AN ABSTRACT OF THE THESIS OF

Jason T. Piasecki for the degree of Master of Science in Sustainable Forest Management presented on 7 August 2023.

Title: Red Tree Voles in Fragmented Forests

Abstract approved: ____

John D. Bailey

The red tree vole (*Arborimus longicaudus*) is an arboreal Arvicoline rodent endemic to conifer dominated forests of western Oregon and northwestern California. While commonly associated with old forests, often inhabiting stands over 80 years old, tree voles have also been found in young forests between 20 and 80 years old. Nonetheless, little is known about the extent of tree vole occupancy and demographic rates in younger stands. Young forest stands may provide ephemeral habitat, connectivity among patches of old forest, and/or long-term habitat that supports multiple generations of tree voles. Whether or not voles occupy young forest may be dependent on factors such as forest age, and the proximity to the nearest patch of old forest habitat from which the species could emigrate.

Due to the elusive nature of tree voles and obstacles of canopy research, knowledge of population dynamics and site-level occupancy in young forests is limited. Since tree voles spend most of their time in nests within the live canopy foliage (hereafter described as 'arboreal'), the distribution and persistence of nests (especially occupied nests) in the live canopy are pertinent metrics for describing habitat. However, detecting nests in the forest canopy can be challenging, especially as forests age and the canopy becomes difficult to survey from the ground. Understanding the implications and extent of imperfect detectability is imperative to accurately assess metrics such as occupancy and density of tree voles and their nests.

I estimated both arboreal and tree vole specific nest persistence rates, interspecific nest use, arboreal nest detectability, survey effort detection rates of tree vole nests, probability of site occupancy by tree voles, and density of arboreal and tree vole nests. I assessed these factors in relation to stand age (20–320 years) and proximity to the nearest >20-hectare patch of old forest estimated to be greater than 80 years old. I conducted plot-based surveys using ground and canopy-based techniques in 63 randomly selected stands stratified by age and distance from patches of old forest in the Oregon Coast Range from 2019 to 2022. I identified and climbed 1,044 arboreal nests within the live canopy and recorded site and nest characteristics, presence of tree vole signs and estimated occupancy state (e.g. recently occupied).

I evaluated multiple models for nest persistence using a known fate modeling framework. Arboreal nest persistence was dependent on nest size while tree vole nest survival was dependent on both stand age and nest size. The probability of tree vole nest persistence was highest 0.98 (95% CI 0.81, 0.99) in old forests where nests were more cryptic and often associated with stable microsites (e.g., cavities). Persistence was lower 0.90 (95% CI 0.79, 0.95) and more variable in young forest and was positively correlated to nest volume. In addition to nest persistence, I examined nest construction and use by other canopy nesting species. I recorded interspecific tree vole nest use by other arboreal species at a higher frequency in young forest than in old forest suggesting possible competition for nesting space in young forests.

To estimate detection rates of tree vole nests I double-surveyed 80 plots across 15 stands in young forests in 2021 and 2022 and conducted census surveys of 9 plots across 3 stands in old forest in 2022. I estimated detection rates in young forests using a Huggins *p* and *c* modeling framework in Program MARK. In old forests, I used the Lincoln-Peterson estimator to quantify detection rates. The detection rate of individual nests was 0.84 (95% CI 0.72, 0.96) using ground-based surveys in young forest and 0.05 (95% CI 0.0, 0.12) using canopy-based surveys in old forest.

Using a case study approach, I conducted a complete census of nests in a single stand in 2020, 2021 and 2022. I simulated 250,000 surveys using randomly generated plots across a range of survey effort (amount of area surveyed) and found that plot-based survey methods that cover 10% of the survey area can effectively estimate stand-level tree vole occupancy at a rate of 66% (95% CI 64, 67%). A survey effort sampling approximately 40% of a stand is required to reliably capture stand level tree vole occupancy at a rate nearing 100%.

I used a single season occupancy model to predict the likelihood of stand level occupancy by tree voles in forests <80 years old across stand age and distance from the nearest old forest patch. My model predicted occupancy probability was highest in the 20-year age class (0.5, 95% CI 0.01, 0.67) and decreased to zero (95% CI 0.0, 0.4) between the 50 and 80-year age classes. Occupancy probability decreased as distance from the nearest old forest patch increased and my modeled data suggested that a young forest stand must be within 1,425m of a patch of old forest beyond which probability of tree vole occupancy approached zero. Empirically, I did not detect any recently occupied tree vole nests more than 1,649m from the nearest patch of old forest.

Using my estimates of detection rates from both young and old forests, I estimated arboreal nest density in 53 stands across stand age and estimated tree vole nest density in 45 stands across stand age that were within the occupancy informed threshold of 1,425m from the nearest patch of old forest. My estimates of arboreal nest density were adjusted for imperfect detection rates and I highlighted the risks of using naïve density especially in older forests where detection probability was low. I estimated the density of recently occupied tree vole nests across stand age and found the recently occupied tree vole nest density to be locally high in the 30-year age class (1.24 per ha, SD = 0.35) and highest overall in the 80-year age class (53.5 per ha, SD = 14.9).

With this understanding of variable nest persistence from year to year, changes in nest detectability across stand age, tree vole occupancy probability and nest density, I suggest management opportunities for this sensitive species in young, managed forests. While old, mature Douglas-fir stands provided complex habitat reflecting the highest density of red tree vole nests, many young stands provided sufficient structural complexity that allowed nesting and supported large nests that were more likely to survive year-to-year. Young forests also exhibited high canopy connectivity which provided dispersal and foraging opportunities. Although expanding my research to include additional stands would help refine predicted trends, young stands within 1,425m of old forest patches contributed to tree vole occupancy and modest levels of tree vole nest density. Given the results of my research, I conclude that young forest can augment, expand, and/or connect habitat for red tree voles in the Oregon Coast Range.

Red Tree Voles in Fragmented Forests

by

Jason T. Piasecki

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jason T. Piasecki, Author

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My thesis research was established as a collaborative effort between Oregon State University, the National Council for Air and Stream Improvement Inc., and many partnering landowners, without whom this project would not have been possible.

Although the Oregon coast range is now a fragmented mosaic of ownerships and land use values, I would first like to recognize the indigenous tribes who were forcibly removed to reservations in western Oregon in 1855, and who's living descendants are part of the Confederated Tribes of the Siletz and the Confederated tribes of the Grand Ronde. They are the original inhabitants and traditional stewards of the land on which this study took place.

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Chapter 1: General Introduction

Jason T. Piasecki

Red tree vole biology and ecology

Despite intriguing naturalists for over a century, relatively little is known about the canopy dwelling red tree vole (*Arborimus longicaudus*), especially in the younger, regenerating forests of the Oregon coast range. The species was first designated, *Phenacomys longicaudus*, in 1890 via a specimen collection from Marshfield, or what is now known as Coos Bay, Oregon (True 1890). Only after an analysis of tree vole blood proteins was conducted in 1968 was the species recommended to the then subgenus *Arborimus* (Johnson 1968). Currently there are three species in the genus *Arborimus*, including the red tree vole, the Sonoma tree vole (*Arborimus pomo*), and the white-footed vole (*Arborimus albipes*). The Sonoma tree vole is genetically and geographically isolated, and found along the coastal region in California from the Klamath river, south into Sonoma County (Bellinger et al. 2005). The white-footed vole occupies a similar range to that of the red tree vole however they are closely associated with deciduous tree species such as alder and hazel (e.g., *Alnus and Corylus*) and are only semi-arboreal (Verts and Carraway 1995; Manning et al. 2003).

The red tree vole, hereafter 'tree vole', is a highly canopy dependent rodent in the Family *Cricetidae*, which includes voles, lemmings, muskrats, and mice. The tree vole is endemic to western Oregon, including the west slope of the Cascade Mountains, and northwestern California. Tree voles inhabit conifer forests, primarily associating with Douglas-fir (*Pseudotsuga menziesii*) dominated stands, although they also inhabit the coastal ecoregion in forests dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) (Walker 1930; Benson and Borell 1931; Maser 1965a; Forsman et al. 2016).

Habitat requirements of the species can vary depending on forest age and composition, but tree voles will often nest where nest supporting structures are readily available and food sources are easily accessible. In areas of mixed conifer forests, such as the coastal ecoregion, tree voles have been found to nest in and feed on needles of Sitka spruce, Western hemlock, Grand fir (*Abies grandis*), and Coast Redwood (*Sequoia sempervirens*) (Jewett 1920; Wight 1925; Walker 1930; Benson and Borell 1931; Maser 1965a; Lesmeister and Swingle 2017). On occasion, tree voles have been found nesting in deciduous tree species such as Bigleaf maple (*Acer macrophyllum*) and Golden chinquapin (*Chrysolepis chrysophylla*) provided there was available branch connections to adjacent conifers from which food could be sourced (Swingle 2005). Because tree voles are highly canopy dependent (Carey 1991; Linnell and Lesmeister 2020) and spend the majority of time in their nests (Swingle 2005; Forsman, Swingle, and Hatch 2009), the nest a tree vole occupies and the surrounding site characteristics are extremely important to understanding habitat/species relationships.

Tree voles subsist primarily on a diet composed of needles from fresh Douglas-fir cuttings, and occasionally fresh twig cambium. Tree voles harvest fresh boughs between 1 – 35cm in length on a nightly basis only leaving the nest to forage for short periods of time (median 27 minutes) (Forsman, Swingle, and Hatch 2009). Tree voles will consume the needles from these cuttings by removing the leaf from the stem and stripping off and discarding the resin ducts before consuming the remainder of the needle (Benson and Borell 1931). Tree voles do not heavily rely on free water and consume the majority of their water from their diet of conifer needles which are high in water content (Forsman and Price 2011). Because the feeding habits of tree voles are so unique, discarded components of their diet such as resin ducts, stripped boughs, and debarked twigs are reliable clues in the identification of tree vole nests (Lesmeister and Swingle 2017).

Tree voles often nest in the live crown of trees where they have easy access to food and can be concealed and sheltered by canopy foliage. Nests are commonly constructed close to the bole in association with dense branch whorls or other available tree structures such as split trunks, broken tops or cavities, although nests have also been found at varying distances from the bole given the availability of nest supporting structures (Jewett 1920; Wight 1925; Howell 1926; Brown 1964; Gillesberg and Carey 1991; Lesmeister and Swingle 2017). Tree vole nests appear to be constructed in a haphazard manner, and generally consist of piled up twigs and branchlet cuttings, discarded resin ducts of conifer needles, and decomposing fecal pellets (Brown 1964; Gillesberg and Carey 1991; Lesmeister and Swingle 2017). Maternal nests can be quite large compared to nests constructed by males or sub-adults and are generally easier to detect from the ground in young forests (Lesmeister and Swingle 2017).

While tree voles can construct their own nests, they have also been found to utilize vacant nests constructed by other species of canopy dwellers such as woodrats (*Neotoma spp.*), tree squirrels (*Tamiasciurus douglasii and Sciurus griseus*), and Humboldt's flying squirrels (*Glaucomys oregonensis*). Conversely, other such arboreal species have been documented utilizing vacant nests constructed by tree voles (Jewett 1920; Howell 1926; Benson and Borell 1931; Brown 1964; Lesmeister and Swingle 2017). Interspecific nest use may occur as a result of limited nesting space and overlapping nesting requirements among canopy-nesting species. Such relationships are unclear in young forests and Weldy et al. (2019) highlighted the benefit of understanding population dynamics of co-occurring species to better address knowledge gaps in the conservation and management of small mammals in forested landscapes.

Because tree voles regularly use a variety of tree structures such as broken topped trees with new apical leading trunks, epicormic branches, and cavities for nest support (Swingle 2005;

Marks-Fife 2016), they may prefer structurally complex forests to more uniform, less structurally complex forests characteristic of commercial timber plantations (Carey 1991; Forsman et al. 2016). These types of structures can provide physical nest support, as well as cover and concealment from predators and positively influence the occupancy and dispersal of small arboreal mammals in areas where available nesting substrates are otherwise limited (Wagner, Feldhamer, and Newman 2000; Linnell et al. 2018). The development of diverse tree structure composition in forests increases niche availability for many species. Although the development of structural complexity is generally related to stand age, many vertebrate species respond to changes in vegetation structure more so that stand age per se (Bunnell, Kremsater, and Wind 1999). Changes in canopy cover as forest structure evolves over time can influence risk perception and foraging behavior of prey species (Potash et al. 2019; Orrock et al. 2004) and reduced availability of nest supporting structures caused by changes in canopy structure can negatively influence species presence (Aitken and Martin 2012; Berthier et al. 2012; Lindenmayer et al. 2017).

While structures associated with old forests such as cavities, epicormic branches, and moss mats take long periods of time to develop (Franklin et al. 2002), alternative nesting structures such as broken topped trees, split trunks, and dense branch whorls are also found in young forests (Swingle 2005; Michel and Winter 2009; Marks-Fife 2016). The development and persistence of these features, hereafter referred to as ‘tree structures’, can increase ecological biodiversity by augmenting habitat quality (Bruce et al. 1985; Bunnell, Kremsater, and Wind 1999). Despite their ecological value, research on the quantification and distribution of tree structures in forests of varying age is limited (Van Pelt and Nadkarni 2004). Michel and Winter (2009) quantified tree structures across age classes of Douglas-fir forests in the Pacific

Northwest and created a replicable example for evaluating such features as an indicator of ecological function. The development and persistence nest supporting structures in younger forests can provide habitat for a variety of arboreal nesting species such as tree voles, Humbolt's flying squirrels, and wood rat species (Linnell et al. 2018). Nonetheless, there is limited quantifiable knowledge on the capacity of young forests to provide sufficient nesting space for canopy dependent mammals.

The persistence of tree voles in stands requires not only nest supporting structure, but an ability for populations to survive and reproduce at a higher rate than predation. Red tree voles are a significant component of the diet of northern spotted owls (*Strix occidentalis caurinia*) in western Oregon (Forsman, Meslow, and Wight 1984). Barred owls (*Strix varia*), northern saw-whet owls (*Aegolius acadicus*), pygmy owls (*Glaucidium gnoma*), and short and long-tailed weasels (*Mustela erminea, Neogale frenata*) also prey on tree voles (Maser 1965b p164; Forsman and Maser 1970; Graham and Mires 2005; Linnell and Lesmeister 2020). Other predators that pose a threat to tree voles and have been recorded disturbing nests include raccoons (*Procyon lotor*), Humboldt's flying squirrel and Steller's jays (*Cyanocitta stelleri*) (Maser 1965b p164; Linnell and Lesmeister 2020). It is presumed that predation rates of tree voles are higher in younger stands than in old stands. Linnell and Lesmeister (2020) conducted the only study providing an index of predation on tree voles and attributed higher rates of predation to weasels rather than owls in young forest. They suggest that the density and cryptic nature of tree vole nests in old forest may increase the difficulty for predators to locate prey based on visual and olfactory senses. Because predation likely differs between old forests and young forests, it is imperative to consider tree vole population dynamics through the lens of stand age and habitat quality.

One of the challenges associated with classifying tree vole habitat in young forests is that robust, systematically collected information regarding the context of nest site features across stand age and location on the forest landscape is largely lacking. Many early reports and studies on tree voles were anecdotal and, while they provide valuable insight on the historical distribution and life history of the species, lack a systematic approach required to make determinations about population metrics. Perhaps the most significant impediment of studying tree voles is that effective surveys require a large time and energy investment. It is impossible to reliably determine the presence and status of tree vole signs at a nest without climbing and carefully inspecting trees where nests are located (Swingle, Forsman, and Sovern 2004; Swingle and Forsman 2009; Huff et al. 2012; Marks-Fife 2016). Tree climbing is both cost and labor intensive and requires specialized training. As such, two other methods have also been employed with varying rates of success. Ground-based traps have been used to assess distribution and presence/absence of tree voles with low success rates (Corn and Bury 1986, 1988; Gomez and Anthony 1998; Suzuki and Hayes 2003). However, because tree voles are canopy dependent, cannot be reliably baited into traps, and rarely come to the ground, this method is ineffective and biased (Swingle et al. 2004; Forsman et al. 2016 p44). For instance, Corn and Bury (1986) continuously operated pitfall traps in Douglas-fir dominated stands aged between 5 and 450 years for 180 days and recorded a capture rate of 0.84% for tree voles (n = 2,104 mammals captured). Alternatively, a more ecologically relevant, creative method of examining landscape scale distribution has been through spotted owl pellet analysis. Forsman et al. (2016 p5) analyzed prey items from spotted owl pellets from 1386 owl territories in 7 geographic sub-regions in western Oregon. They used percentage of tree vole prey items (e.g. bones) to provide an index of tree vole abundance across their study range, finding tree vole occurrence in owl territories varied between 0-73% between sub-regions and constituted an average and standard error of 37±15% of territories among all sub-regions (Forsman et al. 2016 p13). Both methods were valuable in assessing fine scale distribution across forest growth stages and large-scale distribution of the species across its range, however extensive surveying followed by tree climbing allows for a more reliable analyses of tree vole occurrence within stands.

Tree voles have been found and studied in both young and old forests (>80 years old); however, tree voles have been documented in higher densities in old forest leading to the assumption that they are an old forest obligate species (Benson and Borell 1931; Corn and Bury 1986; Gillesberg and Carey 1991; Meiselman and Doyle 1996; Forsman et al. 2016; Marks-Fife 2016). Few studies have focused on younger, managed forests as potential habitat for tree voles. Thompson and Diller (2002) studied a closely related species, the Sonoma tree vole, and found them to be present in young forests managed for timber production in northwestern California. Swingle et al. (2010), Forsman et al. (2016), and Linnell et al. (2018) all documented tree vole occurrence in young forests in western Oregon. Swingle et al. (2010) conducted research on the home range and survival of tree voles at three different sites in young and old forests in the Oregon Coast Range and west slope of the Cascade Range. This research focused largely on the influence of gender and mass on survival and only categorized two age groups of forest (<55yrs and >110yrs). Linnell and Lesmeister (2020) studied colonization, extirpation and predation of tree voles at nests in young forest using remotely triggered cameras, however their inference is limited to artificial nest platforms. Further, several studies that focus on modeling tree vole distribution on a spatial scale, are limited in their scope of inference because they primarily utilize occurrence data collected disproportionately on federally managed lands (Forsman et al. 2016; Rosenberg et al. 2016). Consequentially, federally managed forest land constitutes approximately 25% of the Oregon Coast Range while privately owned forests managed for timber production comprise approximately 41% of the region (Spies et al. 2007). Therefore, there is a significant knowledge gap to be addressed regarding the distribution of tree voles in intensively managed and regenerating young forests commonly occurring on private land.

Although young forests can exhibit characteristics that fulfill the ecological needs of tree voles such as nesting structures, canopy closure, and a stable food source, the function of these forests in relation to tree vole population dynamics is unclear. Individual young forest stands may act as population sinks providing only ephemeral habitat, or they may provide long-term life history requirements sustaining multiple generations of tree voles, or they may primarily facilitate connectivity between patches of older forest. A more comprehensive examination of the role young forests play as habitat for the red tree vole will provide land managers with much needed information on species distribution and status in managed forests. As a result, it is helpful to evaluate prior information and empirically test previous hypotheses regarding the survival, detectability, occupancy rates and density of tree vole nests. Such research could inform on the extent to which tree voles use young managed forests in the Oregon Coast Range.

Survey methods review and detectability

To contextualize the state of current information on tree voles and identify knowledge gaps, it is important to review existing study designs, scope of inference, and implications of various approaches in the analysis of tree vole populations.

Thompson and Diller (2002) conducted systematic surveys for Sonoma tree voles, a biologically similar species, in Humboldt County, California using ground-based transect and grid-pattern surveys across 6 age classes of forest ranging from 10 years old to greater than 60 years old. Although they were able to provide insight to nest site characteristics, nest survival and nest density across a range of forest age, they did not climb trees to verify the status of potential tree vole nests, and they assumed that their detection rates were close enough to 1 that they did not account for imperfect detection in their nest density results.

Price et al. (2015) assessed the distribution and abundance of tree voles in the Tillamook and Clatsop State Forests of Oregon using randomly generated plots across young (0-79yr) and old (80-250yr) forests. They conducted ground-based transect surveys followed by tree climbing to inspect nests for tree vole signs and presence. Although this method is a significant improvement over that of Thompson and Diller (2002) because it involved tree climbing, they concluded that tree voles were largely absent from their study area, documenting tree vole nests in only 4 out of 86 sampling units which further limited their ability to infer on population densities elsewhere in the species' range.

The implementation of the Survey and Manage amendment to the Northwest Forest Plan outlined procedures and requirements for surveying for red tree voles on federal lands (USDI, USDA 2001). Under this protocol, the Forest Service and Bureau of Land Management established the 'Modified Line Transect' method wherein 70% of the survey area is covered, based on a 90m ground transect with an assumed 30m width per acre of survey area; the 'Individual Tree examination Method' where individual trees were surveyed for nests from the ground; and additional guidelines for 'Stands with Large Trees' where 2 trees per 10 acres were climbed and visually searched for nests (Huff et al. 2012). While these methods allow for flexibility based on the survey intent, they do not uniformly account for variability in detection rates across areas of different stand age and/or structure. Swingle and Forsman (2009) found that 48% of nests surveyed were not visible from the ground in both young and old forest and highlighted the need to climb trees to accurately assess tree vole site use and distribution.

Marks-Fife (2016) further quantified detectability using ground-based line transect surveys followed by tree climbing across three different age classes finding that detection rates of trees with active tree vole nests decreased to as low as 0.030 (95% CI 0.004, 0.186) as forest age class increased (>200 years). Because detectability of nests has been a documented challenge in tree vole research that can introduce bias in estimates of nest abundance, density and distribution, it is imperative to quantify detection probability of arboreal nests within the context of any prospective study on tree voles, especially regarding estimations of occupancy, distribution, and density.

The Forest Service provided an updated survey protocol for red tree voles in 2022 in which 'Targeted Tree Climbing' was added to the list of strategies for surveying for tree voles. 'Targeted Tree Climbing' surveys attempt to reduce the occurrence of false negative survey outcomes associated with the previously developed ground-based 'Modified Line Transect' survey method. 'Targeted Tree Climbing' focuses on the selection and climbing of large diameter (32"-59" DBH) trees that are most likely to exhibit structural complexity such as broken tops, split trunks, cavities, etc. (Marks-Fife 2022).

Pre-disturbance surveys following the aforementioned protocol in the Northwest Forest Plan (Huff et al. 2012) were required only under certain circumstances that generally only apply to proposed disturbance in areas of old forest with large diameter trees. There is currently no consistently used protocol for conducting tree vole surveys in young forests. The development of such a protocol, although not currently required, will provide managers with an informed approach to survey for this sensitive species. Further, in the event that young forests are determined to provide critical tree vole habitat, surveys to manage for tree voles in these areas may be required in the future.

Existing tree vole research has established protocols and methods for surveying either focused almost exclusively on old forests or that only include young forests to draw comparisons to old forest. This is not surprising since tree voles continue to be found in high densities in old forests and are regarded as an old forest obligate species. However, the focus on tree vole demographics in old forests leaves much to be determined regarding the status of populations in young, managed forests, which comprise a large area of the coast range patchwork.

Red tree vole legal status and context in Oregon

The state of Oregon identifies the red tree vole as a ‘strategy species’ in its statewide Conservation Strategy defining it as a ‘species of greatest conservation need’ (Oregon Conservation Strategy 2016). The Oregon Department of Fish and Wildlife also lists red tree voles as a ‘sensitive species’ highlighting population decline, and/or species management concerns (Oregon Sensitive Species List 2021). Although tree voles are not listed under the Endangered Species Act (ESA), a distinct population segment (DPS) of the red tree vole in the north coast of Oregon was proposed for listing in 2011. The United States Fish and Wildlife Service (USFWS) decided that although tree voles warranted an ‘endangered’ or ‘threatened’ status, their listing was precluded by higher priority listing objectives (USFWS 2011). The USFWS ultimately declined to list the species, citing that recent habitat models developed by Linnell et al. (2017) showed more available habitat in the vicinity of the DPS than reported in 2011 (USFWS 2019). Despite the ‘not warranted’ listing decision, published surveys for tree voles in the previously proposed DPS area include (Price et al. 2015; Linnell and Lesmeister 2019) and there is little to no current on-the-ground validation that this previously modelled predicted habitat is sustaining reproducing tree vole populations. Following the 2019 ‘not warranted’ listing decision, the USFWS was sued by the Center for Biological Diversity, Oregon

Wild, Cascadia Wildlands and the Audubon Society of Portland wherein the plaintiffs argued the USFWS failed to consider state and private lands when considering habitat loss across the range of the red tree vole DPS (Center for Biological Diversity 2021). Upon settling this lawsuit, the USFWS agreed to rescind the 2019 'not warranted' decision, reassess the candidacy of the DPS to be considered for listing under the ESA, and deliver a decision by January 31, 2024 (USFWS 2022).

Because tree voles are completely dependent on conifer forest canopies for all aspects of life, tree voles are extremely susceptible to all manner of forest disturbance from wildfire to timber harvesting. Forsman et al. (2016 p36-42) found tree voles to be largely extirpated in areas where they had been historically present but had since been burned and/or harvested. While tree voles can potentially return to inhabit regenerated forests, the cycle of intensive forest management and fragmentation through short timber rotations and frequent thinning that currently exists across a large portion of the tree vole's range does not lend itself well to sustaining tree vole populations (Carey 1991; Forsman et al. 2016; Linnell and Lesmeister 2019). The presence and natural succession of large patches of old forest on the landscape can improve habitat across the species' range but large-scale disturbances are still a threat to sensitive species with limited mobility such as the tree vole (Linnell and Lesmeister 2019; Heinrichs et al. 2023). Fragmentation of old forest habitat, which is prevalent throughout most of the coast range, can limit dispersal and gene flow between populations and negatively affect genetic diversity of the species (Miller et al. 2005; Linnell and Lesmeister 2019). Even in areas where young forest provides dense canopy cover and could facilitate movement between large patches of old forest habitat, short timber rotations that disrupt occupied young forests linkages can be detrimental to tree vole dispersal (Linnell and Lesmeister 2019). Concurrently, young forest that is adjacent to, or close to patches of old forest >20 hectares can serve as marginal tree vole habitat (Linnell et al. 2017). Young forests that fill this capacity, if managed with a holistic consideration for marginal habitat and matrix-based processes across such a fragmented landscape (Andrén and Andren 1994; Kupfer, Malanson, and Franklin 2006; Ruffell, Clout, and Didham 2017), could increase the effective patch size for adjacent old forest that is occupied by tree voles (Linnell et al. 2017; Ruffell et al. 2017).

Large-scale research on arboreal nests and red tree vole population metrics would help to provide information for future conservation and management decisions on the species. Comparison of arboreal nest survival and detectability and tree vole population metrics such as density and site occupancy between old and young forests and proximity to mature forest areas would aid in our understanding how forests of different ages fulfill habitat requirements for tree voles and improve habitat modelling accuracy within the Oregon Coast Range.

Chapter 2: The Influence of Forest Age and Nest Size on Red Tree Vole Nest Persistence and Interspecific Nest Use

Jason T. Piasecki

Abstract

Red tree voles (*Arborimus longicaudus*) are largely a nocturnal and highly canopy dependent species spending most of their time in nests constructed within the live tree canopy (hereafter 'arboreal'). As such, the distribution, number, and longevity of nests in the live canopy are pertinent metrics for assessing habitat. Little is known about longevity, or survival probability, of natural tree vole nests, especially in younger forests (<80 years). The composition and occurrence of nest supporting tree structures and patterns of arboreal nest use and survival likely varies significantly between forests that differ in age. I randomly selected 63 Douglas-fir (*Pseudotsuga menziesii*) dominated stands from 2019-2022 in Oregon's central Coast Range mountains. Stand selection was stratified by latitude, age class (20-29, 30-39, 40-49, 50-59, 60-79, and ≥80 years) and distance (up to 5km) from the nearest patch of old forest ≥80 years old and >20 hectares in size. I surveyed for arboreal nests using plot-based ground and canopy surveys and climbed and recorded nest status (present or absent), characteristics and use by other arboreal species and presence of tree vole sign at 1044 nests. I modeled nest persistence as a function of time, stand age, nest size, nest construction type, and latitude using a known-fate modeling framework in *Program MARK*. Tree vole nest persistence rates were highest (0.98 95% CI 0.81, 0.99) in old forests where nests were more cryptic and often associated with stable microsites (e.g., cavities). Persistence rates were lower 0.90 (95% CI 0.79, 0.95) and more variable in young forest and were positively correlated to nest volume. In young stands (<80 years old), nests were often constructed and used by multiple species, most commonly tree voles and Humboldt's flying squirrel (*Glaucomys oregonensis*). These nests were often built on stable structures (e.g. split trunks, broken tops) compared to features commonly used in old forest (>80 years old) such as moss mats and epicormic branches. I describe trends in nest persistence and

interspecific nest construction and use to highlight relationships among nest availability, habitation, and interspecific relationships of a canopy dependent species. This is especially pertinent in young forests where nesting space may be a limiting factor for tree vole density and reproduction.

Introduction

Red tree voles (*Arborimus longicaudus*) are the most canopy dependent mammal in Douglas-fir (*Pseudutsuga menziesii*) dominated forests of western Oregon and northwestern California (Carey 1991). However, tree voles are not the only rodent species that depend on the forest canopy to fulfill key functions of their life history. Humboldt's flying squirrel (*Glaucomys oregonesis*), Bushy-tailed woodrat (*Neotoma cinerea*), and Douglas squirrel (*Tamiasciurus douglasii*) also depend on forest canopies for nesting, foraging and reproduction. One common requirement among these species is the necessity for nesting space within the forest canopy (Maser et al. 1981; Carey 1991; 1996). Arboreal nests, which I define as any nest occurring within the live tree canopy, provide shelter from predators and elements, space to reproduce and rear young, and facilitate dispersal (Berthier et al. 2012). Because they need arboreal nests to fulfill ecological requirements, in addition to building their own nests, tree voles can rely on the construction and temporal persistence of nests built by other species in the forest canopy. While forests of various ages can support arboreal nests, landscape scale disturbances such as wildfire and thinning that lead to a loss of microsite complexity characteristic of older forests can adversely affect populations of such canopy dependent species (Carey 1989; Buchanan, Lundquist, and Aubry 1990; Ritchie et al. 2009; Wilson and Forsman 2013; Forsman et al. 2016).

Although arboreal nests are essential for species survival and reproduction, the quantity and quality of nests may differ between forests of varying age. Old forests and especially forests with old-growth trees (>200 years) provide a higher level of structural complexity compared to younger, managed forests (Ruggiero et al. 1991). Occurrence and retention of nests can increase survival and immigration of canopy dependent species (Berthier et al. 2012). Further, promoting and maintaining nests and nest supporting structures in forests can increase resiliency of canopy dependent species and improve forest biodiversity (Jones, Hanberry, and Demarais 2009; Michel and Winter 2009; Ibarra et al. 2020). For instance, Aitken and Martin (2012) showed the positive response of increased nest-site availability on bird and mammal densities in mature, mixed-conifer forests in British Columbia. Although arboreal nests are presumed at their highest densities in older forests, young forests can exhibit structural complexity in the form of nest supporting tree structures, albeit at lower densities, and can suffice to provide nesting space for arboreal species such as flying squirrels, birds, and tree voles (Maser et al. 1981; Carey 1991; Michel and Winter 2009; Linnell et al. 2018). Depending on forest management practices, which can vary between ownerships and management goals (Cole 1996), forest structure patterns and availability of nest supporting features in young forests can vary (Michel and Winter 2009; Griffey et al. 2020). Low availability of nesting structures can impact presence, survival, and reproductive success of canopy dependent species (Berthier et al. 2012; Jiménez-Franco et al. 2018). Similarly, availability of nesting platforms may be a limiting factor for the persistence of canopy dependent species in young forests across the Oregon Coast Range (Linnell et al. 2018; Linnell and Lesmeister 2020). Linnell et al. (2018) documented increases in occupancy of tree voles, Douglas squirrels, and Humboldt's flying squirrel after installation of artificial nest platforms. As such, younger forests may be limited in their capacity to provide structures to support arboreal nests and for those nests to persist over multiple years.

Tree vole nests are easily distinguished from other arboreal species because of the unique feeding habits of tree voles. Tree voles are unique in that they feed almost exclusively on fresh conifer needles and live twig cambium harvested from fresh boughs in the canopy. Tree voles will strip and discard these small twigs and resin ducts found in conifer needles resulting in accumulations of these by-products at their nest. Additionally, tree voles will collect and store fresh boughs in and on top of their nests from which they harvest needles throughout the day. Arboreal nests can be classified as having been inhabited or used by a tree vole based on the presence of discarded resin ducts, debarked twigs, harvested cuttings of foliage, and their fecal pellets (Lesmeister and Swingle 2017). Because identification of tree vole signs at nests is straightforward, tree vole nests can be used as an indication of tree vole occurrence and activity in a stand.

One reason for improved quantification of nest occurrence, persistence and interspecific nest use for tree voles and other canopy dependent mammals in forests that differ in age is the need to manage forests for multiple values including sustaining or improving wildlife habitat. Both federal (USDA and USDI 1994) and state (Oregon Department of Forestry 2010) forest management plans contain such requirements. This presents a unique challenge combining the difficulty of surveying for canopy dependent species such as tree voles with political requirements to verify their occurrence. Only one such study has evaluated nest characteristics and persistence in western forests, however this study focused on Sonoma tree voles (*Arborimus pomo*), and only covered forests in northwestern California where the species occurs (Thompson and Diller 2002). Thus, a better understanding of canopy nesting dynamics in managed forests is needed to inform decision making on tree voles and their habitat requirements in young forests.

My objectives were to 1) quantify arboreal nest characteristics (supporting structures, volume, use) in forested stands that differ in age, 2) model both arboreal, and more specifically tree vole, nest persistence, and 3) describe nest use by tree voles and other canopy dependent mammals. I predicted nest characteristics and supporting tree structures would differ among forest age as forest composition changes and that tree vole nest persistence would be lower in young forest than in old forest. I also predicted that interspecific nest use would be higher in younger forests based on limited availability of nest supporting structures.

Methods

Study Area

My study area from 2020 to 2022 was comprised of 10 USGS Hydrologic Watershed (HUC 8) units in the Oregon Coast Range (12466km^2, Figure 2.1). There was no ecological significance of these units to tree voles, but they allowed me to easily delineate a study area based on existing watershed boundaries. My study area during the 2019 pilot season was limited to the central Coast Range along the US highway 20 corridor (approx. 830km^2). Approximately 30% of my study area overlapped with the proposed Distinct Population Segment (DPS) of red tree voles that was considered for listing in 2019 and 2023 (USFWS 2019; 2022). Stands were dominated by Douglas-fir (*Pseudotsuga menziesii*) with western hemlock (*Tsuga heterophylla*) commonly appearing as a successional species in older stands. In stands within the coastal ecoregion, Sitka spruce (*Picea sitchensis*) was co-dominant along with western hemlock and Douglas-fir. In some unmanaged stands, grand fir (*Abies grandis*) was sporadically present.

Stand selection

I collaborated with eight different land ownerships and forest management agencies to create a pool of available stands for selection. The US Forest Service Siuslaw NF, and Bureau of Land Management provided stands on federally owned land. The Oregon Department of Forestry provided stands on state owned land. Weyerhaeuser Company, Starker Forests, Manulife Investment Management, Hampton Lumber, and Lone Rock Resources provided stands on privately owned land.

For the purpose of this study, a forest stand is defined as a spatially contiguous community of trees that are similar in age, composition and distribution such that they are distinct from adjacent tree communities (Nyland et al. 2016). I randomly selected stands stratified by stand age classes: 20-29, 30-39, 40-49, 50-59, 60-79, and >80 years of age. For stands under private and state management, I used known age calculated from the planting date provided by the stand owner. To classify older stands (≥80 years) under federal management, I used a compilation of LiDAR derived tree height layers paired with available forest inventory data from the Bureau of Land Management in ArcGIS. I then cross-referenced my layer with a smaller existing old forest layer developed by Linnell et. al. (2017) .

My old forest layer was similarly generated using LiDAR data and represented patches ≥80 years old and ≥20 hectares in size. I cross referenced this layer with the Forest Activity Electronic Reporting and Notification System (FERNS) maintained by the Oregon Department of Forestry to eliminate areas that had been disturbed or harvested since LiDAR was flown. For the purposes of stand age classification in my study design, analysis and discussion, I classified young forest as any Douglas-fir dominated stand between 20 and 79 years old. I classified old forest as any Douglas-fir dominated stand greater than or equal to 80 years old. I classified any patch of old forest assumed to be occupied by tree voles capable of emigrating to nearby young forest as greater than or equal to 80 years old and greater than 20 hectares in size (Linnell et al. 2017). To verify the age of stands classified as greater than or equal to 80 years old, I collected age estimates of trees within each plot using ageing techniques outlined in Van Pelt (2007) and averaged the estimated age for the whole stand. My definition of ‘old forest’ coincides with the typical age of maturation for Douglas-fir forests in the northwest and aligns with other tree vole studies that evaluated forest age (Old-Growth Definition Task Group 1986; Marks-Fife 2016;

Rosenberg et al. 2016; Linnell et al. 2017). My assumption that minimum old forest patch size of 20 hectares is needed to support a tree vole population aligns with the same assertion in previous research established using historical density estimates in old forest (Maser 1965a; Marks-Fife 2016; Linnell et al. 2017).

I placed certain additional requirements on my stand selection for logistical and ecological reasons. I restricted my stand area to a minimum of 10 hectares and a maximum of 30 hectares. Stands could only be selected if they were not scheduled to be harvested in the next 5 years and had not been pre-commercially thinned.

To achieve an equitable distribution of selected stands across the entire study range, I evenly divided the study range into 4 sections from north to south. Red tree vole population density was anticipated to be highest at the southern section of my study area (Forsman et al. 2016 p22) and lowest in the northern section (Price et al. 2015), so geographic partitioning likely provided the most representative gradient of tree vole density. I selected 6 stands in each age class within each of these 4 sections using a random ranking process.

Within each stand, I randomly generated circular 17.8m radius (995.4m^2) survey plots at a density of one per hectare using ArcGIS. The total area of these plots represented approximately 10% of the total stand area.

Ground-based surveys

In forests aged 20-59, I conducted ground-based surveys of each plot where I walked around each plot and used binoculars to search the canopy for arboreal nests. I also opportunistically searched the canopy for nests while travelling between plots. I recorded and stored survey tracklogs using Garmin eTrex 10 handheld GPS units (Garmin Inc.) and estimated sight distance into the canopy within each stand to approximate the total area surveyed. I uniquely marked all nest trees found in this manner with numbered aluminum tree tags and flagging. I recorded geolocation and tree-specific data using S1 Mobile Mapper and Trimble Smart Receivers (Trimble Inc. Model R-1000 #99133). Following my ground survey for nests, all nests discovered in the live crown that were able to be safely climbed were accessed using spur climbing techniques (Berdeen et al. 2015). Tree vole nest status was determined by searching the nest for the presence of chisel-cut Douglas-fir cuttings, discarded resin ducts, chisel-cut debarked twigs, and tree vole fecal pellets (Table 2.1).

Canopy-based surveys

In forests over 60 years of age, I determined that ground surveys would be ineffective given the height of the canopy and complexity of canopy and tree structure especially in old forests over 80 years of age. Marks-fife (2016) estimated nest tree detectability from the ground to be as low as 2%. Instead of conducting ground-based surveys, I searched plots for nests from the canopy using a vertical-climb survey method. Upon entering each plot, I selected a tree within the plot to represent the ‘center’. I selected this tree based on climbing safety, canopy-to-canopy visibility from the plot center tree to other trees within the plot, and the presence of tree structures that could potentially support tree vole nests. Once selected, I climbed the plot center tree using stationary rope climbing techniques (Berdeen et al. 2015). I surveyed for nests within the plot center tree and in the canopy of surrounding plot trees. Following this, any nests that I discovered in adjacent trees were then climbed and inspected for any signs of tree vole presence (Table 2.1).

Nest characteristics

At each nest, I collected data to quantify the physical characteristics of the nest and type of tree structure that physically supported the nest. I identified these structures, which were often the result of normal growth patterns or a prior injury or infection to the bole or branches, using categories established in Swingle (2005), Michel and Winter (2009) and Marks-fife (2016) (Table 2.2). I also estimated nest volume (V) in meters cubed using the cubic volume calculation:

$$V = (L * W * D)/100$$

Where L is nest length in centimeters measured perpendicular to the bole of the tree, W is nest width in centimeters measured parallel to the bole of the tree, and D is nest depth measured in centimeters vertically from the top to the bottom of the nest.

Nest status, construction and use

During nest surveys, I examined physical evidence (e.g. nest composition, materials) to determine nest construction and use by tree voles and other arboreal species. Tree vole nest status was determined by searching the nest for the presence of 45^{o} chisel-cut Douglas-fir cuttings (between 1-35cm long), discarded resin ducts, 45^{o} chisel-cut debarked twigs ($\leq$6cm long), and tree vole fecal pellets (Lesmeister and Swingle 2017) (Table 2.1). I classified tree vole nests as ‘old’, if resin ducts, fecal pellets, and collected Douglas-fir cuttings were dried and brown, or ‘recent’ if resin ducts, fecal pellets, and collected Douglas-fir cuttings were fresh and green. I also examined nests for evidence of other arboreal species. For example, fecal pellets and long Douglas-fir cuttings (>30cm long) associated with Bushy-tailed woodrat or fresh moss and bark shavings associated with Humboldt’s flying squirrel (Maser 1998; Lesmeister and Swingle 2017). I estimated the number of distinguishable nest layers present and assigned each layer a suspected species based on evidence supporting construction of an individual layer by a species or species type (Maser et al. 1981; Maser 1998; Lesmeister and Swingle 2017). For example, a nest might have initially been constructed and/or used by a Humboldt’s flying squirrel evidenced by the presence of a single moss-lined chamber about the size of a grapefruit

(Maser et al. 1981). The same nest may have later been colonized by a tree vole evidenced by the presence of discarded resin ducts and debarked twigs (Lesmeister and Swingle 2017). Since arboreal species may colonize and add nest material on top of or inside existing nests, I quantified and classified nest layers on a temporal scale such that the most recent layer was attributed to the species that most recently constructed or used the nest. For example, if a nest exhibited any recent tree vole sign, I attributed the most recently constructed layer to red tree vole (Figure 2.2). I associated suspected species to individual nest layers only when able to determine distinct signs of species-specific nest material or construction habits.

Estimating nest persistence

I revisited arboreal nests annually once they were initially discovered and recorded nest presence/absence. I classified nests that provided cover and habitable structure as 'present' (1) and classified nests that had been destroyed or decomposed to the point where they would be functionally useless to any canopy dependent species as 'absent' (0) (Figure 2.3). I estimated nest persistence using a known-fate modeling framework in Program MARK (White and Garrott 1990; Cooch and White 2019). I evaluated nest persistence for all arboreal nests, which I classified as a nest structure in the live crown of the tree constructed or inhabited by any species. I also evaluated nest persistence for tree vole nests, which I defined as any arboreal nest in the live crown that exhibited recent tree vole sign or was confirmed as occupied at any survey occasion from 2019 to 2022.

Under my definition of nest persistence as 'present' or 'absent', I treated all surveyed nests as marked individuals that were able to be monitored until they became extirpated (became absent), were removed from the study due to climbing safety issues or reached the end of the study. Because I geolocated and marked nest trees and nests, I assumed the encounter probability of any nests found was ‘1.0’ after initial surveying. I used binomial known-fate modelling in Program MARK to estimate annual probability of nest persistence, modeled as survival (*S*), for arboreal nests (Cooch and White 2006). I modeled arboreal nest persistence across each annual time interval (*t*), stand age at the time of initial survey (*stand age*), and nest size in cubic meters at the time of initial survey (*nest size*). For tree vole nest persistence, I also modeled for nest construction type (*construct*) to determine if probability of nest persistence changed between nests originally constructed by other species and nests constructed by tree voles. Finally, I included latitude in decimal degrees (*latitude*) in my model for tree vole nest persistence, predicting tree vole nest persistence would be highest with increased presumed tree vole density in the southern portion of my study area. Further, I wanted to account for potential differences within the proposed distinct population segment of red tree voles being considered for ESA listing (USFWS 2022) and any changes in nest persistence probability across a latitudinal gradient could augment best available science for land managers. I created *a priori* model sets for both all arboreal nests and tree vole nests using these variables and ranked models by Akaike information criterion (AIC) to determine which model was the most parsimonious with the data (Burnham and Anderson 2004).

Results

I conducted surveys from September to December in 2019 and April to October in 2020, 2021, and 2022. The length of my survey seasons were occasionally impacted by weather conditions, including long periods of dense wildfire smoke during and following the Holiday Farm, Beachie Creek, and Lionshead fires in September 2020 and also late spring snowstorms in the Oregon Coast Range in April 2022.

I surveyed a total of 63 individual stands with increased sampling effort each year across a gradient of stand ages (Figure 2.4). I surveyed 13 stands for 4 years, 20 stands for 3 years, 12 stands for 2 years, and 18 stands for 1 year (Table 2.3). I surveyed a total of 6557 trees and found 1044 arboreal nests. Of the 1044 nests surveyed, I classified 564 as tree vole nests based on the presence of either old or recent tree vole sign (Table 2.1).

I recorded nest dimensions and calculated nest volume for each arboreal nest ($n = 1044$). The largest nest was 4.68m^3 (200cm *W* x 180cm *L* x 130cm *D*) and was initially constructed by a Bald eagle (*Haliaeetus leucocephalus*). The smallest nest measured was 0.000192m^3 (8cm *W* x 8cm *L* x 3cm *D*) and was initially constructed by a red tree vole. Mean nest volume across all age classes of forest was 0.042m^3. Median nest volume was slightly larger in young forest age classes (<60 years) relative to the old forest age class (≥80 years) (Kruskal-Wallis rank sum test, $p < 0.001$) (Table 2.4).

Tree structures that supported arboreal nests varied with forest age. In old forest, where available, cavities ($n=22$) supported the largest arboreal nests with a median volume of 0.06m^3. Mistletoe brooms ($n=8$) also supported large arboreal nests with a median volume of 0.03m^3. In young forest, where cavities and mistletoe brooms were not present, broken tops ($n=233$) and split trunks ($n=154$) support the largest nests with a median volume of 0.02m^3 for both types of tree structures (Figure 2.4). In young forests, most tree vole nest construction was supported by branch whorls, broken tops, and split trunks. For example, using data from 2022 ($n = 564$ nests), in the 20-year age class, these structures supported 46%, 28%, and 19% of tree vole nests respectively. In old forests, tree vole nest construction was supported largely by epicormic branch whorls (33%), large branches (25%), and moss mats (18%) (Table 2.5).

Arboreal nest persistence

I recorded nest presence and absence status for 663 arboreal nests over a total of 980 occasions from 2019 to 2022. I observed nest extirpation across all age classes (Table 2.6). The proportion of nests that became extinct was consistently highest in the 50 and 60-year age classes however sample sizes were low here because of low overall nest density.

I modeled arboreal nest persistence using encounter histories for 663 nests over four annual survey occasions (2019-2022). My top model for arboreal nest persistence included only nest size (*S(nest size)* AICc weight 61.78%) (Table 2.7). The effect of nest size on annual persistence was positive such that persistence increased with nest size ($\hat{\beta}_{nest\ size}$ = 31.82, 95% CI 21.02 42.61). Time period and stand age did not have strong effects on annual persistence probability of arboreal nests. Based on predicted probability of nest persistence, my top model showed an asymptotic relationship between annual nest persistence probability and nest size. As nest size increased, annual persistence probability approached 100% (Figure 2.5).

Tree vole nest persistence

I modeled tree vole nest persistence using encounter histories for 150 nests across four annual survey occasions (2019-2022). My top model included time, stand age, and nest size effects on annual persistence probability (Table 2.8). Nest size had a strong positive effect on annual persistence ($\hat{\beta}_{nest\ size}$ = 22.27, 95% CI 4.72, 39.82) such that the probability of a tree vole nest persisting for one year increased as nest size increased. Stand age had a weak positive effect on annual persistence probability ($\hat{\beta}_{stand\ age}$ = 0.01, 95% CI 0.0, 0.03) meaning tree vole nests were more likely to persist year over year in older forests than in young forests. Each time period also had relatively weak effects on annual persistence of tree vole nests. The time period effect on nest persistence was similar for 2019-2020 ($\hat{\beta}_{time}$ = 0.73, SE = 0.59, 95% CI -0.44, 1.90) and

2021-2022 ($\hat{\beta}_{time}$ = 0.39, SE = 0.48, 95% CI -0.56, 1.33) (reference year), but higher in 2020-2021 ($\hat{\beta}_{time}$ = 1.17, SE = 0.58, 95% CI 0.03, 2.32). (Table 2.9, Figure 2.7).

My model suggests stand age influenced tree vole nest persistence such that annual persistence probability was lower 0.90 (95% CI 0.79, 0.95) and more variable (Range 0.67 to 0.99) in young forests (<80 years) and higher 0.98 (95% CI 0.81, 0.99) and more stable (Range 0.86 to 1.00) in old forests (≥80 years) (Figure 2.7). I found the influence of nest size on tree vole nest persistence to be similar to that of arboreal nest persistence. My estimates of annual persistence probability based on nest size show an asymptotic relationship with nests larger than 0.3m^3 exhibiting annual persistence probability approaching 100% (Figure 2.6 and 2.7).

Interspecific nest construction and use at tree vole nests

I quantified nest layers and identified species associated with layer construction and/or use at every nest from 2020 to 2022. For analysis, I used tree vole nests surveyed in 2022 (n = 439) which was my largest sample size within a survey season.

Of all tree vole nests surveyed in 2022, 72.2% (n = 317) were comprised of a single distinct layer, 25.7% (n = 113) were comprised of two identifiable layers, and 2% (n = 9) were comprised of three identifiable layers. I identified multi-layer nests across all forest age classes but found them to be most common in the 20 and 30-year age classes (44% and 33% of nests respectively) and least common in the 80-year age class (4.3% of nests). Further, I only found nests with 3 identifiable layers in the 20 and 30-year age classes (Figure 2.8). Based on evaluation of nest layer data and suspected species associated with layer construction, tree voles and Humboldt's flying squirrel exhibited the highest occurrence of interspecific nest use compared to other recorded species. In my data, 42.62% of all tree vole nests were originally constructed by Humboldt's flying squirrel and 29.31% of Humboldt's flying squirrel nests were originally constructed by tree voles (Table 2.10). I observed no temporally sympatric nest use among tree voles and arboreal mammals. However, I documented freshly harvested Douglas-fir cuttings pulled into a tree cavity at the base of a Bald-eagle nest. I also documented recent tree vole signs throughout the dense structure of the eagle nest. I had observed a mating pair of bald eagles rearing chicks at this nest prior to climbing the tree after the chicks had fledged. Based on these observations, I suspected both species had been actively using the nest at the same time (Figure 2.9).

Discussion

This research provides a foundation for better understanding the extent to which young forests contribute to arboreal nesting diversity, specifically evaluating tree vole nest use and survival. Although nest persistence in young forests was more variable than in old forests, nests had >70% likelihood of survival in most years especially for nests larger than $0.1m^3$. Interestingly, nests in younger forests were often used and/or constructed by multiple species such as tree voles and Humboldt's flying squirrels. This suggests either 1) a limitation of desirable nest supporting tree structures, which results in competition for space, or 2) a mutually beneficial relationship through interspecific nest construction and use. I also identified split trunks and broken tops as tree structures that commonly support large, longer lasting nests in young forests. Practices that improve the availability of these tree structures and the survival rates of arboreal nests can be used by managers to identify objectives to establish and maintain potential habitat for canopy dependent species in young forests.

Although old forests exhibit high structural complexity compared to young forests, both can support arboreal nesting through the provision of individual tree structures. In old forests, in addition to the presence of some split trunks and branch whorls, the tree structures characteristic of mature trees (e.g., cavities, moss mats and epicormic branches) were used more often by tree voles to support nest construction. Cavities created by insects, fungi or disease can not only provide desirable nest support and concealment from predators but physical cover as well (Bunnell 2013). Moss mats can be common in mature trees covering large branches throughout the canopy (Sillett 1995); tree vole nests created under these moss mats were extremely difficult to locate and almost assuredly provide a high level of concealment from predators. Although I documented moss mat supported nests comprising 18% of tree vole nests in old forests in 2022 (n = 162), these may be underrepresented due to their cryptic nature. Epicormic branch structures not only create stable platforms for nest construction, but also allow reliable access to food without having to travel long distances along the trunk, increasing exposure to predation. These desirable nest supporting tree structures were absent in young forests; however, split trunks and broken tops where one or more leaders diverge from the main stem can support construction of large nests. While these structures provide little concealment from predators, the composition and location of split trunks and broken tops is such that they were often interconnected by high densities of branches. This can facilitate movement and improve the ability to escape from predators via branch pathways throughout the canopy. The availability and persistence of these nest supporting structures likely influences the occurrence and dispersal of tree voles and other canopy dependent species in young forests.

Little is known about arboreal nest persistence and survival for canopy associated mammals in forests that differ in age. I found larger ($>0.3m^3$) arboreal nests had higher annual survival rates. Larger nests often were supported by robust tree structures such as split trunks and broken tops in young forests (<80 years). The availability of these structures that support the construction and persistence of larger arboreal nests can increase nesting space for canopy dwelling mammals such as tree voles. The intentional or unintentional development of trees with broken tops, split trunks or other defects in young stands may bolster the ability for tree voles to construct large nests often used for rearing young (Lesmeister and Swingle 2017; Linnell et al. 2018), supporting the reproduction and dispersal of the species in otherwise unsuitable habitat.

Although the structural complexity of individual trees in old forests is more conducive to the nesting habits of canopy dependent species, trees in young forests can exhibit structural complexity sufficient to support construction and persistence of arboreal nests. However, because structural complexity is lower in young forest, potential nesting space may be limited. Higher rates of interspecific nest use in young forests suggests possible competition for species that would otherwise occupy different nesting space niches in older forests. Nesting space may be a limiting factor for the occurrence and dispersal of tree voles in young forests. In this study, I recorded frequent overlap in nest construction and use between tree voles and Humboldt's flying squirrels in young forests, while recording almost no overlap in nest site use in old forests. The specific dynamic of the relationship is unclear. My interpretation of these occurrences is that tree voles may be competing for nesting space with flying squirrels in young forest. Alternately, nest construction by both species may create a situation where increased availability of existing unused nests benefits both species. Nonetheless, flying squirrels have been documented extirpating tree voles from active nests and occasionally predating tree voles where nest use overlapped (Linnell and Lesmeister 2020). The nesting habits of these two highly canopy dependent species do not overlap in old forests where flying squirrels frequently nest in snags (Carey et al. 1997) that were unattractive to tree voles because of their lack of direct food supply or connections to the live canopy. Further, the availability of tree structures used for nesting is significantly higher in old forest than in young forest. While nest site availability is likely not a limiting factor in old forests, both flying squirrels and tree voles may benefit from increased availability and persistence of arboreally constructed nests in young forest. Existing unoccupied nests in the live canopy can provide concealment and protection from predators at little energy cost to the inhabitant. While tree voles can construct their own nests on branch whorls and other structures (Table 2.5), the energy requirements involved in nest construction and prolonged exposure to predators is a significant trade-off. Therefore, tree voles would likely choose pre-existing nests (this study) or artificial nests (Linnell et al. 2018) if available, especially when those nests were large (>0.3m^3) and supported by stable tree structures.

As expected, nests within the canopy hosted a diversity of species. I documented interspecific nest construction and use by tree voles, Humboldt’s flying squirrels, bushy-tailed woodrats, other tree squirrels, and Bald eagle (*Haliaeetus leucocephalus*) (Figure 2.9). Despite recording almost 50% of tree vole nests in young forest as having multiple distinct layers initially constructed by another arboreal species, sympatric nest use is extremely rare and has only been documented at occupied tree vole nests with deer mice (*Peromyscus maniculatus*) and grey squirrel (*Sciurus griseus*) (Brown 1964; Maser 1965a). I suspect this behavior may only occur in situations where the nest size permits sufficient allocation of nesting space and where species interaction is limited and non-detrimental. Despite this assumed rarity, I recorded the first known occurrence of sympatric nest use by tree voles and Bald eagles. Although Bald eagles prey on mammals, it is likely that tree voles do not present themselves as a good prey species for bald eagles due to their small size and primarily nocturnal habits. Further, nests constructed by bald eagles offer good protection from predators, structural stability, and because of their size, can fulfill space requirements for tree vole reproduction.

Within my study, I observed a paucity of arboreal nests in forests in the 50 and 60-year age classes (Table 3.6). As such, nest survival estimates from 50-79 year old stands have limited precision and results should be interpreted with caution. Additionally, the scale at which I examined forest age as an independent variable varied between young forest (<80 years) and old forest (≥80 years). The smaller range of forest age (20 to 79 years) within young forest allows for more continuous sampling of age than that of old forest, which spans a much larger range of forest age (80 to 320 years). Additionally, my sampling of stands was weighted towards learning more in younger stands while having sufficient data to draw comparisons to older forests. In young forest, I had a high sample size of stands (n=54) and a small range of forest age (21-69 years) whereas in old forest, I had a comparatively low sample size of stands (n=9) and a high range of forest age (97-320 years). I encountered two major challenges while surveying in the old forest age class. First, stand age was not easily quantified in old forests using remote sensing or forest inventory data. Age estimation in these stands was problematic because older forests under natural succession are often composed of trees from different age cohorts, so assigning a singular value to stand age did not capture the structural and developmental variability present in such areas. My second challenge was the increased effort associated with conducting effective surveys in old forest. My established canopy-based survey method required a considerably greater amount of time (approx. 5.51 person hours per nest surveyed) compared to surveying in young forest (approx. 2.07 person hours per nest surveyed) where it is practical to survey for nests from the ground. As such, my sampling efforts allowed me to show comparisons between young forests and old forests but limited my ability to draw substantial inferences solely within the scope of old forests.

I implemented a large-scale study in Oregon’s central coast range over four years investigating site characteristics and persistence of arboreal and tree vole nests and documenting nest construction and use by a variety of canopy nesting species. I obtained a robust sample size of stands and nests allowing me to generate substantive discussion on the dynamics of tree vole nest use and arboreal and tree vole nest persistence among forests that differ in age. Differing forest management practices in the coast range can have impacts on nest site availability and persistence of arboreal nests. The relationships I presented can better inform managers concerning the nesting dynamics of canopy dependent species such as tree voles.

Tables and Figures

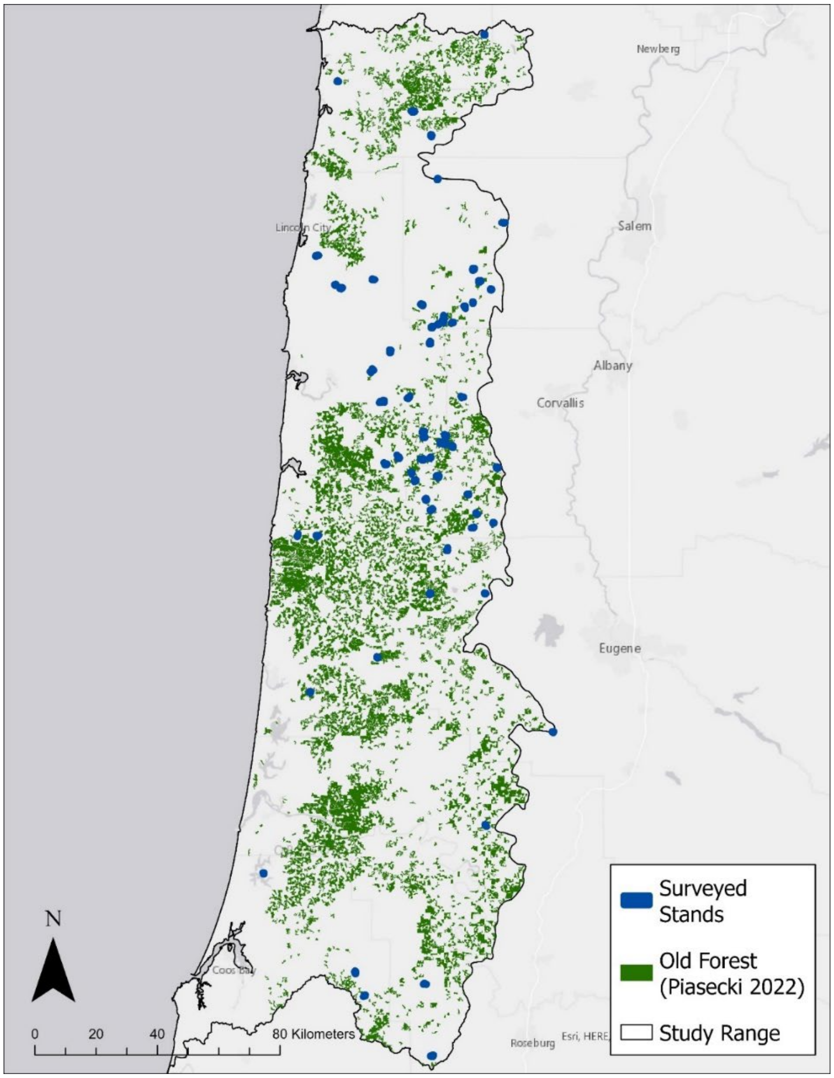

Figure 2.1. Map of study range (2020-2022), LiDAR derived old forest (green. ≥80 years of age), and all stands surveyed for arboreal and red tree vole (*Arborimus longicaudus*) nests (blue dots.).

Table 2.1. Description of arboreal and tree vole nest status classification used in this study using key signs of tree vole activity to determine status.

		Nest status	Description
Arboreal Nest		No Sign	No tree vole signs of any type found
	Tree vole nest	Old Sign	Any combination of 45^{0} chisel cut brown, dried cuttings, brown resin ducts, 45^{0} chisel cut debarked twigs, and/or black or brown tree vole fecal pellets
		Recent Sign	Any combination of 45^{0} chisel cut fresh, green cuttings, green resin ducts, and/or green tree vole fecal pellets
		Occupied	Tree vole occupancy confirmed by either remote camera or live capture

Table 2.2. Definitions of nest supporting structures quantified in this study based on a classifications found in (Swingle 2005; Michel and Winter 2009; Marks-Fife 2016).

Tree Structure	**Definition**
Broken Top	Structure created when main stem of tree partially or completely shears off creating one or more new leaders
Cavity	Hole in bark or wood where the opening is at least 5cm wide in which an arboreal nest could be constructed
Epicormic	Developed branch formation from a dormant bud on the main stem below the main canopy
Mistletoe	Dense aggregation of branchlets resulting from an infection or parasite
Split Trunk	‘V’ shaped structure formed from two or more diverging main stems
Moss Mat	Thick blanket of moss covering the top portion of a large diameter (>5cm) limb
Large Branch	Branch larger than 5cm in diameter
Whorl	Annual growth of multiple branches growing in a circular pattern from the main stem
Defect	Structural deformity capable of supporting arboreal nest construction not classified in an above category

Table 2.3. Sample sizes of stands surveyed from 2019 to 2022 to evaluate arboreal and tree vole nest survival.

Year	Stand Age Class						Total
	20[1]	**30[1]**	**40[1]**	**50[1]**	**60[1]**	**80[1]**	
2019	6	4	0	2	0	0	12
2020	12 (6)	9 (4)	5 (0)	7 (2)	2 (0)	5 (0)	40
2021	13 (12)	12 (9)	6 (5)	7 (7)	4 (4)	6 (5)	48
2022	15 (11)	15 (12)	7 (4)	8 (6)	1 (1)	7 (4)	53

[1] Total number of stands surveyed (resurveys)

Figure 2.2. Example of a multi-layer nest with signs of recent red tree vole occupancy. In this case, the original nest was primarily composed of moss and contained a spherical chamber characteristic of nests constructed by Humboldt’s flying squirrel. It was later occupied by a red tree vole. Green resin ducts, freshly harvested Douglas-fir cuttings, and fecal pellets were present inside and just below the initially constructed nest.

Figure 2.3. Example of nest persistence from 2020 (nest present) to 2021 (nest absent)

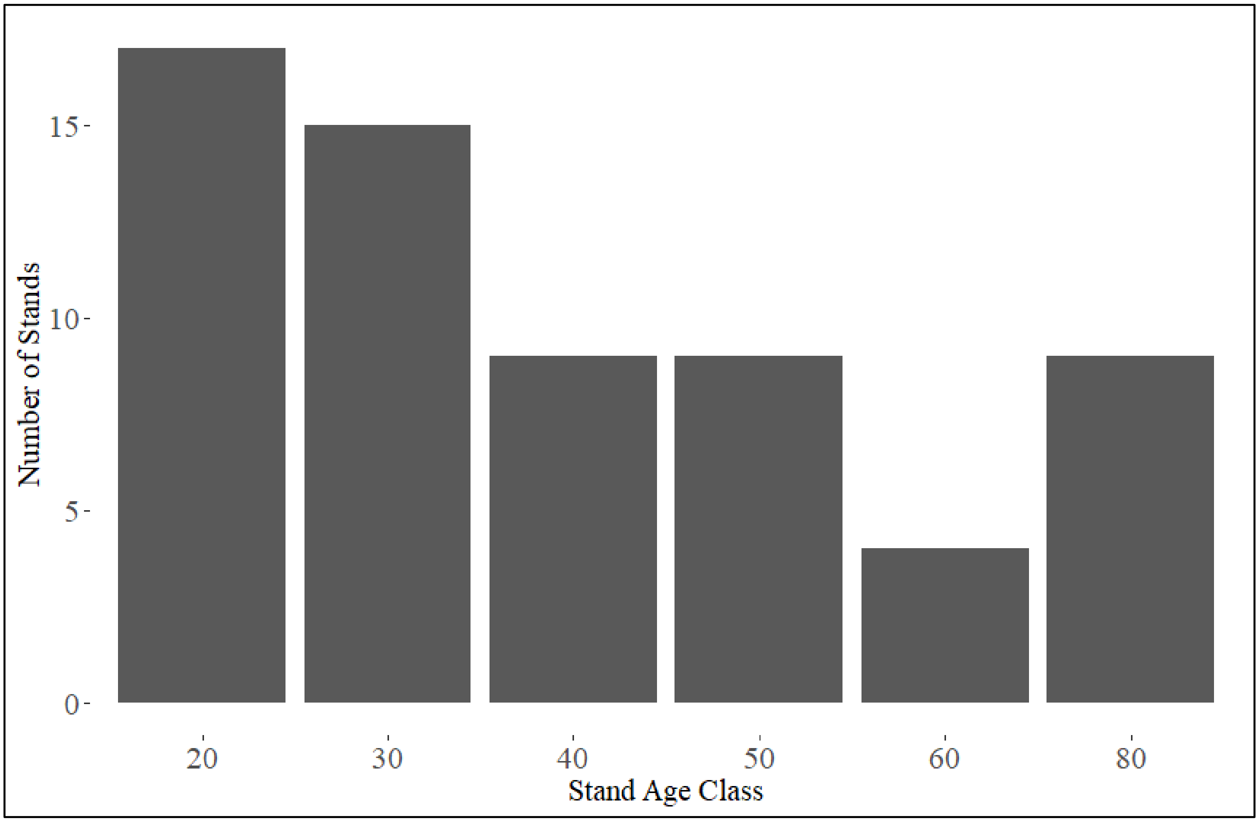

Figure 2.4. Distribution of surveyed stands for red tree voles in the Oregon Coast Range by stand age class.

Table 2.4. Median and interquartile range (IQR) nest volume in cubic meters measured at the time of initial survey.

	Stand Age Class						
	20, N = 437[1]	**30**, N = 338[1]	**40**, N = 37[1]	**50**, N = 52[1]	**60**, N = 11[1]	**80**, N = 169[1]	**p-value**[2]
Nest Volume	0.02 (0.03)	0.02 (0.03)	0.03 (0.04)	0.02 (0.03)	0.01 (0.02)	0.01 (0.01)	<0.001

[1] Median (IQR)

[2] Kruskal-Wallis rank sum test

Table 2.5. Number and proportion of supporting tree structures for tree vole nests across forest age class in 2022 (n = 564 nests).

Tree Structure	Stand Age Class					
	20, N = 180[1]	**30**, N = 169[1]	**40**, N = 23[1]	**50**, N = 25[1]	**60**, N = 5[1]	**80**, N = 162[1]
Broken top	51 (28%)	56 (33%)	14 (61%)	9 (36%)	1 (20%)	5 (3.1%)
Cavity	-	-	-	-	2 (40%)	18 (11%)
Defect	9 (5.0%)	12 (7.1%)	-	5 (20%)	-	3 (1.9%)
Epicormic	-	-	-	-	-	53 (33%)
Large branch	1 (0.6%)	1 (0.6%)	-	1 (4.0%)	-	40 (25%)
Mistletoe	1 (0.6%)	-	-	3 (12%)	-	-
Moss mat	-	-	-	-	-	29 (18%)
Split	35 (19%)	30 (18%)	4 (17%)	2 (8.0%)	1 (20%)	5 (3.1%)
Branch whorl	83 (46%)	70 (41%)	5 (22%)	5 (20%)	1 (20%)	9 (5.6%)

[1] n (%)

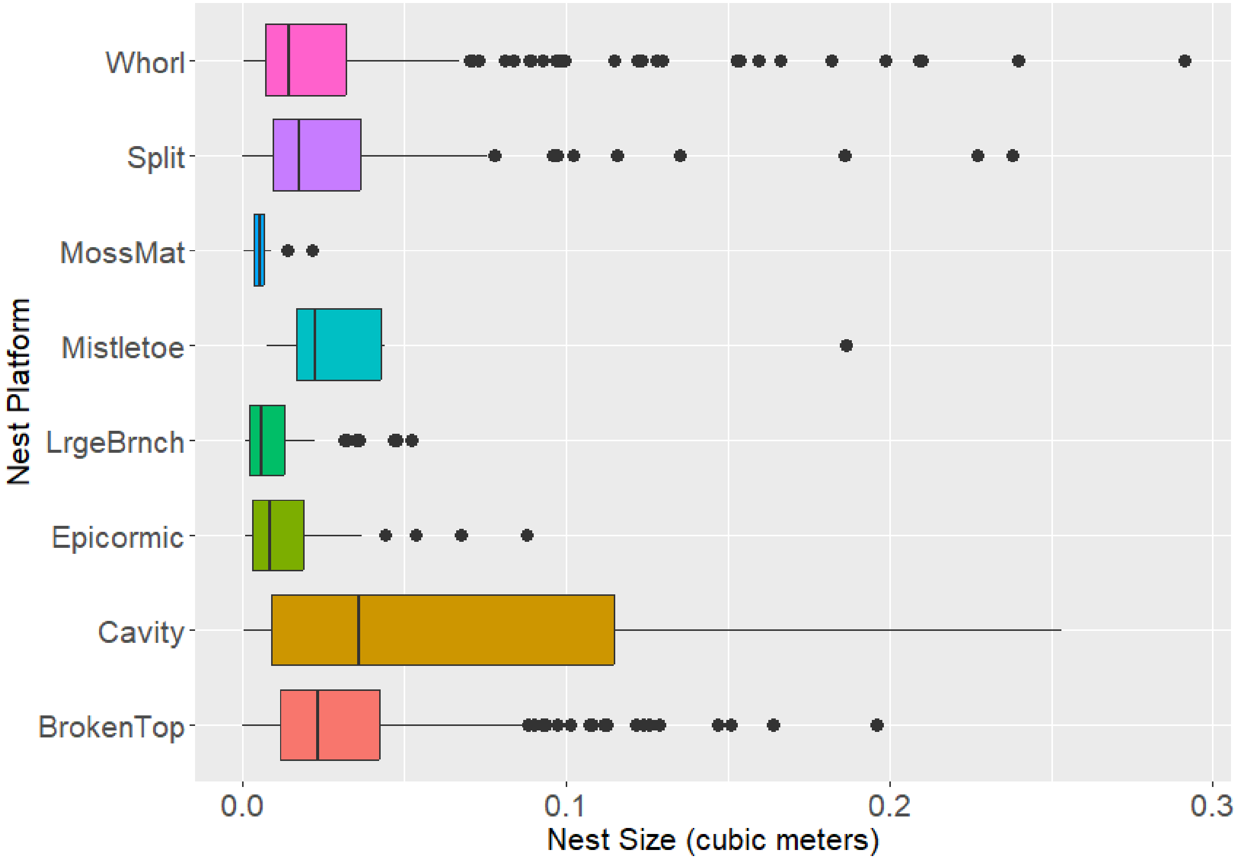

Figure 2.4 Distribution of calculated nest volume in cubic meters for each type of nest supporting structure (n=1033). Nests larger than $0.3m^3$ (n=11) were removed from the plot to better visualize data.

Table 2.6. Proportion of surveyed arboreal nests that became absent, or were no longer functional as a nest, between years.

Age Class	Time Period		
	2019-2020	**2020-2021**	**2021-2022**
20	0.14 (n=77)	0.11 (n=148)	0.19 (n=216)
30	0.11 (n=46)	0.14 (n=116)	0.18 (n=193)
40	-	0.08 (n=13)	0.12 (n=17)
50	0.18 (n=11)	0.22 (n=23)	0.22 (n=23)
60	-	0.4 (n=5)	1 (n=1)
80	-	0.36 (n=25)	0.11 (n=66)

Table 2.7. *A priori* model selection results from analysis of annual persistence probability (*S*) of 663 arboreal nests across 3 time periods from 2019-2020, 2020-2021, and 2021-2022. Models are listed in order of increasing AIC$_c$ values.

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**
S(nest size)	829.36	0	0.618	1	2
S(stand age + nest size)	831.36	1.99	0.23	0.37	3
S(t + nest size)	832.76	3.40	0.11	0.18	4
S(t + stand age + nest size)	834.78	5.42	0.04	0.07	5
S(.)	893.05	63.69	0	0	1
S(stand age)	894.89	65.53	0	0	2
S(t)	896.64	67.28	0	0	3
S(t + stand age)	898.54	69.18	0	0	4

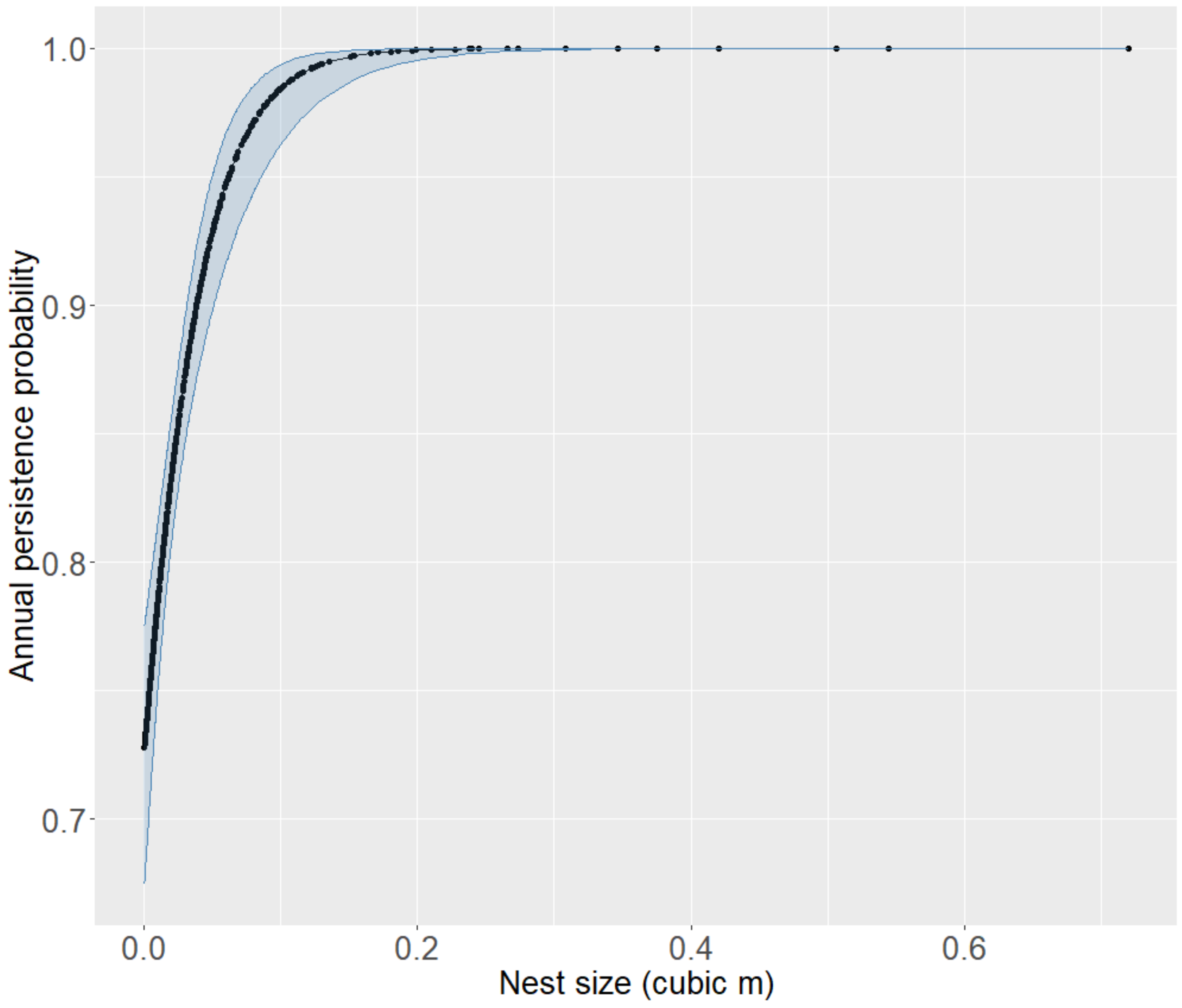

Figure 2.5. Annual persistence probability of arboreal nests based on nest volume in cubic meters measured at the time of initial survey.

Table 2.8. *A priori* model selection results from analysis of annual persistence probability (*S*) of 150 tree vole nests across 3 time periods from 2019-2020, 2020-2021, and 2021-2022. Models are listed in order of increasing AIC_c values.

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Model Likelihood**	**Num. Par**
S(t + stand age + nest size)	158.44	0.00	0.35	1.00	5
S(stand age + nest size)	159.56	1.12	0.20	0.57	3
S(t + construct + stand age + nest size)	160.11	1.66	0.15	0.44	6
S(construct + stand age + nest size)	160.87	2.43	0.11	0.30	4
S(t + construct + stand age + nest size +	162.06	3.62	0.06	0.16	7
S(construct + stand age + nest size + latitude)	162.88	4.44	0.04	0.11	5
S(nest size)	163.49	5.05	0.03	0.08	2
S(t + nest size)	163.97	5.53	0.02	0.06	4
S(construct + nest size)	164.39	5.95	0.02	0.05	3
S(construct + nest size + latitude)	166.30	7.86	0.01	0.02	4
S(t + stand age)	167.26	8.82	0.00	0.01	4
S(stand age)	167.59	9.15	0.00	0.01	2
S(construct + stand age)	169.49	11.05	0.00	0.00	3
S(.)	170.85	12.41	0.00	0.00	1
S(construct + stand age + latitude)	171.54	13.10	0.00	0.00	4
S(t)	171.55	13.11	0.00	0.00	3
S(construct)	172.58	14.14	0.00	0.00	2
S(latitude)	172.84	14.40	0.00	0.00	2
S(t + latitude)	173.52	15.08	0.00	0.00	4
S(t + construct + latitude)	175.39	16.95	0.00	0.00	5

Table 2.9. Means and standard deviation of annual persistence probability estimates for tree vole nests across 3 time periods from 2019 to 2022. These estimates were derived from the *S(t + stand age + nest size)* model.

	2019-2020 *n = 150*[1]	**2020-2021** *n = 150*[1]	**2021-2022** *n = 150*[1]
Persistence	0.93 (0.06)	0.95 (0.04)	0.87 (0.10)

[1] Mean (SD)

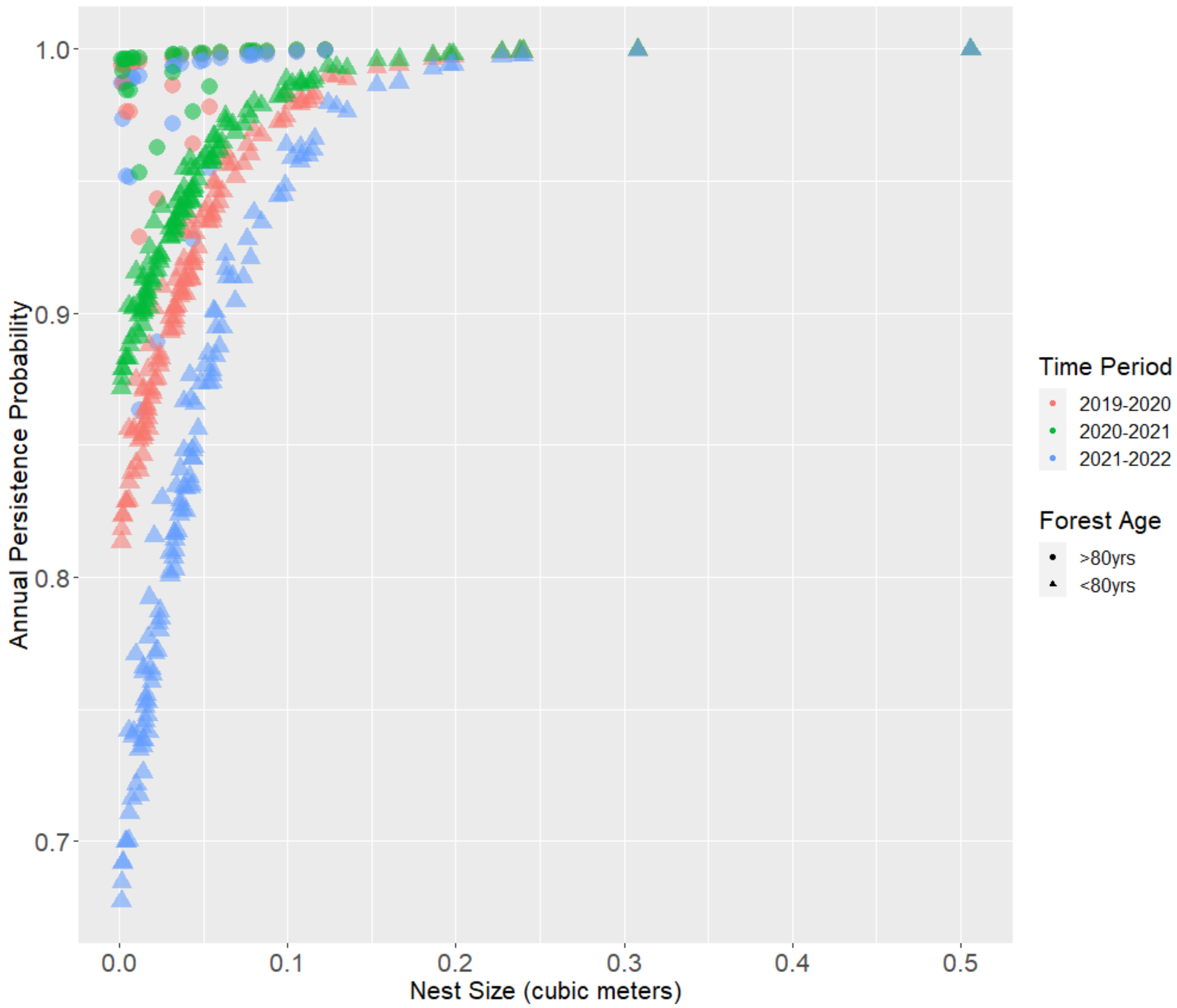

Figure 2.6 Annual persistence probabilities of recently occupied red tree vole nests (n = 151).

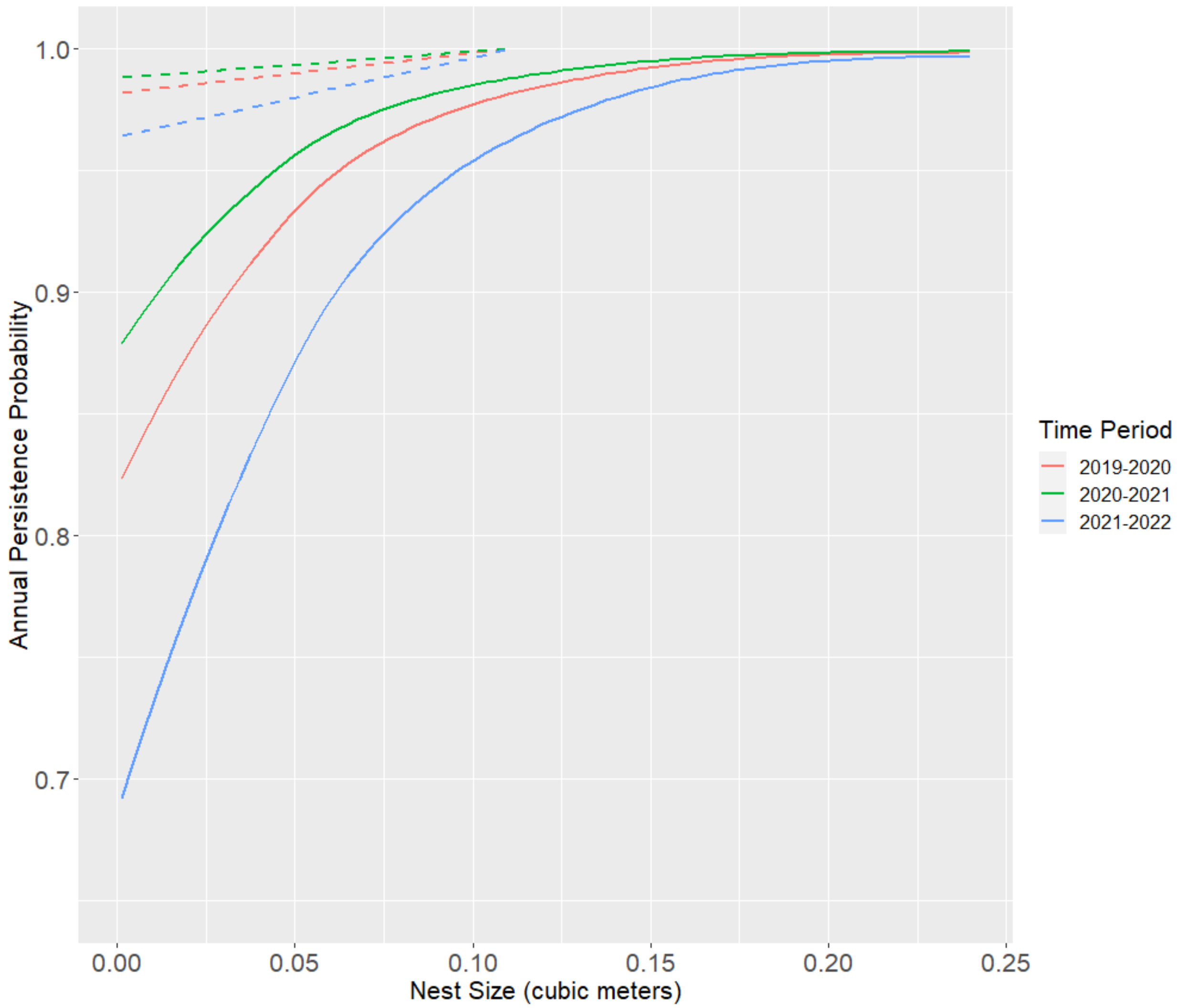

Figure 2.7. Annual persistence probabilities and modeled persistence estimates of recently occupied red tree vole nests (n = 151). Dashed trendlines represent linear models fit to data for each time period for forests over 80 years old. Solid trendlines represent generalized additive models fit to data for each time period for forests under 80 years old.

Table 2.10. Percentage of multi-layer tree vole nests originally constructed by another arboreal species (n=61) and multi-layer nests originally constructed by tree vole and later colonized by another arboreal species.

	Existing nest colonized by tree vole (n=61)	**Tree vole nest colonized by other arboreal species** (n=58)
Bird spp.	4.91%	8.62%
Bushy-tailed woodrat	6.56%	1.72%
Humboldt's flying squirrel	42.62%	29.31%
Tree squirrel spp.	16.39%	25.86%
Unknown	26.23%	29.31%

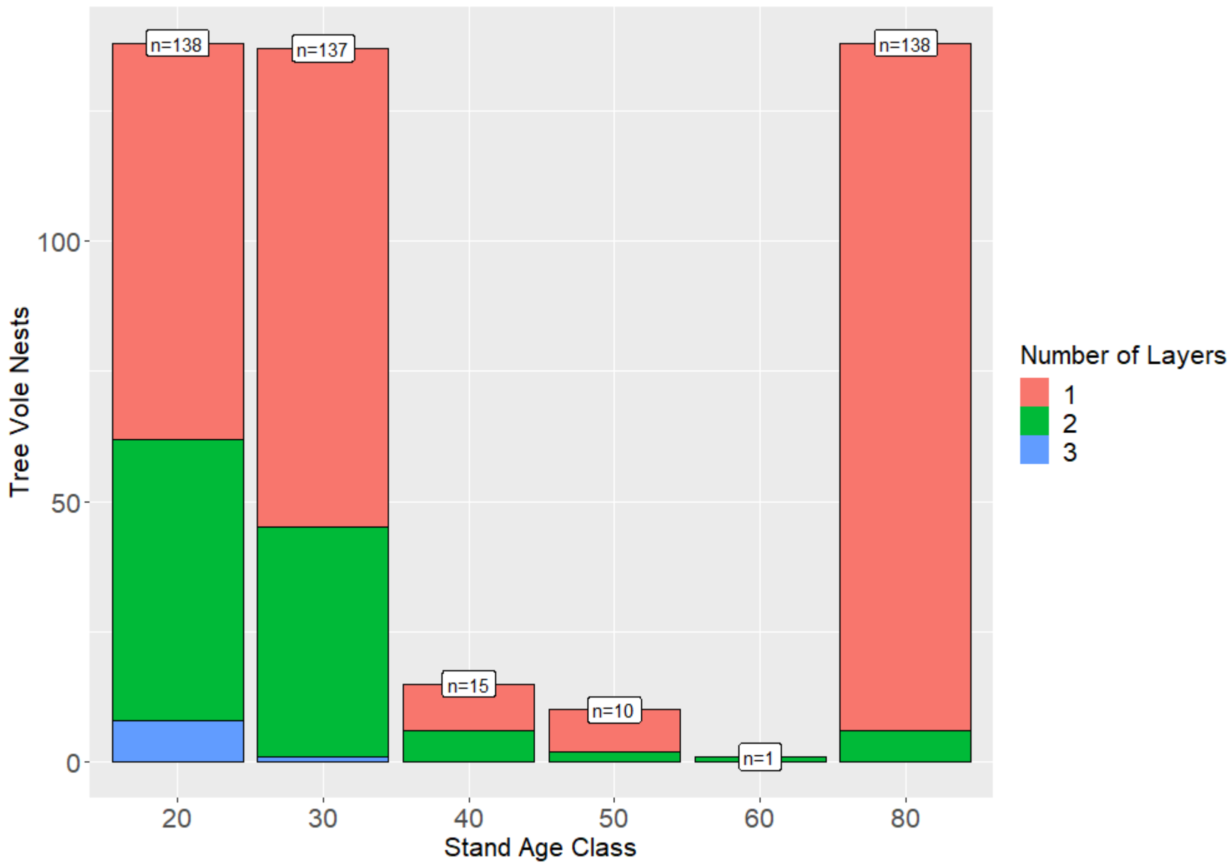

Figure 2.8. Bar plot showing the number of tree vole nests comprising one, two or three distinct layers constructed by other canopy nesting species.

Figure *2*.9. Interspecific nest use between Bald eagles and tree voles. Signs of recent tree vole activity were found in the hollow tree cavity created by a decaying broken top that was supporting an active bald eagle nest. Tree vole sign was also interspersed throughout the structure of the eagle nest. The eagle nest was confirmed to be active during the Bald eagle breeding season prior to climbing.

Chapter 3: Estimates of tree vole occupancy, arboreal nest detectability, and density in Douglas-fir forests of the central Oregon Coast Range with an emphasis on young stands

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Abstract

While red tree voles (*Arborimus longicaudus*), hereafter ‘tree vole’, are commonly regarded as an old forest obligate species, they have been regularly documented in younger forests. Due to the elusive nature of tree voles, challenges of canopy research, and lack of research on privately managed young forests, the extent of use and value of young forests to tree voles is unclear. While multiple tree vole studies included a young forest age category, most lacked the resolution to illuminate tree vole population metrics across the short temporal scale at which harvest rotations commonly occur. Probability of occupancy in young forests has never been modeled and nest density estimates can be easily confounded because of difficulties of finding tree vole nests. Detectability of tree vole nests can be limited in mature forests by extreme canopy heights, and in young forests by low canopy visibility resulting from high tree densities in stands managed for timber production. My goals included assessing nest detectability, likelihood of tree vole occupancy, and quantifying nest density across a range of forest age and distance from patches of old forest habitat.

I randomly selected and surveyed a 63 Douglas-fir (*Pseudotsuga menziesii*) dominated stands stratified by age and distance from patches of old forest (>20 hectares and $\geq$80 years old) in the central Oregon Coast Range from 2019 to 2022. I used differing methods to survey young (<60 years) and older ($\geq$60 years) stands to maximize my ability to detect arboreal nests. To estimate detectability within forests that differ in age, I conducted ground-based double sampling surveys in 80 plots across 15 young forest stands aged 22-50 years and conducted systematic canopy-based surveys in 9 plots across 3 old forest stands aged 160-212 years. I estimated detection probabilities in young forest using a closed-capture Huggin’s *p* and *c* model in program MARK. In young forests, I found nest detection rates to be constant (0.84, 95% CI 0.72, 0.96),

and significantly higher than in old forests where I estimated detection rates using a conventional abundance estimator and found that nest detection rates were low (0.05, 95% CI 0.0, 0.12). Directly estimating detection probabilities of my survey methods allowed me to more accurately interpret my nest density results.

Although random sampling allows inference to a broader population, it's often unknown how much sampling is needed to have the capacity to detect rare species. Using a case study approach, I conducted a census survey of an entire stand for arboreal nests and verified tree vole occupancy. I quantified the effectiveness of plot-based surveys across a range of survey effort defined as the percent of stand area surveyed. I ran 250,000 survey simulations of randomly selected hypothetical plots across continuous survey effort from 1 to 100% to detect at least one recently occupied tree vole nest given a stand is occupied. My simulation results suggest that surveying 10% of the stand would accurately assign stand-level occupancy on approximately 66% of the simulated occasions. Because I surveyed an average of 42% of the area within each of my young stands, I conclude that my survey methods were appropriate to accurately evaluate stand occupancy.

To estimate stand occupancy probability across stand age and distance from the nearest patch of old forest, I used my highest sample size of 48 young forest stands (<80 years) surveyed in 2022 in a single season occupancy model. I adjusted my occupancy prediction estimates to account for detection bias introduced from using spatial replicates instead of temporal replicates. My data suggested occupancy probability was highest (0.5, 95% CI 0.01, 0.67) in 20-year-old stands and declined as stand age increased to just over 50 years when occupancy reached near-zero (0.0, 95% CI 0.0, 0.4). Predicted occupancy probability decreased as distance from the nearest old forest patch increased to where tree voles no longer occupied young forest at modeled distances greater than 1,425m. Empirically, I did not detect any recently occupied tree vole nests in stands more than 1,649m from the nearest old forest patch.

Using my estimated results of detection rates of arboreal nests, I estimated density of arboreal nests and recently occupied tree vole nests for each stand. I demonstrated minor differences between detectability informed estimates and naïve estimates of arboreal nest density in young forest. In old forest, my naïve estimates were significantly lower than nest density estimates that accounted for detectability. Estimated density (in nests per hectare) of arboreal nests in young forest was highest in the 20-year age class ($\bar{X} = 3.76$, *SD* = 0.49) and declined as stand age increased. In old forest, my estimate of arboreal nest density was significantly higher than in young forest ($\bar{X} = 152.9$, *SD* = 76.82) and increased with stand age. Estimated density of recently occupied tree vole nests was locally high in the 30-year age class ($\bar{X} = 1.24$, *SD* = 0.35) within young forests, and overall highest in stands ≥80 years old ($\bar{X} = 53.5$, *SD* = 14.9). Based on my estimates and observations, I predict tree vole density is similarly bimodal with modest densities of tree voles in stands between 20-30 years, little to no tree voles in stands 50-80 years, and reaching highest densities in forests ≥80 years old.

Based on my observations and results, I maintain that nests must be climbed to determine species presence or absence, and imperfect detection rates must be accounted for when estimating population metrics for any species inhabiting arboreal nests. With my estimations for arboreal nest detectability across stand age, density estimates of red tree vole nests along with other canopy dependent species can be more accurately assessed. Further, my model of occupancy probability in young forests is the first to provide detailed resolution within young forests. I provide explanations and considerations regarding potential biases using a ‘space for time’ survey approach. Despite challenges I encountered in modeling occupancy, I believe my framework can help managers better assess likelihood of tree vole presence in young forests based on stand age and distance from patches of old forest.

Introduction

The red tree vole (*Arborimus longicaudus*), hereafter 'tree vole', is an elusive, canopy-dwelling species found in the coniferous forests of western Oregon and northwestern California. Because of their near exclusive association with the forest canopy, they can be challenging to study especially on a landscape scale. Tree voles have been well documented in older forests where high canopy volume provides a stable food source and structurally complex trees are conducive to arboreal nesting (Benson and Borell 1931; Corn and Bury 1986; Gillesberg and Carey 1991; Meiselman and Doyle 1996; Forsman et al. 2016; Marks-Fife 2016). While tree voles have also been documented nesting and reproducing in young forests (Clifton 1960; Brown 1964; Maser 1965a; Swingle 2005; Marks-Fife 2016; Linnell et al. 2018), very little information is available to better assess the likelihood of their occurrence or density by stand age or forest characteristics.

Privately owned forests, often young stands managed for timber production, make up over 41% of the Oregon Coast Range (Spies et al. 2007). Federal and state forests in some areas are also managed for timber resources. Nonetheless, forest management practices can differ significantly between stands leading to variation in forest age and composition (Cole 1996; Franklin et al. 2002). For land managers, expectations of site occupancy and population densities as influenced by forest age and composition may be useful for assessing conservations strategies for disturbance-sensitive species such as tree voles.

The extent to which young Douglas-fir (*Pseudotsuga menziesii)* forests provide conditions suitable for species like tree voles is unclear. The description that tree voles are obligates of old forests, only residing in stands with large multi-story Douglas-fir may be due, in part, to sampling bias. For instance, distribution maps created from northern spotted owl (*Strix* *occidentalis caurinia*) pellet contents are restricted in their scope because spotted owls were not common in younger stands (Forsman, Meslow, and Wight 1984; Forsman, Anthony, and Zabel 2004; Forsman et al. 2016). Other reasons for this assumption stem from the expansion of old-growth forest research created by the Northwest Forest Plan (USDA and USDI 1994). Many early (before 1985) museum and personal collection specimens collected via logging and pitfall traps were from mature and old-growth forests while specimens collected via tree climbing were primarily in young forests (Forsman et al. 2016 p19), highlighting opportunistic bias in early capture methods.

Regardless of effort, available information suggests tree vole abundance and density was highest in old forests compared to younger, regenerating stands (Price et al. 2015; Forsman et al. 2016; Marks-Fife 2016; Linnell et al. 2017). However, only one study has focused primarily on the relationship between young forests and arboreal voles, albeit a related species, the Sonoma tree vole (*Arborimus pomo*), which is similar in habitat requirements to the red tree vole but only occurs in northwestern California (Thompson and Diller 2002). Although their study design did not include tree climbing to verify nest occupancy, Thompson and Diller (2002) evenly balanced survey effort for stands within each decade of growth from 10-19 years to >60 years and found active Sonoma tree vole nest density was high in 30-39, 40-49 and >60 year age classes (3.40, 3.99, and 6.21 nests/hectare respectively) (Thompson and Diller 2002 Table 1.1). In western Oregon, which contains the majority of the red tree vole range, most studies have lacked resolution in, or ignored young forests, or were in areas with low tree vole population numbers such that generalizing characteristics within young forests would be problematic. For instance, Dunk and Hawley (2009) predicted tree vole nest occupancy in plots on federally managed land (USDA Forest Service and Bureau of Land Management); however, their positive observations included nests where only old tree vole sign was found. Tree vole habitat and distribution has also been evaluated using systematic surveys conducted primarily on state (Price et al. 2015) and federally-managed lands; however, these surveys have often collapsed young forest into a single age or size (DBH) class (Forsman et al. 2016; Rosenberg et al. 2016; Linnell et al. 2017), which could be problematic in capturing variation within young forests. Further, while surveys of tree vole abundance conducted by Price et al. (2015) included a large sample of plots in young forest (0-79 year) stands (n = 82), they only discovered tree vole nests in 1 young forest stand (aged 65 years), and 3 old forest stands (aged 90-125 years). As such, Price et al. (2015) concluded that tree voles were mostly absent in the northern Oregon Coast Range, suggesting a limited scope of inference in their assessment of tree vole abundance in areas where large portions of the landscape are unsuitable for tree voles.

Although commonly included in study designs, young forests were often misrepresented in tree vole literature. Many studies ‘binned’ or combined young forest into one age class and therefore lacked the resolution to predict non-linear relationships across stand age (Table 3.1). According to these studies, simply comparing young forest to old forest seemingly yields linear trends with young forest exhibiting a lower predicted density of tree voles than old forest. However, this approach is likely an oversimplification of the relationship between stand age and tree voles. Because the composition of young forest changes rapidly from 0 to 80 years (Franklin et al. 2002), further investigating tree vole occurrence within the range of stand-level succession and growth would help provide insights as to whether and to what degree young forests function as potential habitat for tree voles.

A variety of stand- and tree-specific characteristics may affect nesting habits of tree voles in young forests. Because tree voles are canopy dependent, they utilize branch connections in the canopy to travel between trees for food and escape from predators (Carey 1991). Branch and tree connections that create canopy pathways may play an important role in the nesting preferences of tree voles in young forests. Further, the availability of nest supporting structures and pre-existing arboreal nests improves habitat suitability for tree voles and other arboreal species in young forest (Linnell et al. 2018). These fine-scale features, referred to as 'tree structures' play an important role in facilitating forest biodiversity (Bruce et al. 1985). While the structural complexity of old forest greatly outweighs that of young forest (Michel and Winter 2009), the capacity of young forest to harbor highly canopy dependent species such as tree voles likely depends on the availability of these structures as well as the presence of pre-existing arboreal nests which tree voles can colonize.

While robust, stratified sampling is necessary to effectively capture distributions of rare species (Thompson 2004; Delgado 2022), accurate assessments of site occupancy and population density require the application of study designs and analyses that account for imperfect detection of the target species (MacKenzie et al. 2002; Kellner and Swihart 2014). For a small, elusive canopy dwelling mammal such as the tree vole, this was especially applicable. Forsman et al. (2016 p43) specifically highlighted the need for assessments of detection probabilities in tree vole population studies. Difficulties and biases involved with searching for arboreal nests from the ground has been thoroughly documented in tree vole research (Swingle 2005; Dunk and Hawley 2009; Forsman et al. 2016 pp42-43; Marks-Fife 2016). For instance, Swingle and Forsman (2009) tracked tree voles in their nests using radio telemetry and found that only 48% of nests were detectable from the ground. Although Dunk and Hawley (2009) determined that false negative observations via ground-based surveys were low (approx. 6%) in areas where tree voles actually occur, detection rates of ground-based transect surveys decrease in effectiveness from 0.27 (95% CI 0.090, 0.586) in young forest (25-79 years) to as low as 0.03 (95% CI 0.004, 0.186) in old forest (> 200 years) as stand age increases and canopy height becomes too great for reliable observation (Marks-Fife 2016 p111).

While accurate identification of a tree vole nest is difficult from the ground, when a tree is climbed to investigate a nest, signs of tree vole presence are discernable from other arboreal species. Tree voles are the only species that strips and discard the resin ducts of the conifer needles they consume. Tree voles will harvest needles directly from branchlets close to their nest, often leaving petioles attached to the live branchlet. They also collect and store these live branchlets in or on their nest from which they will later harvest needles (Lesmeister and Swingle 2017). These cuttings, which are typically collected on a nightly basis (Forsman, Swingle, and Hatch 2009), are cut at 45-degree angles and generally at lengths between 1-35cm making them discernable from cuttings collected by woodrats (*Neotoma spp.*) which are often longer and contain more auxiliary branchlets than those collected by tree voles (Lesmeister and Swingle 2017). Tree voles will also feed on the fresh cambium of live twigs and will cut these twigs at 45-degree angles on either end at lengths of up to 6cm. Such twigs break down at a slower rate than other signs and can offer clues about tree vole presence long after fecal pellets and resin ducts have decomposed (Lesmeister and Swingle 2017). While such signs are often easily discernable at nests, classification of species use is unlikely to be accurate without the application of tree climbing. Nonetheless, the detection of nests from the ground continues to present a challenge in surveying for tree voles and has implications on the accuracy of various populations analyses such as occupancy and density estimates.

In addition to understanding the rate of detection for arboreal nests to inform population metrics, a better understanding of the extent of survey effort required to maximize the likelihood of detecting tree voles in occupied areas has been a long-standing information gap. Forsman et al. (2016 p43) suggest that when survey plots (area surveyed) are large, the likelihood of detecting no tree vole nests in an area where tree voles are present was low. Further, Dunk and Hawley (2009) concluded that the rate of false negatives in tree vole surveys was only 6%. However, the amount of survey effort required to accurately classify an area as occupied or unoccupied by tree voles was unknown. Such an assessment would benefit the development of any formal survey protocols for tree voles and help improve the effectiveness of any occupancy-based study designs.

Because sampling for tree vole nests includes the potential for observers to miss locations of nests, it is useful to account for such error through statistical analyses. Occupancy model frameworks that account for imperfect detection rates (MacKenzie et al. 2002) can be used to better understand the influence of young forest characteristics on the likelihood of tree vole presence in a stand. Because tree voles have been described as an old forest obligate, distance to the nearest patch of old forest has been predicted to be a contributing factor to tree vole occurrence in young forests (Price et al. 2015; Forsman et al. 2016; Rosenberg et al. 2016; Linnell et al. 2017; Linnell and Lesmeister 2019). Linnell et al. (2017) suggested that patches of old forest >80 years old and at least 20 hectares in size were required to sustain a reproducing genetically diverse population of tree voles capable of dispersing into nearby young forest. Linnell et al. (2019) describe young forest ‘matrix’ (20-80 years old) as suboptimal for tree voles. Under this assumption, modelled connectivity between patches of old forest for tree vole populations with limited dispersal had the best conservation network when distances between patches were <4km (Linnell and Lesmeister 2019 Appendix Figure S1). Forsman et al. (2016 p32, 44) reported that 38% of tree vole nests in the central Oregon Coast Range were found in young forest that was adjacent to old forest. They further concluded that occupancy of young forests was ephemeral in nature and that colonization of such areas by tree voles was dependent on the presence of a source population in adjacent old forest. Based on this and other work, it is assumed that tree vole occurrence is limited in young forest landscapes and that probability of occupancy becomes less likely with increasing distance from the nearest patch of old forest. As such, any estimates of occupancy within young forest should be relative to nearest patch of old forest.

Although commonly accepted that tree voles occur in higher densities in old forests than in younger forests (Benson and Borell 1931; Gillesberg and Carey 1991; Meiselman and Doyle 1996; Price et al. 2015), few density estimates have been reported. Maser estimated a density of 1.03 individual tree voles per acre (or ~2.47 per hectare) (Maser 1965a). While much of Maser's research provides foundational knowledge on the species, his estimate was based on a census-style survey of a single stand and did not account for imperfect detection rates of arboreal nests. Marks-Fife (unpublished data) provided a density estimate of 1.91 ± 1.2 'occupied' tree vole nest trees per hectare and 1.6 ± 0.4 tree vole home ranges per hectare in stands 25- >200 years old (n=48). These estimates, although they do not specifically quantify the density of individual tree voles, are an improvement upon Maser's (1965a) initial estimate because stands were randomly selected and sampled and estimates accounted for imperfect detection rates of nests. Although Marks-Fife (2016) identified occupied nests throughout different age classes of forest, the study lacked sufficient sample size to draw conclusions about differences in density across stand age. Estimates from both Maser's (1965a) and Marks-Fifes's (2016) research apply to individual tree voles/home ranges. While there is merit in directly addressing tree vole population density, issues of detectability persist on multiple levels. In addition to accounting for the imperfect detectability of arboreal nests, such studies would also need to confirm and quantify unique individuals, requiring the use of labor intensive mark/recapture techniques such as radio telemetry (Swingle, Forsman, and Sovern 2004). Alternatively, estimating the density of recently occupied tree vole nests in a stand offers a simpler approach, can reduce required survey effort and would likely allow for a more robust sample of stands. Although the numerical relationship between recently occupied tree vole nests and individual tree voles is unclear, it is reasonable to assume that comparatively, high densities of recently occupied nests allude to high densities of individual tree voles as suggested in Thompson and Diller (2002). Nonetheless, reliable estimates of either approach to quantify population density are lacking specifically in young forests. Because young forests develop rapidly and can exhibit sufficient structural complexity and canopy connectivity to support arboreal nesting (Bingham and Sawyer 1991; Franklin et al. 2002; Linnell et al. 2017), and the availability of pre-existing arboreal nests in these forests can increase nesting space and facilitate movement for tree voles (Linnell et al. 2018), estimates of both arboreal nest density and recently occupied nest density would provide insight into the capacity of young forests to support tree voles.

Because information on the effects of forest age, specifically within young forests, on tree vole occupancy and tree vole nest density is limited, and distance from the nearest patch of old forest has been previously identified as likely influencing tree vole use in young forests, the development of models including these variables as predictors of occupancy and tree vole nest density is needed. Further, estimates of arboreal nest density, including tree vole nests, should be informed by the assessment of detection rates associated with survey methods. Thus, my objectives were to 1) quantify my ability to detect arboreal nests and nests recently occupied by tree voles in both young and old forest stands using multiple survey techniques, 2) assess survey effort needed to accurately classify stand-level occupancy by tree voles, 3) estimate tree vole occupancy using recently occupied nests in young stands by age and distance to old forest, and 4) estimate arboreal nest density and recently occupied tree vole nest density in stands that differ in age. I predicted that detection rates in young forest would be high, albeit imperfect, and that detection rates in old forest would be low, leading to underestimates of nest density. I predicted that occupancy probability in young forests would be modest, but greater than zero in stands that were close to patches of old forest. Finally, I predicted that both arboreal nest and tree vole nest density likely would not adhere to a simple linear trend across stand age, but instead reflect a rise, decline, and increase similar to a bimodal curve with locally high density in forests between 20 and 40 years of age, and the highest density in forests ≥80 years old.

Methods

Study Area

My study area from 2020 to 2022 was comprised of 10 USGS Hydrologic Watershed (HUC 8) units in the Oregon Coast Range (12466km^2, Figure 2.1). The significance of these units on tree voles is arbitrary, but they allowed me to easily delineate a study area based on existing landscape features. My study area during the 2019 pilot season was limited to the central Coast Range along the US highway 20 corridor (approx. 830km^2). Approximately 30% of my study area overlapped with the proposed Distinct Population Segment (DPS) of red tree voles that was considered for listing in 2019 and 2023 (USFWS 2019; 2022). Stands were dominated by Douglas-fir (*Pseudotsuga menziesii*) with western hemlock (*Tsuga heterophylla*) commonly appearing as a successional species in older stands. In stands within the coastal ecoregion, Sitka spruce (*Picea sitchensis*) was co-dominant along with western hemlock and Douglas-fir. In some unmanaged stands, grand fir (*Abies grandis*) was sporadically present.

Stand selection

I collaborated with eight different land ownerships and forest management agencies to create a pool of available stands for selection. The US Forest Service Siuslaw NF, and Bureau of Land Management provided stands on federally owned land. The Oregon Department of Forestry provided stands on state owned land.Weyerhaeuser Company, Starker Forests, Manulife Investment Management, Hampton Lumber, and Lone Rock Resources provided stands on privately owned land.

For the purpose of this study, a forest stand is defined as a spatially contiguous community of trees that are similar in age, composition and distribution such that they are distinct from adjacent tree communities (Nyland et al. 2016). I randomly selected stands stratified by stand age classes: 20-29, 30-39, 40-49, 50-59, 60-79, and >80 years of age. For stands under private and state management, I used known age calculated from the planting date provided by the stand owner. To classify older stands (≥80 years) under federal management, I used a compilation of LiDAR derived tree height layers paired with available forest inventory data from the Bureau of Land Management in ArcGIS. I then cross-referenced my layer with a smaller existing old forest layer developed by Linnell et. al. (2017).

My old forest layer was similarly generated using LiDAR data and represented patches ≥80 years old and ≥20 hectares in size. I cross referenced this layer with the Forest Activity Electronic Reporting and Notification System (FERNS) maintained by the Oregon Department of Forestry to eliminate areas that had been disturbed or harvested since LiDAR was flown. For the purposes of stand age classification in my study design, analysis and discussion, I classified young forest as any Douglas-fir dominated stand between 20 and 79 years old. I classified old forest as any Douglas-fir dominated stand greater than or equal to 80 years old. And I classified any patch of old forest assumed to be occupied by tree voles capable of emigrating to nearby young forest as greater than or equal to 80 years old and greater than 20 hectares in size (Mark A. Linnell et al. 2017). To verify the age of stands classified as greater than or equal to 80 years old, I collected age estimates of randomly selected trees at 1/hectare within each stand using ageing techniques outlined in Van Pelt (2007) and averaged the estimated age for the whole stand. My definition of 'old forest' coincides with the typical age of maturation for Douglas-fir forests in the northwest and aligns with other tree vole studies that evaluated forest age (Old-Growth Definition Task Group 1986; Marks-Fife 2016; Rosenberg et al. 2016; Mark A. Linnell et al. 2017). My assumption that minimum old forest patch size of 20 hectares is needed to support a tree vole population is based on the same assertion established in previous research using historical density estimates in old forest (Maser 1965a; Marks-Fife 2016; Mark A. Linnell et al. 2017).

I placed certain additional requirements on my stand selection for logistical and ecological reasons. I restricted my stand area to a minimum of 10 hectares and a maximum of 30 hectares. Stands could only be selected if they were not scheduled to be harvested in the next 5 years and had not been pre-commercially thinned.

To achieve an equitable distribution of selected stands across the entire study range, I evenly divided the study range into 4 sections from north to south. Red tree vole population density was anticipated to be highest at the southern portion of my study area (Forsman et al. 2016 p22) and lowest in the northern portion (Price et al. 2015), so geographic partitioning likely provided the most representative gradient of tree vole density. I selected 6 stands in each age class within each of these 4 sections using a random ranking process.

Within each stand, I randomly generated circular 17.8m radius (995.4m^2) survey plots at a density of one per hectare using ArcGIS. As such, each plot represents a survey effort of ~10% of one hectare meaning the total area of these plots represented approximately 10% of the total stand area.

Ground-based surveys

In forests aged 20-59, I conducted ground-based surveys of each plot where I walked around each plot and used binoculars to search the canopy for arboreal nests. I also opportunistically searched the canopy for nests while traveling between plots to increase the area of the stand that was surveyed. I recorded and stored survey tracklogs using Garmin eTrex 10 handheld GPS units (Garmin Inc.) and estimated sight distance into the canopy within each stand to approximate the total area surveyed. I uniquely marked all nest trees found in this manner with numbered aluminum tree tags and flagging. I recorded geolocation and tree-specific data using S1 Mobile Mapper and Trimble Smart Receivers (Trimble Inc. Model R-1000 #99133). Following my ground survey for nests, all nests discovered in the live crown that were able to be safely climbed were accessed using spur climbing techniques (Berdeen et al. 2015). Tree vole nest status was determined by searching the nest for the presence of chisel-cut Douglas-fir cuttings, discarded resin ducts, chisel-cut debarked twigs, and tree vole fecal pellets (Table 3.2).

Estimating detectability of nests in young forest using double-observer sampling

To assess detection rates of arboreal nests from the ground I conducted double-observer (or double-sampling) surveys at plots within stands. Double-observer techniques have been used in a variety of studies to assess detection rates and abundance of bird species during point count surveys (Nichols et al. 2000; Moore, Scheiman, and Swihart 2004; Smith et al. 2009). I applied the fundamentals of this methodology to ground-based nest surveys to assess the detectability of arboreal nests from the ground. I randomly selected a subset of 4 plots in each stand to conduct double-sampling surveys. I only double-sampled plots in new stands such that observers had no prior knowledge of any nests that were present in plots. When a plot was selected, the first observer would enter the plot and search for nests from the ground. Any nest detected was recorded by the first observer but not marked in any detectable way. The first observer would then leave the plot and the second observer would conduct a second independent ground survey of the plot for nests. Neither observer would communicate visually or verbally about the presence or absence of nests until both independent surveys were complete. Finally, both observers would compare results and record detections of each nest found by each observer. For example, a nest discovered by the second observer, but not the first observer would be assigned

"0, 1", whereas a nest discovered by both observers would be assigned a "1, 1". Observers were randomly selected (4 observers in 2021, 6 observers in 2022).

Since the initial survey was immediately followed by the second plot survey, I assumed that nest presence did not change between survey occasions. I also assumed that all nests were equally likely to be discovered by both observers. To reduce bias associated with this assumption, I only conducted double-observer surveys with crew members having >3 months of arboreal nest survey experience.

I estimated the detection rate of arboreal nests in my young forest plots using a Huggins closed capture model in Program MARK (Huggins 1989). The Huggins closed capture model is designed to estimate abundance (N) while accounting for the probability of initial detection (p_i) and the probability of redetection (c_i). It also allows for modeling p_i and c_i in relation to covariates associated with each plot or individual nest (Cooch and White 2019). I included stand age as a continuous covariate in my *a priori* model set to determine if stand age played a role in detection rates of arboreal nests from the ground. While abundance (N) can be derived from the Huggins model, the estimate only applies to plots that were included in the double-observer survey method where nests were found (n = 18 plots with nests across 16 stands). Because plots are distributed randomly throughout each stand and I was interested in extrapolating plot-level detection rates to the entire stand, I assumed that any heterogeneity in detection rates affected by variation in stand composition was accounted for. As such, I applied the detection rate from double-observer surveys in plots to the whole stand.

Canopy-based surveys in forests > 60 years of age

In forests over 60 years of age, I determined that ground surveys would be ineffective given the height of the canopy and complexity of canopy and tree structure especially in old forests over 80 years of age. Marks-fife (2016) estimated nest tree detectability from the ground to be as low as 2%. Instead of conducting ground-based surveys, I searched plots for arboreal nests from the canopy using a vertical-climb survey method. Upon entering each plot, I selected a tree within the plot to represent the 'center'. I selected this tree based on climbing safety, canopy-to-canopy visibility from the plot center tree to other trees within the plot, and the presence of tree structures that could potentially support arboreal nests. Once selected, I climbed the plot center tree using stationary rope climbing techniques (Berdeen et al. 2015). I surveyed for nests within the plot center tree and in the canopy of surrounding plot trees. Following this, any nests that I discovered in adjacent trees were then climbed and inspected for any signs of tree vole presence (Table 3.2).

Estimating detectability of nests in old forest stands using canopy-based census surveys

To assess detection rates and the effectiveness of identifying arboreal nests in adjacent trees using canopy-based surveys in old forest stands, I conducted a systematic census of a random subset of plots in old forest stands with estimated ages from 160-210 years (n = 3 stands, n = 9 plots). Following the initial canopy-based survey, I systematically climbed every conifer tree able to be safely climbed within each plot to verify the presence or absence of any nests. In this manner, assuming a detection rate of 1 for finding nests in trees that were climbed, I was able to assess the complete distribution of all arboreal nests within the plots.

I used the conventional Lincoln-Peterson abundance estimation equation (Seber 1982) to estimate the true detection rate (*p*) for each of the nine plots by algebraically rearranging the equation to solve for detection rate.

$$N = \frac{n}{p} \quad \text{solved to} \quad p = \frac{n}{N}$$

Where *N* represents the known abundance of nests within the plot which was determined through the census survey and *n* represents the number of nests identified by an observer within the plot during the initial survey. Because plots are distributed randomly throughout each stand, I assumed that any heterogeneity in detection rates affected by stand composition was accounted for. As such, I calculated the detection rate of arboreal nests (to include tree vole nests) in old forest as the mean of detection rates from each plot.

Plot-based surveys to detect stand occupancy

To estimate the effectiveness of my plot-based surveys at detecting recently occupied tree vole nests in young forest stands given the presence of tree voles, I used a case study approach. For three years from 2020 through 2022, I conducted comprehensive, census survey of a 31-year old, 15 hectare stand. Following my initial ground survey, I used GPS tracklogs to identify areas of the stand that were not yet surveyed. I repeated surveys in excluded areas until 100% of the stand area was surveyed. I then climbed all trees with nests found in the live crown and inspected them for evidence of recent tree vole activity (Table 3.2).

Following these comprehensive surveys, I used ArcPro to generate interconnected hexagonal plots throughout the entire stand. These simulated plots were set at an area of 995m^2 to mimic my standard 17.8m radius (995m^2) circular plots. The number of recently occupied nests found in 2021 (n=10) in each simulated plot was recorded. I then conducted a bootstrapped simulation of the resulting binomial dataset where I assessed the probabilities of simulated plot-based surveys to detect at least one recently occupied tree vole nest across a range of spatial survey efforts from 1-100% of the stand area surveyed.

First, I collapsed the number of recently occupied nests found in each simulated plot to either ≥1 nest detected, or 0 nests detected. The generated plots were assigned values to represent presence or absence of any recently occupied tree vole nests where a '1' meant a plot contained at least one recently occupied nest, and a '0' meant a plot contained no recently occupied nests. I randomly sampled 2500 simulated surveys across a continuous scale of survey effort in stand area surveyed from 1 to 100% (e.g. 30 * 995m^2 plots = 20% of the stand area). Within each simulation I calculated the probability within 100 simulated surveys of each amount of survey effort to detect at least one recently occupied nest within the stand. This resulted in a continuous dataset with 25 simulated values for each percent of survey effort (n=250000 simulated surveys).

Surveys of stand-level occupancy

Predicting stand-level occupancy with respect to tree voles is challenging for multiple reasons. First, tree voles are an elusive species and difficult to detect with certainty even if the surveyor is present at the nest. To reliably confirm occupancy, camera trapping or live capture methods must be used. Because tree voles can use multiple entrances/exits at a nest, even camera trapping cannot assume a perfect rate of detection (Damm, Grand, and Barnett 2010; Palencia et al. 2022). Further, a tree vole nest that exhibits sign of recent tree vole activity does not necessarily constitute tree vole occupancy (Marks-Fife 2016). Individual tree voles have been documented using between 1 and 6 nest trees within their home range (James K Swingle and Forsman 2009). Assigning a definitive, numerical relationship between recently occupied nests and individual tree voles is problematic (Forsman et al. 2019; Rosenberg 2019). To overcome this challenge, I decided to evaluate presence or non-detection of tree voles at a given site based on the occurrence of signs of recent tree vole activity at nests. While recently occupied nests do not necessarily equate to the same number of individual tree voles, occupancy is not a question of density or abundance, but simply of presence of a species. Therefore, I used recently occupied nests as an indicator of tree vole presence. I classified recently occupied nests as any tree vole nest where green resin ducts, freshly harvested conifer cuttings, and/or fresh fecal pellets were found, or where one or more tree voles were seen via remote nest camera (Table 3.2).

Another challenge associated with estimating stand occupancy is that detectability of tree vole nests from ground-based and from canopy-based surveys is imperfect. This challenge requires the application of an occupancy modeling framework that considers a state where the species is present, but not detected. Therefore, I used a single season occupancy model framework established by MacKenzie et al. (MacKenzie et al. 2002) that accounts for species occurrence when detection rates are less than 100%.

To sample for occupancy, I used randomly generated 17.8m^2 circular plots within each stand and defined plots as spatial replicates. I generated plots at a density of 1 per hectare in each stand such that approximately 10% of the stand area was surveyed. Using my plot-based survey methods in both young and old forest, I assigned each plot a '1' if it contained any recently occupied tree vole nests and a '0' if no recently occupied tree vole nests were detected within the plot. Based on stand area, encounter histories contained a minimum of 10 and maximum of 30 numeric values representing plot occupancy status. A value of 'NA' was assigned for unsurveyed plots or as a placeholder in stands where the total number of plots was less than 30. For example, the following encounter history represents a 22 hectare stand in which 3 plots were occupied.

'0, 1, 0, 0, 0, 1, 1, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, 0, NA, NA, NA, NA, NA, NA, NA, NA'

I generated encounter histories for each stand and year from 2019 to 2022. I modeled occupancy in R using the 'occu' function in the 'unmarked' package (Fiske and Chandler 2011; R Core Team 2022) which is based on single season occupancy models developed by

MacKenzie et al. in 2002 (MacKenzie et al. 2002). This model estimates two parameters, ψ and p, where ψ was the probability that the target species was present at a stand, and p was the probability that the target species was detected at a stand given the stand was occupied. I included stand age and distance from the nearest old forest patch as continuous covariates. Because I predicted that the relationship between occupancy and stand age was non-linear, I also included a quadratic parameter of stand age in my global model. I conducted model selection in R using the 'dredge' function in the 'MuMIn' package (R Core Team 2022; Barton 2023) which conducted model selection based on all possible subsets of a global model. My initial global model was: $p(\textit{stand age}), \psi(\textit{stand age} + \textit{stand age}^2 + \textit{distanceOF})$ where *stand age* was the age of the stand in years recorded at the time of initial survey and *distanceOF* was the distance (in meters) to the nearest patch of old forest ≥80 years and ≥ 20 hectares measured in ArcGIS from the edge of the stand to the edge of the old forest patch.

My statistical model was not ideal to accurately portray my data. In a traditional occupancy model, each stand is visited multiple times within a survey season to generate an encounter history (MacKenzie et al. 2002). To adhere to the closure assumption associated with a traditional occupancy modeling approach, using temporally replicated surveys of each stand, independent surveys would have to be conducted consecutively, requiring multiple weeks to complete a single stand. However, when implementing surveys on a large scale in remote areas, it would not be practical to survey a stand multiple times within a season. I instead used each randomly generated plot as replicates within a stand. I made this decision because my study area was large (>12,000km^2), my stands were often located in remote areas in the Oregon Coast Range, and conducting surveys for tree voles required a time and energy-intensive climbing effort. As such, to increase my stand-level sample size, I sampled randomly selected plots, or spatial replicates, without replacement, meaning I only surveyed each plot once within a season. The method I used for modeling is referred to as substituting ‘space for time’ (Kendall and White 2009; Guillera-Arroita 2011; MacKenzie et al. 2018 pp452-458).

Using a ‘space for time’ model can significantly bias the occupancy prediction (Kendall and White 2009; Guillera-Arroita 2011; Srivathsa et al. 2018). Under the conventional approach using temporally replicated surveys, when a stand was found to be occupied on one occasion, it must be occupied on every other occasion. Therefore, any recorded ‘0’ during replicated surveys would traditionally be interpreted as the target species was present but not detected. Under a ‘space for time’ approach, because plots (replicates) were randomly distributed throughout the stand, plots within an occupied stand could be absent of recently occupied tree vole nests even when other plots within the stand contained recently occupied tree vole nests. Implications of this violation of the closure assumption are apparent through the underestimation of detectability (p) and the subsequent inflation of the occupancy estimator (ψ). In other words, when the ratio of plots with tree vole detections compared to total plots surveyed was low, my model would assume the ability to detect tree voles was low and ultimately the connected hierarchical model would incorrectly increase the probability of occupancy. Sampling plots with or without replacement also has implications in the estimation of occupancy probability. Kendall and White (2009) determined that under scenarios where a fixed number of spatial subunits (plots) are occupied, sampling with replacement is desirable because it limits bias of the occupancy estimator. However, because the presence of recently occupied tree vole nests in plots was not constant, and sampling plots with replacement would be prohibitively and logistically challenging when surveying and climbing for tree vole nests, adjusting my survey protocol to sample with replacement as suggested by Kendall and White (2009) was not possible. Guillera-

Arroita (2011) conducted simulations under a similar framework and presented scenarios where occupancy of spatial subunits (plots) was based on a probability instead of a fixed number. Under this scenario, Guillera-Arroita (2011) determined that sampling plots without replacement introduced the least amount of bias to the occupancy estimator based on an approximated value of root mean square error (RMSE). As such, I decided to adjust my modeled estimates of occupancy using a root mean square error derived in simulations conducted in Guillera-Arroita (2011 supplemental information). I coarsely estimated my likely bias under the scenario of sampling subunits (plots) without replacement where the simulated proportion of occupied subunits was equal to 0.1, and the simulated detectability at occupied subunits was equal to 0.5. These simulated values were closest to my observed values for detectability and proportion of occupied plots and I believe this adjustment to my occupancy estimation was effective. Before publication, I will reanalyze these data using a Bayesian hierarchical model where my estimations for detectability can be included as a prior for each age class, but this was beyond my skill and time for this thesis.

I assumed probability of occupancy was equal across all stands and any heterogeneity between stands was modeled by covariates. I included stand age and distance from the nearest old forest patch in my global model to capture any heterogeneity in occupancy between stands.

I assumed probability of detection was equal across all stands and any heterogeneity was modeled by covariates. Because forest age drastically affects detectability (Marks-Fife 2016), I included stand age in my global model to capture any heterogeneity in detection probability between stands.

I assumed the detection of recently occupied tree vole nests at one stand was independent of detecting recently occupied tree vole nests at other stands. Because tree voles are not a highly mobile species and I did not select any stands adjacent to another selected stand, I am confident that my methods maintain this assumption.

Nest tree characteristics

To assess the availability of tree structures in each stand, I counted the total number of each structure type encountered in each plot. Since my plot area represents 10% of the stand area, I extrapolated to the stand level to create an estimate of tree structure density in each stand. In old forest, where it is difficult to visually survey an entire tree from the ground, I verified the occurrence of available tree structures through climbing. To examine the preferences for tree vole nesting in trees with tree structures, I quantified the number of structures both in randomly selected plot center trees in each stand and in trees where tree vole nests were discovered (Table 3.3).

To evaluate canopy connectivity at nest sites, I quantified the number of branch connections and tree connections for each nest. I counted physical branch connections to other live conifer trees within one branch whorl above and below the nest. I counted tree connections as the total number of live conifer trees in direct connection to the nest tree.

Nest Density Estimates

I estimated density of both arboreal nests and recently occupied tree vole nests in each stand using estimates of detection rates from my double sampling approach in young forest and my plot census surveys in old forest. Because my classification of arboreal nests includes all tree vole nests, I used the same detection rates for both arboreal nests and recently occupied tree vole nests. I used the Lincoln-Peterson abundance estimator (Seber 1982) to determine the relative abundance (N) for each stand based on nests found within fixed plots (n), the estimated detection rate (*p*), assigned to 0.84 in forests <60 years old and 0.055 in forests >80 years old (this study), and the stand area represented by fixed plots (10%).

$$N = \left(\frac{n}{p}\right) * 10$$

Using relative abundance (*N*) and known values of stand area in hectares (*A*), I calculated density estimates (*Dp*) for each stand.

$$Dp = N/A$$

I calculated confidence intervals for estimated density using 95% confidence intervals of detectability. Using both estimated density and naïve density, I visualized differences based on varying detection rates in both young and old forests.

Results

Stand, tree, and nest attributes

I surveyed a total of 63 stands from 2019 to 2022 (Table 3.4). Stand age at the time of initial survey ranged from 21 to an estimated 320 years old (Figure 3.2). Distance from the nearest patch of old forest was calculated in ArcPro as the distance from the center of the stand to the edge of the nearest old forest patch and ranged from 0 to 6710 meters (Table 3.5).

From 2019 to 2022, I surveyed a total of 6179 trees, and climbed and identified 1043 individual nests. Of these, 92.9% were found in Douglas-fir, 6.2% were found in Western hemlock and <1% were found in Sitka spruce. I positively identified tree vole sign at 564 nests. Overall number of arboreal nests in the 60-year age class were lowest compared to other age classes with no recently occupied tree vole nests found in any year. The mean proportion of arboreal nests with tree vole sign present was highest (0.97) in the 80-year age class and lowest (0.35) in the 20-year age class (Table 3.6). The maximum distance from the nearest old forest patch where I identified recent tree vole sign at a nest was approximately 1649 meters.

The average number of branch connections and tree connections at tree vole nests decreased as stand age increased (One-way ANOVA, $p < 0.001$; Table 3.7). I found 93.8% of tree vole nests in young forest had at least one branch connection within one whorl above and below the nest compared to only 16.7% of tree vole nests in old forest. I observed 97.3% of tree vole nest trees in young forest had at least one tree connection to an adjacent live conifer compared to only 62.3% of tree vole nest trees in old forest.

Tree structure density increases with stand age ($p < 0.001$). This was the overall trend when examining both young and old forests (Figure 3.3). However, when I only considered young forest, I did not observe a clear trend in structure density across stand age (Figure 3.4).

The mean number of tree structures for trees with tree vole nests was higher than a random sample of trees in each age class, which was statistically significant in all age classes except for the 60 year age class (ANOVA $p<0.05$) (Table 3.8). Visualizations of these differences across forest age can be seen in Figures 3.5 and 3.6.

Arboreal nest detection rates in young forest

I conducted double observer surveys in 54 plots in 16 stands in young forests (22 to 50 years old) and discovered 25 arboreal nests in 18 plots. I used encounter histories for each nest to generate a table of model results using Huggins closed-capture framework (Table 3.9).

Using the top model of constant detection rate with no variation across stand age (AICc weight 32.9%), I estimated the detection rate of arboreal nests from ground-based surveys to be 0.84 (95% CI 0.72, 0.96). While my next top model with an AICc weight of 18.3% included stand age as having an effect on detection rate, the confidence interval for stand age overlapped zero ($\hat{\beta}_{stand\ age} = 0.05$, 95% CI -0.05, 0.16). In young forest stands, stand age had no effect on detection rates in my study.

Arboreal nest detection rates in old forest

I conducted canopy-based census-style surveys in 9 randomly selected plots in 3 stands aged 160-212yrs. I climbed a total of 131 trees during these surveys and detected 35 arboreal nests. Only 5% (n=5) of nests found during the census survey were detected during the initial survey and all of these nests were located in the plot center tree from which the initial survey was being conducted. Using the Lincoln-Peterson abundance estimator, I estimated a detectability (p) value for each of the 9 plots and calculated a mean detection rate of arboreal nest from canopy-based surveys of 0.055 (95% CI 0.0, 0.12) in old forest stands ≥80 years.

Plot-based survey detectability (case study)

The likelihood of plot-based surveys to detect at least one recently occupied tree vole nest within a stand, given they were present, appeared as an asymptotic relationship with survey effort (percent of area surveyed) (Figure 3.8). To achieve 100% chance of detecting at least one recently occupied tree vole nest given the stand is occupied, my simulations suggested 38% of the stand area must be ground surveyed and climbed. Using randomly generated 17.8m radius circular plots, this would correlate with a density of 3.8 plots per hectare (assuming no opportunistic surveys between plots). Because my plots were generated at 1 per hectare, equating to 10% of the stand area, the probability of detecting at least one recently occupied tree vole nest by only surveying in plots was estimated at 0.66 (95% CI 0.64, 0.67) (Table 3.11). Since I ground-surveyed opportunistically between plots in young forest stands and recorded my survey route using GPS tracklogs and estimated my effective survey distance linearly at each stand, I added the area surveyed between plots to the area surveyed in plots to estimate the total area surveyed for each stand. I calculated my average survey effort of 42.4%, with a minimum survey effort of 20% and a maximum survey effort of 65% in stands with complete GPS tracklogs (n = 33). Using my average survey effort, I estimated my probability of detecting at least one recently occupied tree vole nest, given their presence in the stand, ranged from 0.89 (SD = 0.03) to 1.00 (SD = 0.0). My estimates were based on a case specific estimated density of recently occupied tree vole nests of 0.82 nests per hectare (95% CI 0.72, 0.96).

Occupancy

My preliminary analysis of occupancy using an initial global model of ‘*p(.), ψ(stand age + stand age*^{2} *+ distanceOF)*’ revealed that detection rates increased as stand age increases, which was ecologically incorrect. This occurred because I recorded higher proportions of occupied plots in old forest stands leading to the model predicting a higher detection rate than in young forest where I recorded lower proportions of occupied plots in stands. Recall that any stand wherein at least one plot is assigned a '1' (occupied), results in the model assuming that all other plots within that stand must be occupied such that any plot assigned a '0' (unoccupied) negatively impacts the estimated detection rate (p) (see methods). Based on my estimates of detection rates and stand age and results from other research focused on detectability across forest age (Marks-Fife 2016), detectability was estimated to be much lower in old forest (approximately 5%) than in young forest (approximately 84%) – opposite of the initial global model output. Therefore, I could not reliably model detectability as a function of stand age using my complete dataset or even hold detectability constant across both young and old forests. However, through my analysis of detection rates in young forest, I estimated detectability to be constant in forests from 20 to 59 years old (this study) and predicted similar detectability in forests between 60 and 79 years old. Therefore, I excluded old forest data from my final model. I adjusted my global model in stands 20-79 years old to '$p(.),\ \psi(stand\ age + stand\ age^2 + distanceOF)$'.

I used presence/non-detection tree vole nest data from 906 plots within 48 young forest stands (20-69yrs) conducted during 2022 to estimate stand occupancy. I selected data from 2022 because we had the highest sample size of young forest stands surveyed in that year. I generated encounter histories from a total of 906 plots across the 48 stands for input to a single season occupancy model. I generated a table of model results ranked by AICc (Table 3.12). My top model was $\psi(stand\ age + distanceOF)\ p(.)$ (AICc weight 39.7%) and included stand age ($\hat{\beta}_{stand\ age} = -0.95 \pm 0.65$) and distance from the nearest patch of old forest ($\hat{\beta}_{distanceOF} = -1.45 \pm 0.96$). Both variables were significant in predicting the probability of tree vole occupancy.

Using the top ranked model, I predicted likelihood of occupancy across stand age for young forest stands adjacent to patches of old forest (*distanceOF* = 0). Because the 'space for time' approach underestimates detection rates, the predicted value of occupancy was overestimated. I referenced simulations run by Guillera-Arroita (2011 supplemental information) based on sampling spatial subunits (plots) without replacement to reduce my predicted occupancy values by a root mean squared error (RMSE) of 0.3 (Figure 3.9). I plotted observed values for mean occupancy rate for each age class which align with the adjusted predictions for occupancy probability (Figure 3.10). The occupancy rate for recently occupied tree vole nests was highest in the 20-year age class and declined as stand age increased to the 60-year age class.

I predicted likelihood of occupancy in 20-year-old stands across increasing distance from the nearest patch of old forest based on the top ranked model. I adjusted for underestimated detection rates using a RMSE of 0.3 (Guillera-Arroita 2011 supplemental information). My model predicted that occupancy probability steadily declined as distance from the nearest patch of old forest increased (Figure 3.11). The distance at which the adjusted estimate of occupancy probability reached zero was 1425m.

Finally, I predicted the likelihood of occupancy in young forests across a continuous range of both stand age and distance from the nearest patch of old forest using the adjusted predicted occupancy values based on a RMSE of 0.3 (Guillera-Arroita 2011 supplemental information) as a tile plot (Figure 3.12).

Arboreal nest density and forest age

I recorded more tree vole nests per tree (range 0-11) in old forest than in young forest (range 0-2). Mean nests per tree were higher in old forest than in all young forest age classes. (Table 3.12).

With an estimated detection rate of 0.84 (95% CI 0.72, 0.96), ground surveys followed by tree climbing for arboreal nests in forests between 20 and 59 years-old resulted in slight underestimates of estimated nest density. Because overall naïve nest density in young forest was low, adjustments for imperfect detectability did not drastically increase the estimated values for arboreal nest density (Figure 3.13). In young forest, estimated arboreal nest density (in nests per hectare) was highest in the 20-year age class ($\bar{X} = 3.76$, *SD* = 0.49) and declined as stand age increased to 60yrs (Table 3.13).

Density estimates for stands in the 60-year age class were omitted for two reasons. First, the occurrence of arboreal nests in this age class of forest was very low (Table 3.6). In the 60-year age class, I surveyed 1425 trees across 4 stands. I found a total of 11 arboreal nests across all 4 years of surveys. Of these 11 nests, none were determined to be recently occupied by tree voles. Second, I did not assess the detectability of canopy-based surveys used in these stands. Without an estimate of detectability, any prediction of arboreal nest density would be biased.

With an estimated detection rate of 0.055 (95% CI 0.00, 0.12), canopy-based surveys in forests aged 97 to an estimated 320 years old drastically underestimated arboreal nest density. Because detectability of arboreal nests was so low in old forests, accurate predictions of nest density were difficult and naïve values of nest density were vastly different from detectability informed estimates of arboreal nest density (Figure 3.14). In old forest, estimates of arboreal nest density (in nests per hectare) were significantly higher than in young forest ($\bar{X} = 152.9$, *SD* = 76.82) (Table 3.13) and increased with stand age (Figure 3.14). Confidence intervals for predicted nest density were large. Since the lower confidence interval of detectability surpassed 0, the upper confidence interval of predicted nest density was inestimable. For example, in one 10.3 hectare old forest stand, I recorded a total of 19 arboreal nests across 10 plots. Using a detection rate of 0.055 resulted in an estimated density of approximately 345.45 nests per hectare. The lower limit of nest density using a detection rate of 0.12 was approximately 158.33 nests per hectare and the upper limit of nest density using a detection rate of 0.0 was inestimable.

Using trendlines based on linear models (Figures 3.13 and 3.14) I showed that surveys that do not account for imperfect detection of arboreal nests likely underestimate nest density in both young and old forests. Because estimated nest densities were drastically lower in young forest than in old forest, a visual comparison of nest density between young and old forest on the same scale was difficult. In young forest stands, estimated nest density declined as stand age increased (Figure 3.13). Estimated arboreal nest density in young forest ranged from 0.41 to 9.10 nests per hectare (n = 45 stands). In old forest stands, estimated nest density increased with stand age (Figure 3.14). Estimated arboreal nest density in old forest ranged from 17.82 to 682.35 nests per hectare (n = 7 stands).

Density estimates of recently occupied tree vole nests

Estimated densities of recently occupied tree vole nests follow a similar trend to arboreal nests with the exception of being dependent on the distance to the nearest old forest patch. In young forest within 1425m from the nearest old forest patch, I used a detection rate of 0.84 to estimate density. Mean density estimates (in nests per hectare) of recently occupied tree vole nests in stands where recently occupied nests were found were locally high in the 30-year age class ($\bar{X} = 1.24$, *SD* = 0.35, all years) and ranged from 0.61 to 1.19 in 2019 (n = 7 stands), 0.5 to 0.9 in 2020 (n = 9 stands), 0.77 to 2.02 in 2021 (n = 10 stands), and 0.4 to 1.37 in 2022 (n = 10 stands) (Table 3.14). In old forest I used a detection rate of 0.055. Mean density estimates of recently occupied tree vole nests in stands where recently occupied nests were found were 51.1 in 2020 (n = 2 stands), 40 (*SD* = 57.56) in 2021 (n = 6 stands), and 69.41 (*SD* = 28.73) in 2022 (n

= 6 stands) with a mean of 53.5 (*SD* = 14.9) across all years (Table 3.14). While density estimates were highest in the 80-year age class, I did not find recently occupied nests in all old forest stands. Recently occupied tree vole nests were found in 40% of old forest stands in 2020, 100% of old forest stands in 2021, and 86% of old forest stands in 2022.

I plotted estimated densities of recently occupied tree vole nests across all age classes and years using boxplots to visualize the relationship between density and stand age. I show a modest peak in density in the 30-year age class followed by a decline in the 40 and 50 year age classes and a sharp incline in density in the 80 year age class (Figure 3.15).

Discussion

I believe my research provided a much-needed foundation on population metrics and aframework for the management of tree voles in young forests should such a priority be identified by managers. To contextualize the function of young forests on tree vole populations, I provided occupancy estimates, detection rates and density estimates of recently occupied tree vole nests across forest age and distance from the nearest patch of old forest. While there is still room for refinement and a need for further research on the species, I discuss important metrics to help inform future management decisions in areas where existing research is otherwise limited.

While I initially hypothesized a quadratic relationship for stand age in young forests where tree vole occupancy would begin low (e.g., no tree voles present in newly harvested/replanted stands), increase, peak, and lessen at approximately 50 years when arboreal nest density declined, I did not find evidence of this trend. Although I suspect a quadratic trend accurately portrays tree vole occurrence in young stands, I did not survey any stands under 20 years where the occurrence of recently occupied tree vole nests is low to none (Thompson and Diller 2002; Forsman et al. 2016 p19, 24). Surveys for recently occupied nests would need to be conducted in 10-19 year old stands to test my prediction.

My occupancy model showed that distance from the nearest old forest patch was negatively correlated with likelihood of tree vole presence and is an important variable to consider evaluating the function of young forests as tree vole habitat. In an ecological sense, the interpretation and predictive utility of this model parameter assumes that the nearest patch of old forest was occupied by a population of tree voles large enough to facilitate emigration into nearby young forests (Linnell et al. 2017). I did not detect recently occupied tree vole nests in 100% of stands >80yrs. Although my detection rate in old forests was extremely low, and I observed recently occupied tree vole nests at higher densities than in young forest, I caution against assuming that all patches of forest >80yrs are occupied by tree voles. Additionally, the simple classification of all Douglas-fir dominated old forest into a category encompassing all forest >80 years was somewhat rudimentary. It has been well documented that this age class contains multiple developmental stages of both horizontal and vertical forest composition and canopy structure (Bingham and Sawyer 1991; Franklin et al. 2002; Van Pelt and Nadkarni 2004; Van Pelt 2007). For instance, Van Pelt (2007; figure 55) identified four different age and crown vigor classes within forests ≥80 years old. This structural diversity found in old forests suggests that forests within the 80-year age class likely differ in their capacity to support populations of tree voles. From my experience, I recommend any future tree vole research that addresses distance from patches of old forest accounts for this variation in development of horizontal and vertical canopy structure and also patch size.

Despite the alignment of my adjusted estimates of occupancy with my naïve estimates of occupancy (Figure 3.10), I recommend further analysis of occupancy under an approach other than 'space for time' such as a Bayesian hierarchical framework where detection rates are understood as prior knowledge instead of derived from the model and heterogeneity in spatial subunit (plot) occupancy is accounted for (Dupuis, Bled, and Joachim 2011; Outhwaite et al. 2018). While the 'space for time' approach was a viable method given the constraints of my study design and certainly improved the feasibility of surveying more stands over a large study area, the bias introduced on detectability and occupancy through the modeling process cannot be ignored even when adjusted based on simulated error. My adjusted estimates of occupancy based on stand age and distance from the nearest old forest, while novel and informative, still exhibit large confidence intervals and are likely to include bias. As such, I recommend a cautionary approach should my results be applied in any conservation and management framework.

Because occupancy in young forest, even in close proximity to old forest is not guaranteed, and because my density estimates of recently occupied tree vole nests in such areas were variable, I predict there were likely other unmeasured factors that I did not include in my model. While stand age provides a simple and effective mechanism to explain differences in tree vole occupancy, I suggest that the availability of tree structures in young forests may provide an additional and potentially more refined lens through which to examine occupancy probability.

I recorded tree vole nests in association with a variety of tree structures. In some cases, I found nests under moss mats, against the bole on whorls, and on large branches. Quantifying the occurrence of these structures is difficult and I did not account for these types of nest supporting structures in my estimates of tree structure density. As such, my estimates were likely an underestimate of the actual density of nest supporting structures in both young and old forests. Regardless of the omission of moss mats and large branches in my quantification of tree structure availability, the density of tree structures on or in which tree voles will construct nests is an order of magnitude greater in old-growth forests (>200yrs) than in young forests. While availability of tree structures in young forest is variable and there is no clear trend between 20- and 60-year age classes, I suggest that young forests that exhibit comparatively high structural complexity were more likely to support tree voles at high densities.

Although tree structures can be quantified down to the individual tree, I support considering tree vole conservation and management on a larger scale. Some research suggests that silviculture management decisions only affect tree voles at fine scales such as individual tree prescriptions (e.g., legacy tree retention) (Wilson and Puettmann 2007). While the availability of tree structures at fine scales, such as the individual trees, are important for tree vole nesting, foraging and reproduction, these factors may not ultimately contribute to dispersal and long-term persistence of the species on an intensively managed forest landscape. Despite their small home range, tree voles are likely to respond to larger-scale stand management practices and forest disturbances that can suppress canopy connectivity and reduce overall availability of tree structures such as pre-commercial thinning and wildfire. I highlight the declining trajectory of canopy connectivity as stand age increases through reduction in both branch connections and tree connections. While these measurements of canopy connectivity were lowest in old forest, the capacity of older, larger and often more structurally complex trees to harbor tree voles likely outweighs the need for canopy connectivity in old forest. Contrarily, individual tree complexity was far lower in young forest and canopy pathways are likely necessary to expand movement and nesting space for tree voles. While thinning, either mechanical or natural, may not immediately affect resident tree voles, lower tree densities would constrict the movement of tree voles throughout the forest. Open canopies also may lead to increased predation. These stand metrics and landscape-scale spatial relationships should be considered within the scope of any conservation and management priorities for red tree voles in managed forests.

Because tree voles nest in the forest canopy and are difficult to detect even when recently occupied nests have been identified, I believe almost all analyses on tree vole populations must account for imperfect detection rates. My analysis of detectability of canopy-based surveys in forests >80 years revealed that detection rates of arboreal nests were still very low. Compared to ground-based transect surveys for trees with ‘active’ nests conducted by Marks-Fife in 2016, my canopy-based surveys exhibited similar detection rates. The majority of tree vole nests I found during surveys in old forest were extremely cryptic and difficult to detect even when the climber was in the same tree. In my study, many nests were found at the base of epicormic branches, hidden inside cavities or concealed under moss mats. These types of tree structures occur at high densities in older forests and increase the difficulty in finding tree vole nests from the ground or in adjacent trees from the canopy. My double-sampling approach in young forest revealed that although detection rates were not perfect, they were high. Although excluded from the top model, stand age did have a weak effect on detection rate, which is likely a result of changes in canopy height and cover as stands develop over time. This relationship would become more clear with the application of double-sampling surveys in more stands between 20 and 59 years of age.

Although I did not conduct systematic sampling to assess canopy-based surveys in forests in the 60-year age class, I do not believe such an assessment would be productive since I recorded extremely low nest density in climbed trees and adjacent trees despite relatively open canopies. Because structural complexity and canopy height in the 60-year age class is significantly lower than old forest (Franklin et al. 2002; Van Pelt 2007) and the open canopy likely allows for easier detection of nests, I expect detection rates in 60-79 year forests to be more closely aligned to my estimated detection rate in young forests rather than my estimated rate of detection in forests >80 years old. As such, I do not expect my low abundance of observed nests to be a product of low detection rates in 60-79 year old forests. Instead, low canopy density and connectivity combined with limited availability of nest supporting tree structures in these stands likely limit the suitability of the canopy for nesting for both tree voles and other arboreal species.

My estimates of detection rates across different ages of forest allowed me to develop estimates of nest density across forest age. I provided estimates of density (nests/ha) for both arboreal nests and recently occupied tree vole nests across stand age. These estimates accounted for imperfect detection rates and highlighted significant differences in nest density between young and old forests. My range of arboreal nest density estimates in old forest was large (17.82 to 682.35 nests/hectare). This was most likely a result of low detection rates in old forest leading to large confidence intervals of nest density. I recorded locally high densities of recently occupied tree vole nests in the 30-year age class followed by a decline in nest density across the 40 and 50 year age classes. While a simple linear regression of recently occupied tree vole nest density may appropriately fit the data when comparing young forest to old forest, I predict a finer scale examination of estimated nest density in young forest would suggest recently occupied tree vole nest density follows a bimodal trend across all age classes. Based on my estimates I conclude that stand level characteristics of 50–79-year-old forests were not suitable for tree voles based on structural changes to the canopy that take place as stem exclusion occurs in young forests. Swingle (2005) highlighted the importance of canopy connectivity and canopy closure for tree voles in young forests . As young forest ages and increases in canopy height, tree density (stems/ha) decreases and canopy connectivity declines (Bingham and Sawyer 1991). I predict that the lack of physical canopy connectivity, low availability of tree structures, and small canopy volume results in an unsuitable environment for the emigration and persistence of tree voles in stands between 50-79yrs. Additional surveys for recently occupied tree vole nests in the 60-year age class would likely result in a better model fit. However, based on my observations over 4 years of surveying, I predict the likelihood of discovering arboreal nests of any species in this age class is low to none.

While I provided estimates of recently occupied tree vole nest density across stand age, the relationship between such nests and individual tree voles is unclear. Swingle (2005) determined through radio telemetry that the mean number of nests used by adult tree voles was

2.2 with a range of 1-6. It may seem plausible to use this mean value to estimate tree vole density from nest density, however such an estimate would be based on numerous assumptions leading to statistically questionable results. However, my data suggest trends in tree vole density likely follow similar trajectories as recently occupied nest density across stand age. Further, my estimates of recently occupied nest density across all age classes of young forest within an occupancy informed threshold of 1425m from the nearest old forest patch allow for a more expanded scope of inference than provided by previous density estimates of occupied tree vole nests only in occupied stands (Marks-Fife 2016).

I emphasize the importance of evaluating estimates of density within the scope of imperfect detectability. While I have provided analysis and estimates of detection rates of arboreal nests in the canopy, I recommend further development and analysis to determine the accuracy of extrapolating abundance and density estimates from sampled area to stand area. In instances where plot-based surveys are practical to survey for tree voles or other arboreal species, it is imperative to understand the effectiveness of surveys to accurately determine presence or absence of the target species. Through my case study, I was able to simulate the amount of survey effort (in area surveyed) needed to 1) capture the true abundance and spatial distribution of recently occupied nests in a 31-year-old stand, and 2) reliably detect at least one recently occupied tree vole nest in a stand, given that a stand is occupied. Since the relationship between survey effort and the likelihood of detecting at least one recently occupied tree vole nest is asymptotic, I can conclude that a survey effort of 30-40% would be sufficient to provide reliable information on stand occupancy, assuming other stands were similar in age and structure to my randomly selected 31-year-old case study stand. Although my sample size was extremely small, the approach could be used to validate thresholds in required survey effort and statistical power. Similar approaches using empirical data suggest that greater than 25% area surveyed is necessary to achieve 80% power and accurately assign occupancy (Tucker et al. 2021). These simulations, particularly the probability to detect at least one recently occupied nest, provide a realistic estimate to inform survey needs for tree voles or other arboreal species in the future.

Although young forests can provide habitat requirements of tree voles at some capacity, my observations were that not all young forests, even those adjacent to old forest, provide the habitat features necessary for tree vole occupancy. Based on my surveys, young forest stands with open canopies that lack physical connectivity were likely unsuitable for tree voles. I predict this openness in the young forest canopy creates limited ability to facilitate dispersal and protection from predators (see Linnell et al. 2020). My observations were that young forest stands with high tree densities, interconnected canopies, and high availability of nest supporting tree structures were more likely to be suitable for tree voles. However, young forests are far from comparable to old forests in terms of providing tree vole habitat. In my study, I observed forests ≥80yrs old exhibited availability of nest supporting tree structures at an order of magnitude higher than I recorded in young forests. Although tree density is higher in young forests leading to higher physical connectivity represented by branch and tree connections, individual trees in old forest exhibit much higher individual structural complexity than trees in young forest. This observed structural complexity of individual trees combined with the large canopy volume means they can provide superior nesting support than individual trees in young forest. I highlight this relationship by recording occurrences of up to 11 tree vole nests per tree in old forest and conclude that forests ≥80 years old provide the highest quality habitat for tree voles.

In summary, I planned and conducted a large-scale study focused on the relationship between young forests and tree vole populations. I estimated detection rates of arboreal nests including tree vole nests, predicted occupancy probability using stand age and distance from the nearest patch of old forest, and estimated densities of arboreal nests and recently occupied tree vole nests to highlight differences across forest age. My research provides evidence for the capacity of young forests to support tree voles. I emphasize the need to account for detectability in both arboreal nest survey methodology and application of survey effort to accurately assess tree vole stand occupancy. While old forests significantly outperformed young forests in their capacity to support tree vole populations, my data suggest that young forests have a moderate likelihood to contain tree voles specifically stands between 20 and 40 years of age within 1425m of the nearest patch of old forest. I encourage future research on tree voles in young forests to investigate individual tree vole survival, dispersal, and reproductive rates. If reproductive rates are higher than survival, it seems likely that young forests can augment existing habitat for tree voles both improving the resiliency and movement of tree voles across the fragmented forest landscape of the Oregon Coast Range.

Tables and Figures

Table 3.1: Review of forest age classifications and stand sample sizes used in tree vole studies. All studies were designed using a random sampling approach and employed systematic survey methods.

Forest Age classification	Sample size	Ownerships	Method	Comments	Source
0-79 (young) / 80-250 (mature/old-growth)	82 / 4	ODF, BLM	ground survey followed by climbing		Price et al. 2015
≤80 (young) / >80 (old)	365	USFS, BLM	ground survey followed by climbing	Stand age not used in results. Presence defined as any nest with tree vole sign.	Dunk and Hawley 2009
10-19 / 20-29 / 30-39 / 40-49 / 50-59 / ≥60	6 / 7 / 9 / 8 / 8 / 8	Private	ground survey only	Sonoma tree voles. Assumed 1 nest = 1 vole.	Thompson and Diller 2002
<100 (young) / 100-200 (mature) / >200 (old-growth)	3 / 3 / 3	Private	ground survey followed by climbing		Meiselman and Doyle 1996
25-79 (young) / 80-200 (mature) / >200 (old)	10 / 16 / 10	USFS, BLM	ground survey followed by climbing		Marks-Fife 2016
22-55 (young) / 110-260 (old)	2 / 2	USFS, BLM	ground survey followed by climbing		Swingle 2005
5-9 (pre-canopy) / 30-69 (young) / 76-150 (mature) / 195-450 (old-growth)	3 / 3 / 4 / 8	USFS	Pitfall traps	Study did not specifically target tree voles	Corn and Bury 1986

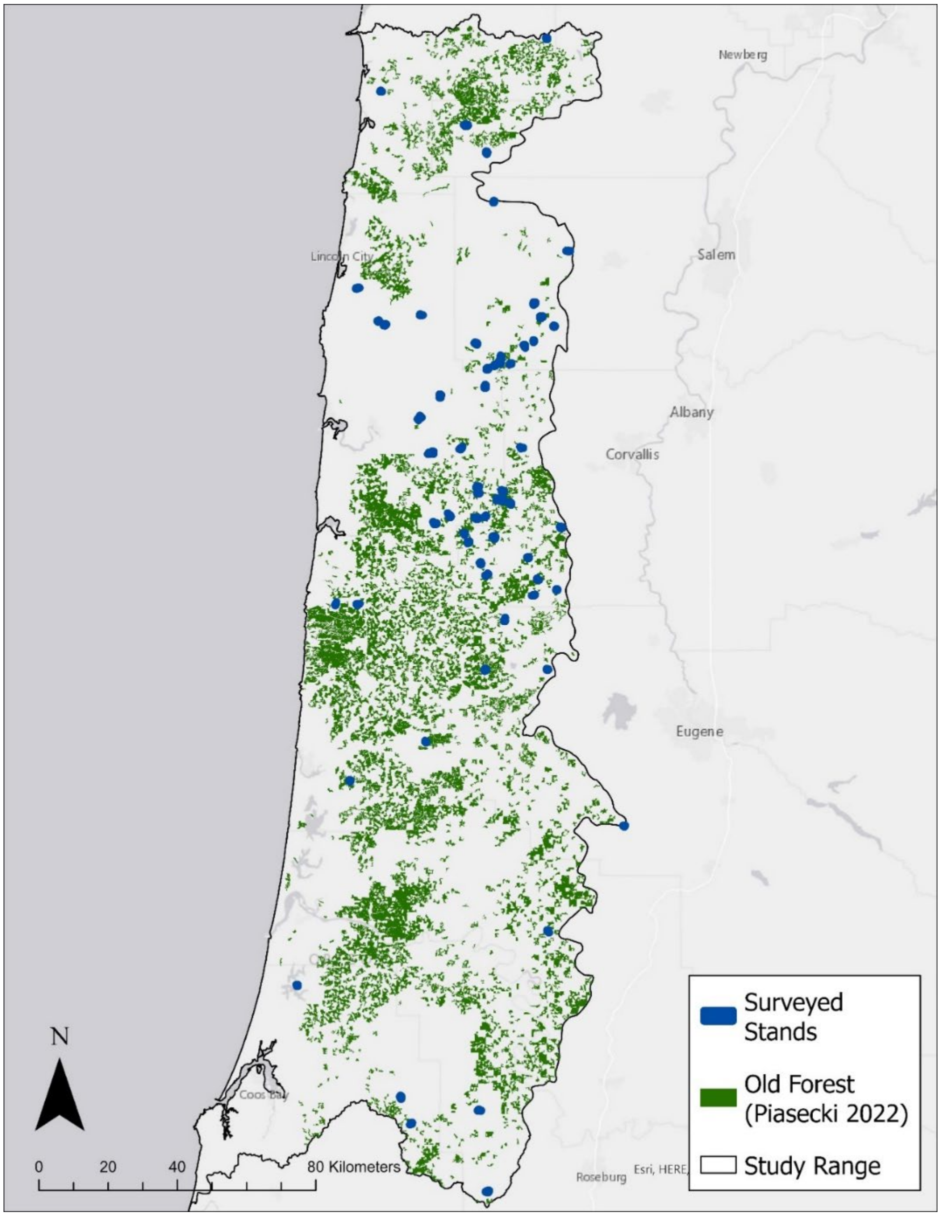

Figure 3.1. Map of study range (2020-2022), LiDAR derived old forest (green. >80 years of age), and all surveyed stands (blue dots).

Table 3.2. Tree vole nest status classification was based on presence of signs specific to nesting and feeding habits of red tree voles (Lesmeister and Swingle 2017).

			Nest status	**Description**
Arboreal nest			No Sign	No tree vole signs of any type found
	Tree vole nest		Old Sign	Any combination of brown, 45° chisel cut dried cuttings, brown resin ducts, 45° chisel cut debarked twigs, and/or black or brown tree vole fecal pellets
		Recently occupied tree vole nest	Recent Sign	Any combination of fresh, 45° chisel cut green cuttings, green resin ducts, and/or green tree vole fecal pellets
			Occupied	Tree vole occupancy confirmed by either remote camera or live capture

Table 3.3. Definitions of nest supporting structures quantified in my study based on a classifications found in (Swingle 2005; Michel and Winter 2009; Marks-Fife 2016).

Tree Structure	Definition
Broken Top	structure created when main stem of tree partially or completely shears off creating one or more new leaders
Cavity	hole in bark or wood where the opening is at least 5cm wide
Epicormic	developed branch formation from a dormant bud on the main stem below the main canopy
Mistletoe	dense aggregation of branchlets resulting from an infection or parasite
Split Trunk	'V' shaped structure formed from two or more diverging main stems
Moss Mat	thick blanket of moss covering the top portion of a large limb
Large Branch	branch larger than 5cm in diameter
Whorl	annual growth of multiple branches growing in a circular pattern from the main stem
Defect	structural deformity capable of supporting arboreal nest construction not classified in an above category

Table 3.4. Sample sizes of stands surveyed and (resurveyed) in each forest age class from 2019 to 2020

Year	Stand Age Class						Total
	20[1]	30[1]	40[1]	50[1]	60[1]	80[1]	
2019	6	4	0	2	0	0	12
2020	12 (6)	9 (4)	5 (0)	7 (2)	2 (0)	5 (0)	40
2021	13 (12)	12 (9)	6 (5)	7 (7)	4 (4)	6 (5)	48
2022	15 (11)	15 (12)	7 (4)	8 (6)	1 (1)	7 (4)	53

[1] Total number of stands surveyed (resurveys)

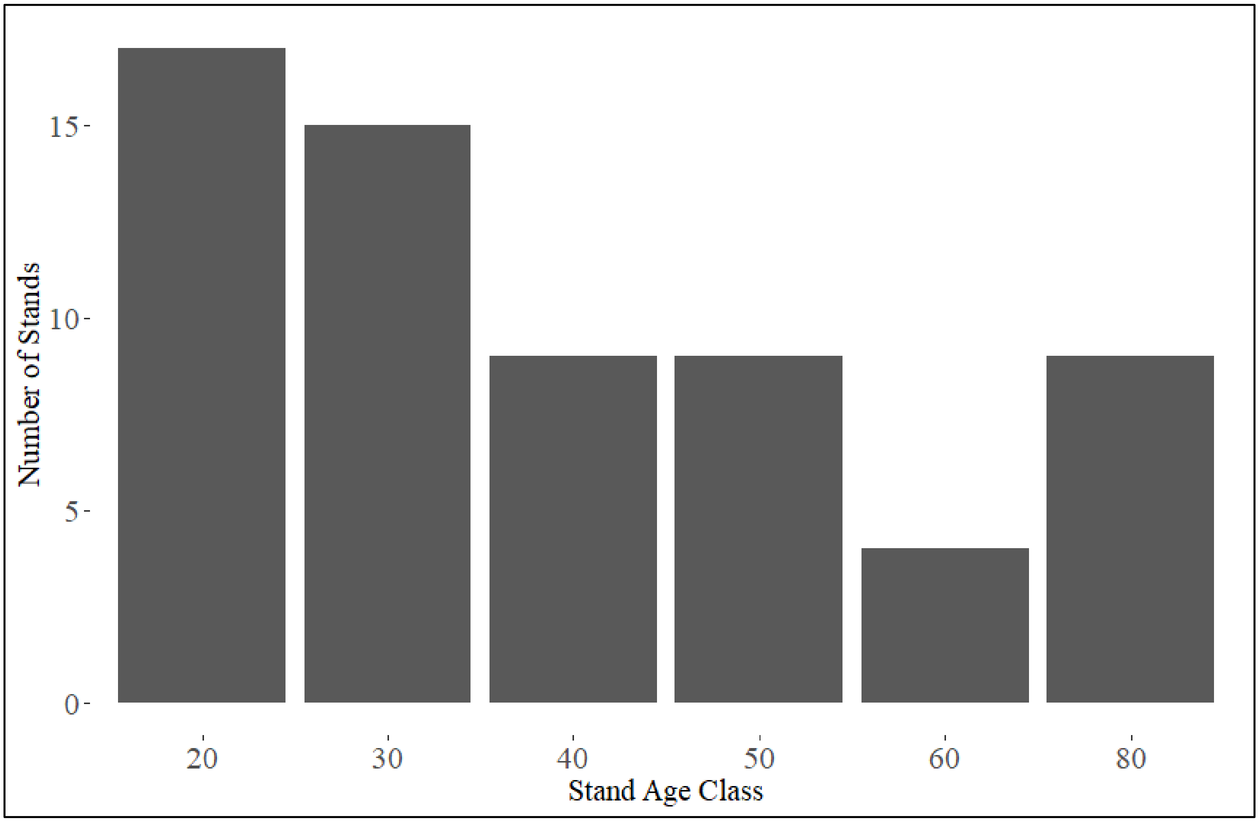

Figure 3.2. Distribution of surveyed stands by stand age class.

Table 3.5. Sample sizes of surveyed stands across a gradient of stand age and distance from the nearest patch of old forest.

Distance from old forest (m)	**Stand Age Class**					
	20	30	40	50	60	80
Adjacent	5	5	3	5	0	9
1-500	6	4	2	1	1	NA
501-1000	2	2	1	2	1	NA
1001-2000	2	3	2	0	1	NA
>2000	2	1	1	1	1	NA
Total	**17**	**15**	**9**	**9**	**4**	**9**

Table 3.6. Number of nests of each status (Table 3.2) found in each stand age class from 2019 to 2022. Young forest stands ranged from 0-6170m from the nearest old forest patch. Remote camera data from 2022 has not been recovered at the time of writing therefore counts of occupied nests may instead be represented in nests with recent tree vole sign.

Year	Stand Age Class					
	20[1]	**30**[1]	**40**[1]	**50**[1]	**60**[1]	**80**[1]
2019	46/18/5/8	21/12/4/9	NA	4/4/2/0	NA	NA
2020	114/24/3/11	64/36/3/15	5/6/0/2	13/7/1/2	2/3/0/0	3/15/3/4
2021	171/53/4/21	117/54/10/21	9/11/3/3	17/11/4/0	5/3/0/0	2/43/10/11
2022	193/87/35/16	134/102/27/9	10/14/1/0	20/9/1/0	0/1/0/0	2/105/33/0

[1] No tree vole sign/old tree vole sign/recent tree vole sign/occupied {stands surveyed}

Table 3.7. Mean branch and tree connections at nests across all age classes of forest

	Stand Age Class						
	20 n = 180[1]	**30** n = 169[1]	**40** n = 23[1]	**50** n = 25[1]	**60** n = 5[1]	**80** n = 162[1]	**p-value**[2]
Branch Connections	8.41 (4.61)	6.53 (4.78)	5.00 (3.61)	3.84 (3.13)	4.20 (4.27)	0.30 (0.80)	<0.001
Tree Connections	5.23 (1.84)	4.66 (1.77)	4.35 (1.61)	3.28 (1.59)	3.20 (1.10)	1.11 (1.14)	<0.001

[1] Mean (SD)

[2] One-way ANOVA

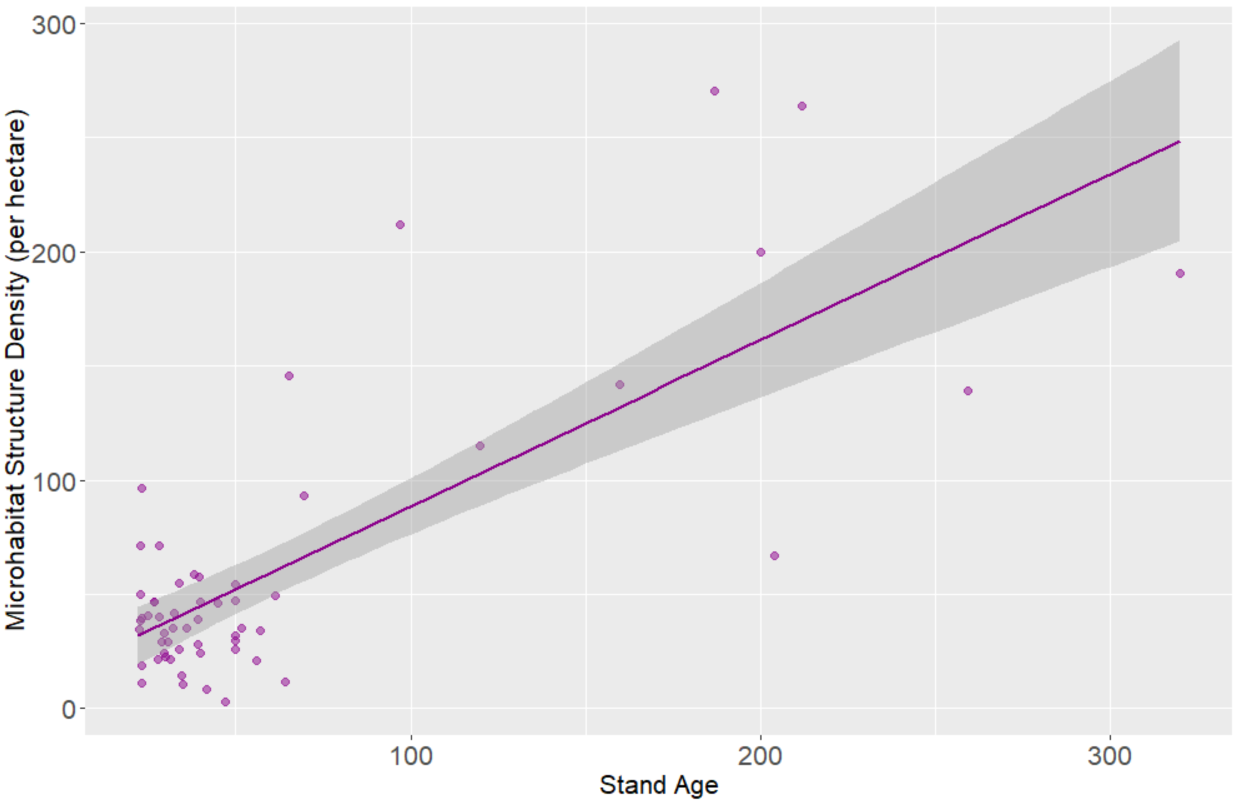

Figure 3.3: Estimates of tree structure density (per hectare) derived from plot surveys in each stand (n = 58).

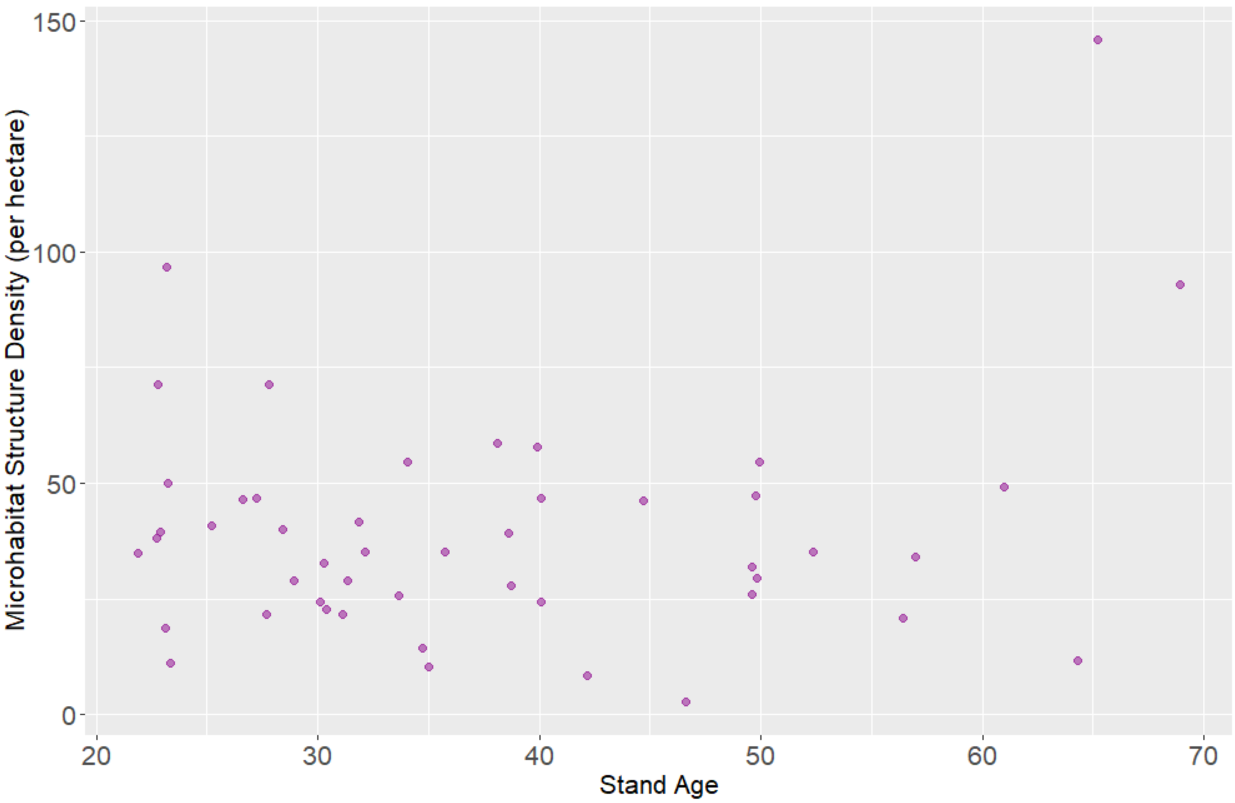

Figure 3.4. Estimates of tree structure density (per hectare) derived from plot surveys in each young forest stand (n = 48).

Table 3.8 Mean number of tree structures per tree showing significantly greater values in trees with tree vole nests across all ages except the 60-year age class.

Stand Age Class	**Structures per Tree**		
	Random Sample[1]	**RTV Nest Trees**[1]	**p-value**[2]
20	0.22 (0.47)	0.77 (0.78)	<0.001
30	0.15 (0.45)	0.80 (0.79)	<0.001
40	0.23 (0.51)	0.91 (0.52)	<0.001
50	0.21 (0.56)	0.60 (0.50)	0.001
60	0.96 (3.64)	2.80 (3.03)	0.28
80	3.40 (6.84)	5.57 (7.18)	0.007

[1] Mean (SD)
[2] One-way ANOVA

Figure 3.5. Younger forests exhibit different stand characteristics depending on age. **Left**: 27 year old stand with higher tree density and a highly interconnected canopy. **Right**: 65 year old stand with comparatively lower tree density and a canopy that is more open and less connected.

Figure 3.6. Forest estimated at >200yrs old exhibiting a complex, multi-story canopy. Although tree spacing is less dense than a younger forest, individual trees have high structural complexity necessary for nesting.

Table 3.9. Model selection results for analysis of the detection rate (*p*) of arboreal nests in forests aged 20-59 years. Models ranked by AICc weight.

Model	**AIC_c**	**ΔAIC_c**	**AIC_c Weights**	**Model Likelihood**	**Parameters**
p(.)=c(.)	41.4351	0	0.32912	1	1
p(.)=c(.) + Stand Age	42.6062	1.1711	0.18325	0.5568	2
p(.), c(.)	43.4637	2.0286	0.11936	0.3627	2
p(.), c(.) + Stand Age	44.6434	3.2083	0.06617	0.2011	3
p=c + Stand Age	44.7292	3.2941	0.06339	0.1926	3

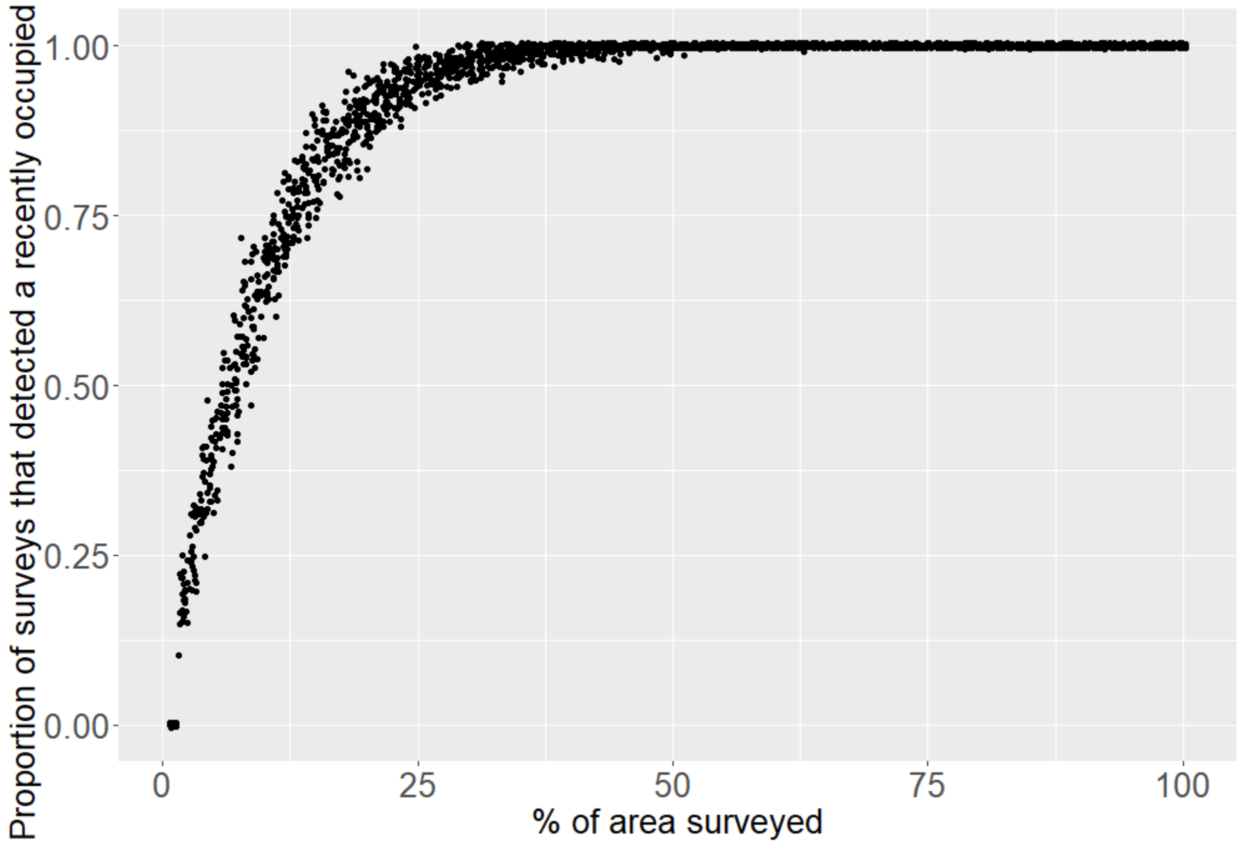

Figure 3.8. Likelihood to detect at least one recently occupied nest, given the area is occupied by tree voles. Simulations of 25 surveys for each survey effort from 0 to 100% based on case study data (n = 2500).

Table 3.10. Mean probabilities that percent of stand area surveyed will detect at least one recently occupied tree vole nest

	Percent Area Surveyed						
	5, N = 25[1]	**10**, N = 25[1]	**15**, N = 25[1]	**20**, N = 25[1]	**25**, N = 25[1]	**50**, N = 25[1]	**75**, N = 25[1]
Detection Probability	0.39 (0.05)	0.66 (0.04)	0.82 (0.04)	0.89 (0.03)	0.96 (0.02)	1.00 (0.00)	1.00 (0.00)

[1] Mean (SD)

Table 3.11. Model selection results for single season occupancy model using presence/absence data of recently occupied tree vole nests from 2022. Models ranked by AICc weight.

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Log Likelihood**	**Num. Par**
Ψ(stand age + distance)	247.20	0	0.40	-119.60	4
Ψ(stand age + stand age^2 + distance)	249.18	1.98	0.15	-119.59	5
Ψ(stand age)	249.21	2.01	0.15	-121.61	3
Ψ(.)	249.87	2.67	0.10	-122.94	2
Ψ(stand age + stand age^2)	251.05	3.85	0.06	-121.53	4
Ψ(distance)	251.63	4.43	0.04	-122.82	3

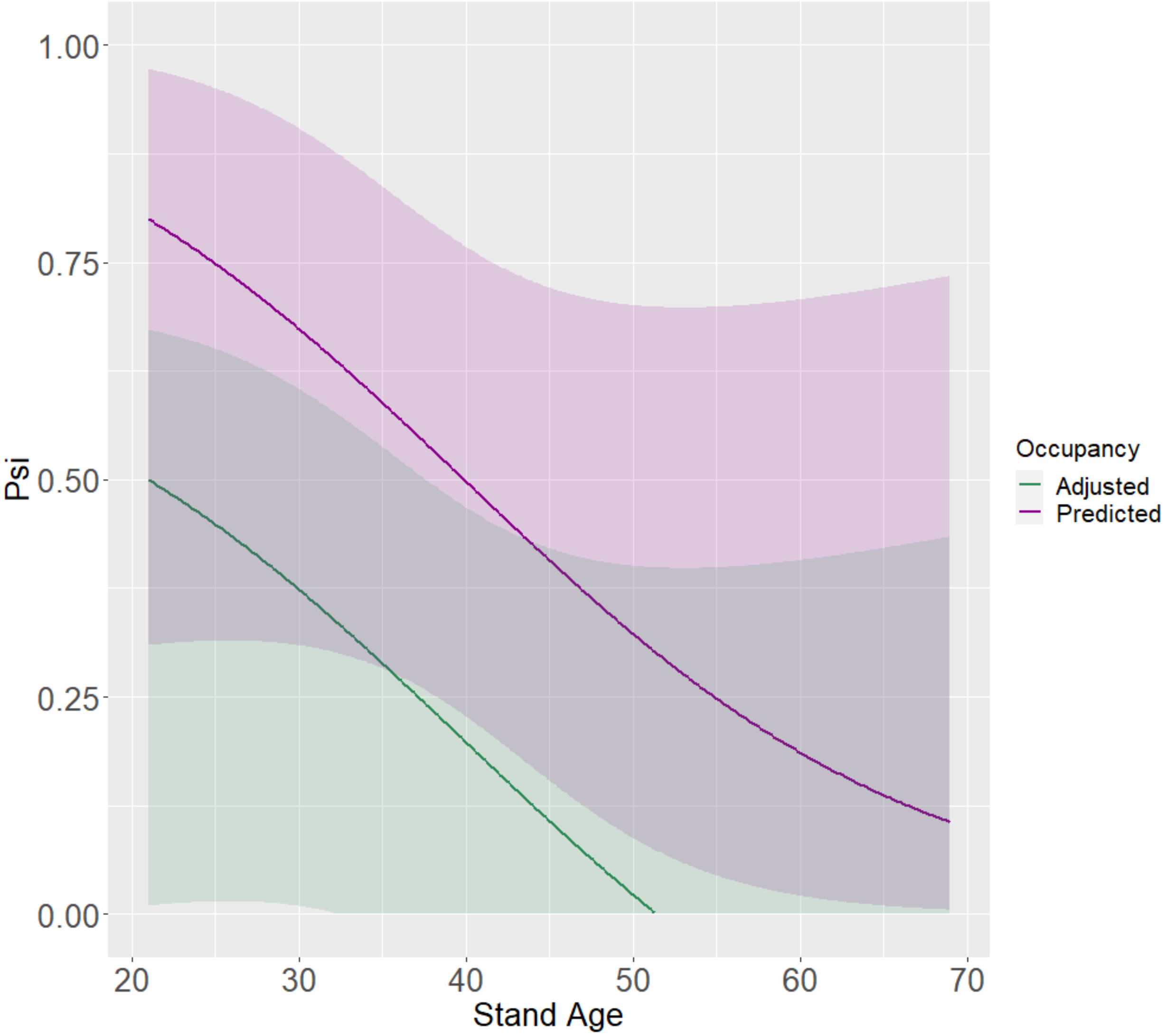

Figure 3.9. Predicted and adjusted occupancy (Psi) of recently occupied tree vole nests in young forest stands adjacent to patches of old forest. Predicted values were based on a ψ(Stand Age + Distance) p(.) model. Adjusted values were based on a RMSE value of 0.3 derived from Guillera-Arroita 2011 simulations. Data from stands surveyed in 2022 (n = 53).

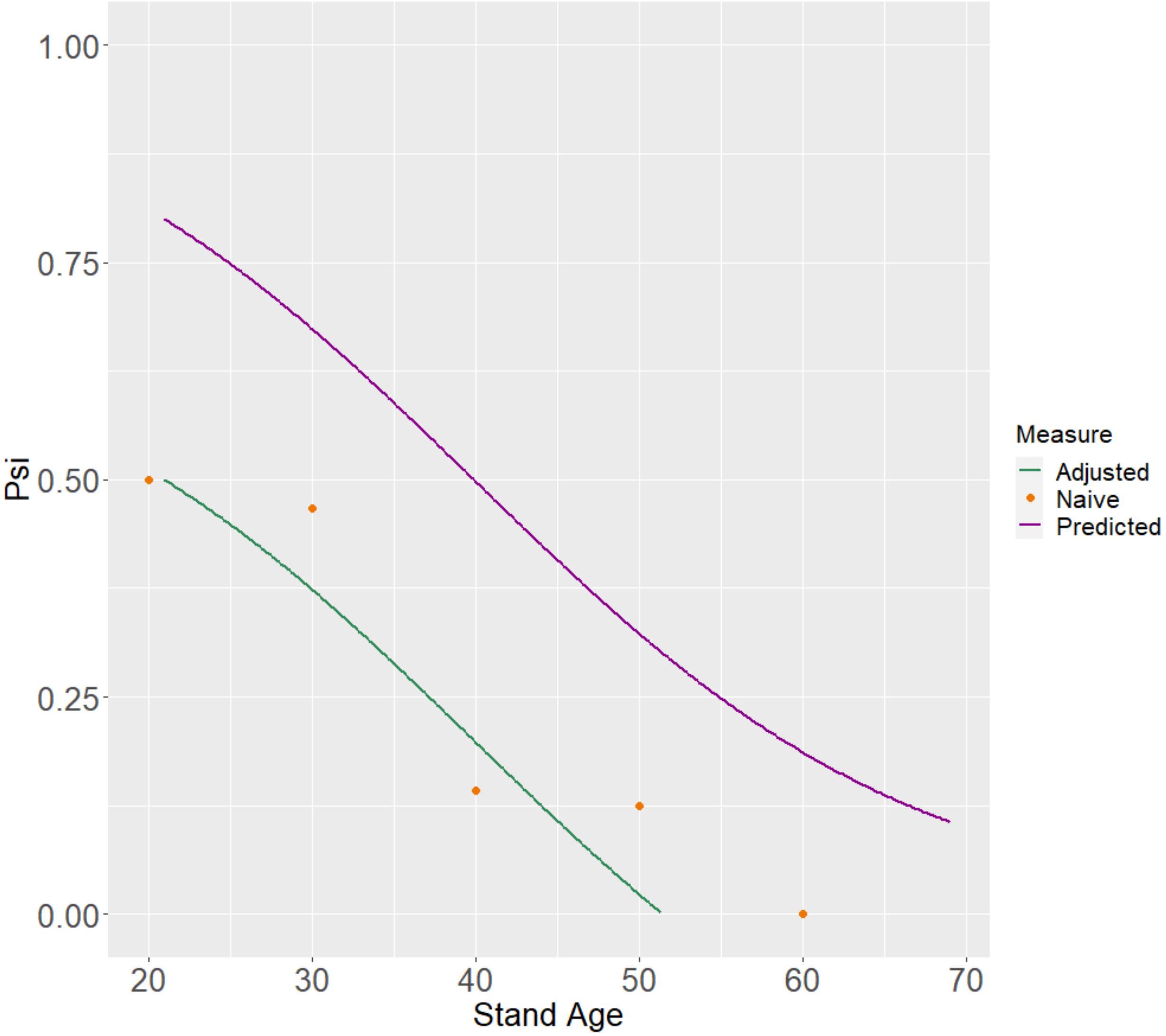

Figure 3.10. Predicted and adjusted occupancy (Psi) of recently occupied tree vole nests in young forest stands adjacent to patches of old forest. Naïve values were plotted for each age class from 20 – 60. Naïve values provide support for the 0.3 RMSE adjustment to predicted occupancy. Adjusted values were based on a RMSE value of 0.3 derived from Guillera-Arroita 2011 simulations. Data from stands surveyed in 2022 (n = 53).

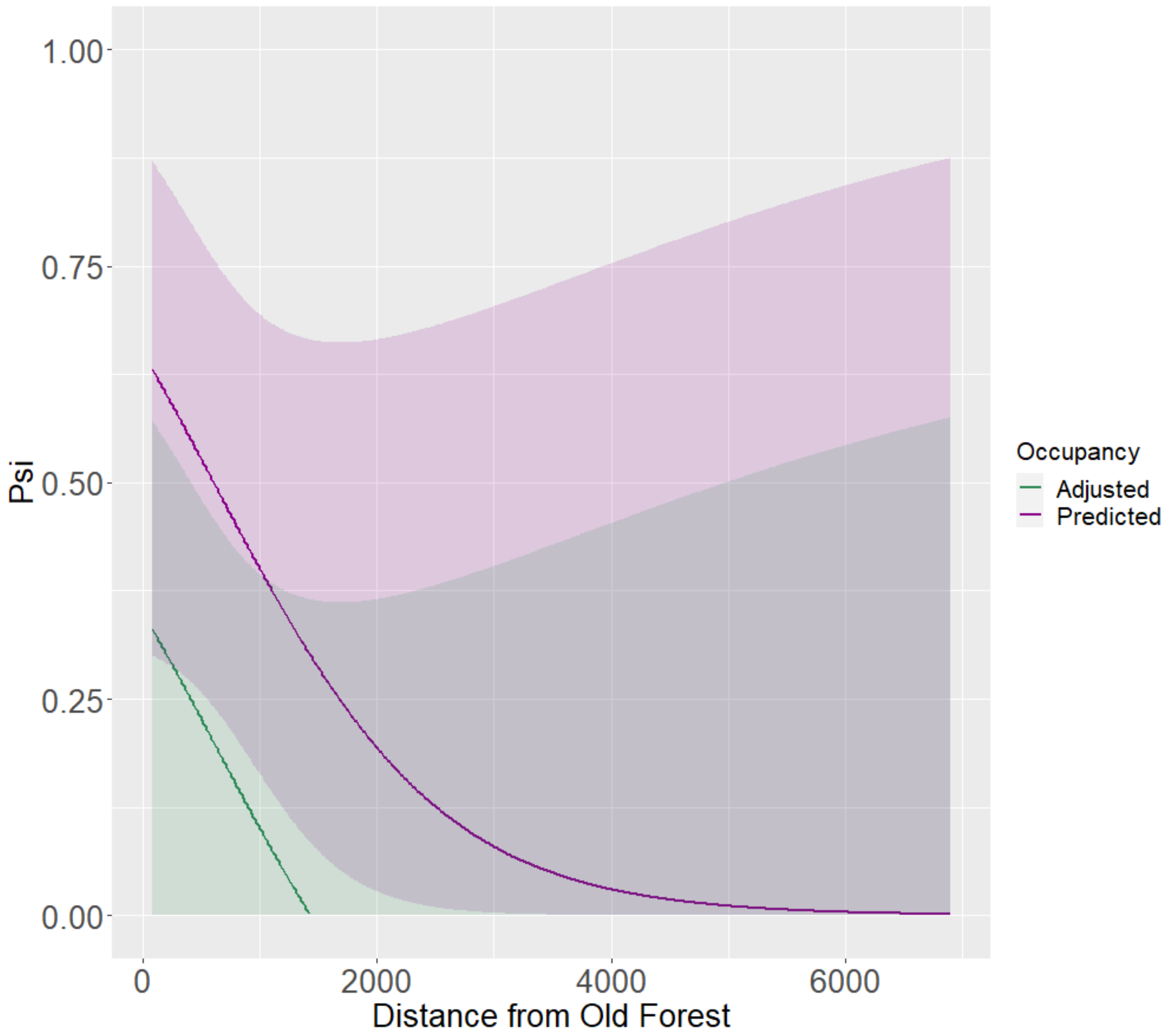

Figure 3.11. Predicted and adjusted occupancy (Psi) of recently occupied tree vole nests in 20 year old forests across a range of distance from the nearest patch of old forest >20ha and >80yrs. Predicted values were based on a *ψ(stand age + distanceOF) p(.)* model. Adjusted values were based on a RMSE value of 0.3 derived from Guillera-Arroita 2011 simulations. Data from stands surveyed in 2022 (n = 53).

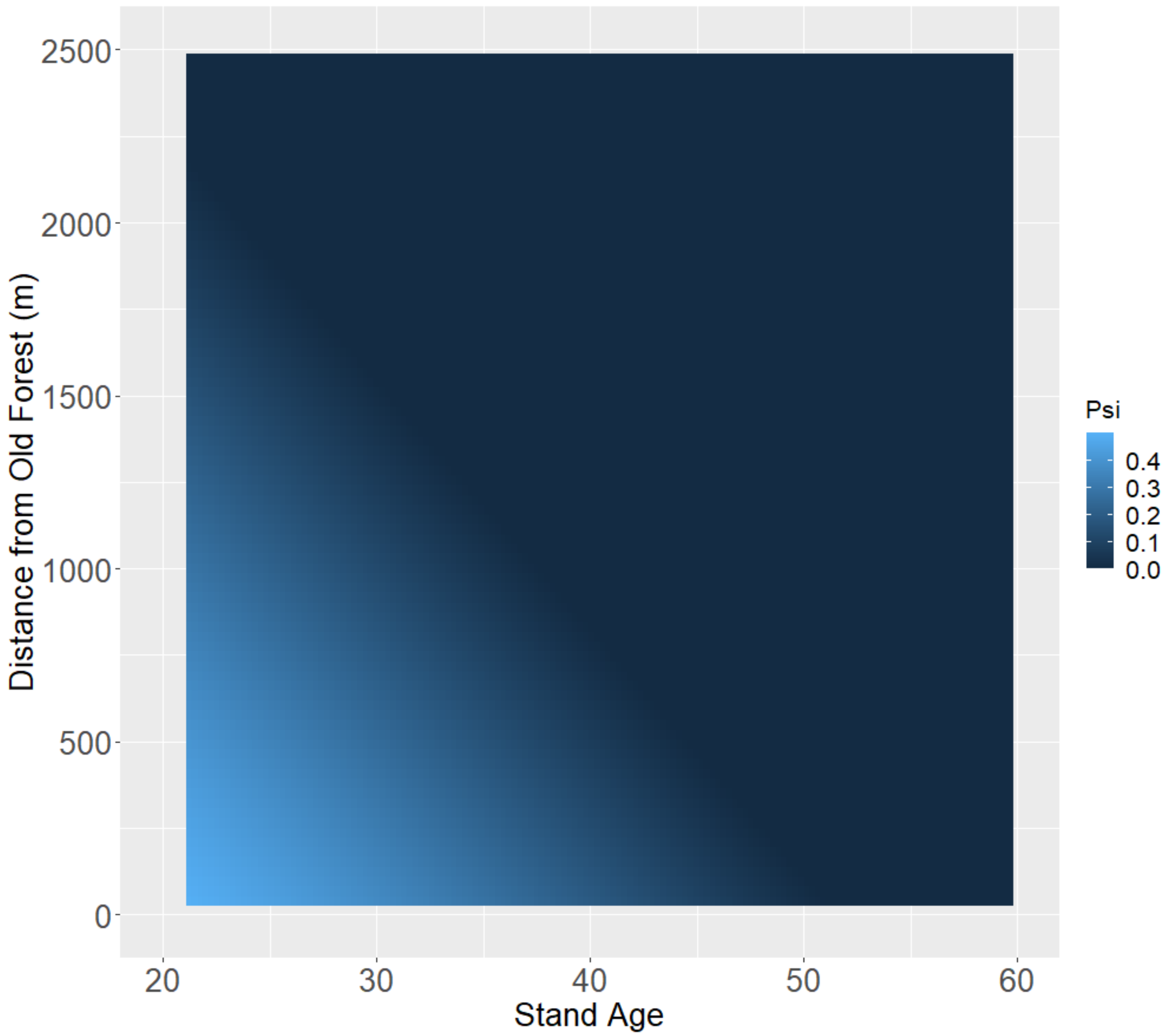

Figure 3.12. Adjusted occupancy of recently occupied tree vole nests plotted continuously across stand age from 21 to 60yrs and distance from the nearest patch of old forest >20ha and >80yr from 0 to 2500m. Adjusted values were based on a RMSE value of 0.3 derived from Guillera-Arroita 2011 simulations. Data from stands surveyed in 2022 (n = 53).

Table 3.12 Mean and maximum recorded tree vole nests per tree by stand age class.

	Stand Age Class					
	20 n = 180[1]	**30** n = 169[1]	**40** n = 23[1]	**50** n = 25[1]	**60** n = 5[1]	**80** n = 162[1]
Nests per tree	1 (1)	1.02 (2)	1 (1)	1.04 (2)	1 (1)	1.86 (11)

[1] Mean (Max)

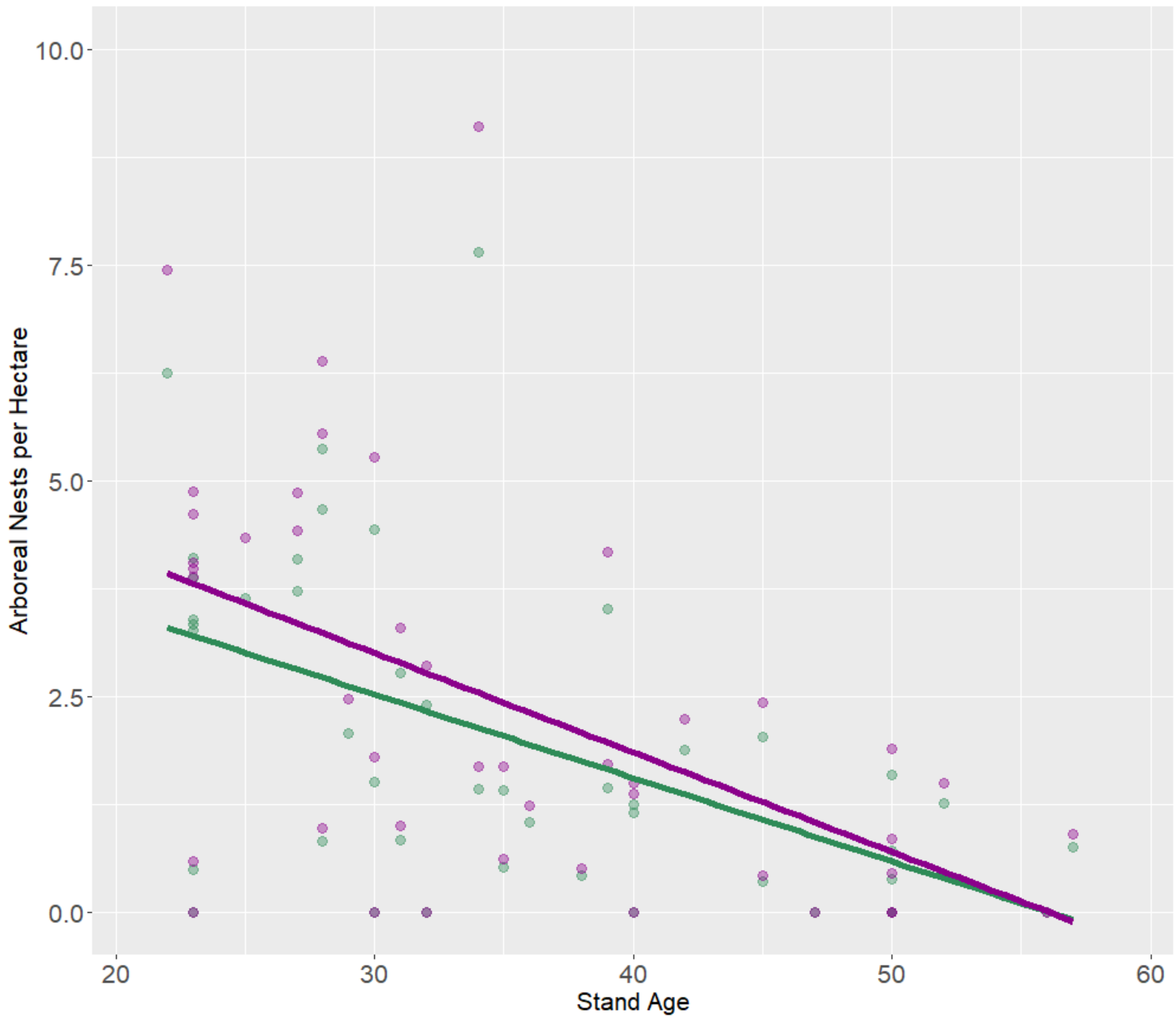

Figure 3.13. Estimates of arboreal nest density across young forest stands up to 59yrs (n = 45). Green represents naïve estimates and fitted linear trend assuming a detection rate of 1. Purple represents derived estimates and fitted linear trend assuming a detection rate of 0.84. Data from stands surveyed in 2022 (n = 53).

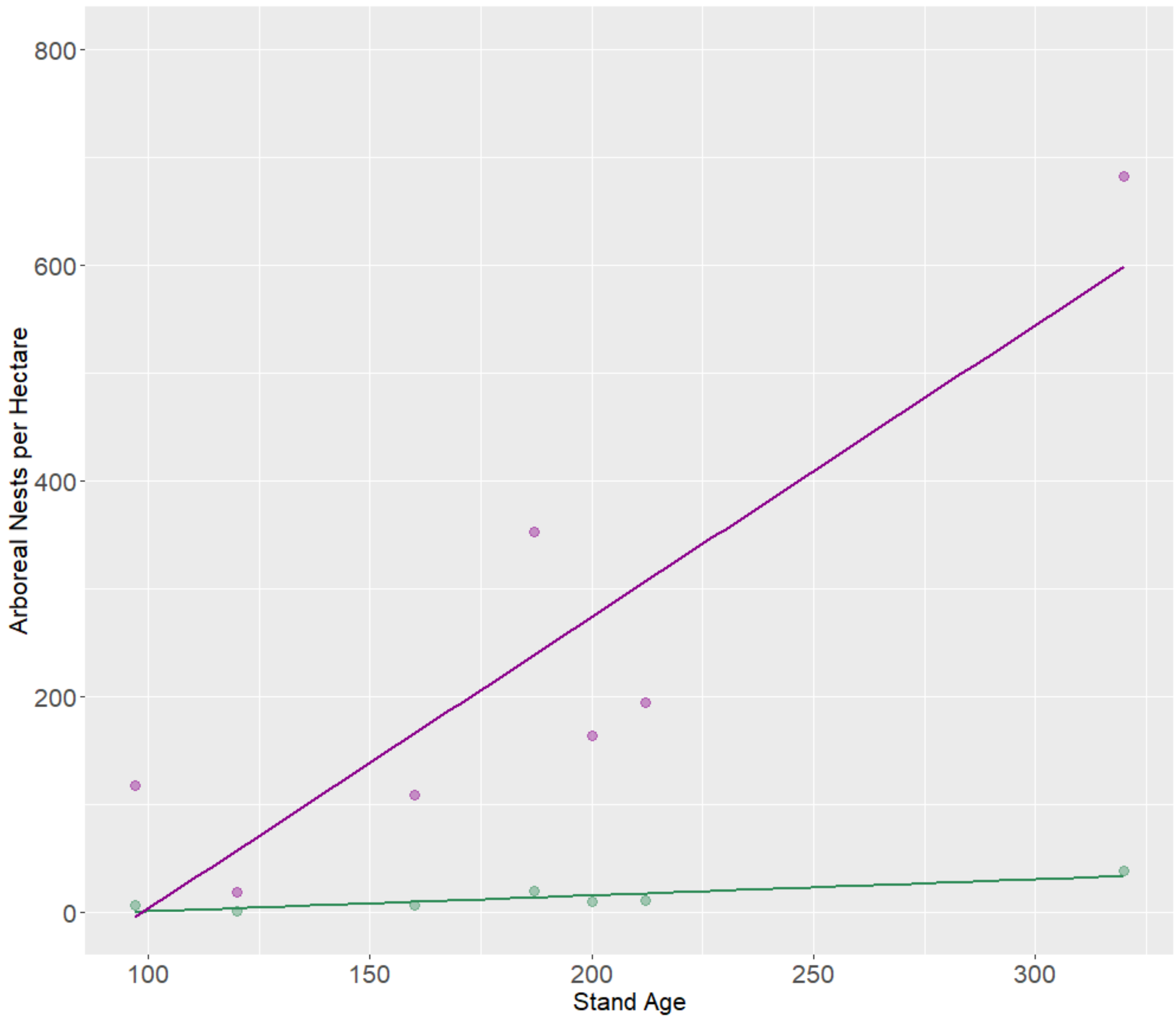

Figure 3.14. Estimates of arboreal nest density across old forest stands from 97 to 320yrs (n = 7). Green represents naïve estimates and fitted linear trend assuming a detection rate of 1. Purple represents derived estimates and fitted linear trend assuming a detection rate of 0.05. Data from stands surveyed in 2022 (n = 53).

Table 3.13. Mean, standard deviation and sample sizes of estimated density of arboreal nests for each stand age class from 2019 to 2022. Detection rates of 0.84 and 0.055 were used in young forest and old forest respectively. N is the total number of stands surveyed in each age class whereas n is the number of stands used in the mean calculation where the estimated density of arboreal nests was > 0. Stands in the 60-year age class were omitted because occurrence of arboreal nests in general was low to none (Table 3.6) and I did not quantify detection rates in that age class.

Year	Stand Age Class					
	20[1]	**30**[1]	**40**[1]	**50**[1]	**60**[1]	**80**[1]
2019	3.47 (1.43) {6/6}	1.83 (0.71) {4/4}	NA	1.05 (NA) {2/2}	NA	NA
2020	3.23 (1.35) {12/12}	2.04 (1.07) {8/9}	1.37 (0.82) {3/5}	1.37 (0.57) {4/7}	NA	81.06 (54.24) {5/5}
2021	4.18 (1.40) {13/13}	2.33 (1.13) {10/12}	1.41 (1.02) {4/6}	1.34 (1.21) {5/7}	NA	141.03 (174.25) {6/6}
2022	4.17 (1.86) {14/15}	2.69 (2.38) {12/15}	1.59 (0.80) {5/7}	1.12 (0.57) {5/8}	NA	233.60 (222.76) {7/7}
All Years	**3.76 (0.49)**	**2.22 (0.37)**	**1.45 (0.12)**	**1.22 (0.16)**	**NA**	**152.9 (76.82)**

[1] Mean (SD) {n/N}

Table 3.14. Mean, standard deviation and sample sizes of estimated density of recently occupied tree vole nests for each stand age class from 2019 to 2022. Detection rates of 0.84 and 0.055 were used in young forest and old forest respectively. N is the total number of stands surveyed in each age class whereas n is the number of stands used in the mean calculation where the estimated density of recently occupied tree vole nests was > 0. Stands in the 60-year age class were omitted because occurrence of arboreal nests in general was low to none (Table 3.6) and I did not quantify detection rates in that age class.

Year	Stand Age Class					
	20[1]	**30**[1]	**40**[1]	**50**[1]	**60**[1]	**80**[1]
2019	0.92 (0.41)	1.19 (0.53)	NA	0.61 (NA)	NA	NA
	{3/6}	{3/4}		{1/2}		
2020	0.90 (0.38)	0.79 (0.18)	0.81 (NA)	0.50 (NA)	NA	51.1 (NA)
	{4/12}	{3/9}	{1/5}	{1/7}		{2/5}
2021	0.77 (0.49)	1.62 (0.60)	2.02 (NA)	0.95 (NA)	NA	40 (57.56)
	{4/13}	{3/12}	{1/6}	{2/7}		{6/6}
2022	1.04 (0.94)	1.37 (1.14)	0.40 (NA)	NA	NA	69.41 (28.73)
	{6/15}	{3/15}	{1/7}	{0/8}		{5/7}
All Years	**0.91 (0.11)**	**1.24 (0.35)**	**1.08 (0.84)**	**0.68 (0.24)**	**NA**	**53.5 (14.9)**

[1] Mean (SD) {n/N}

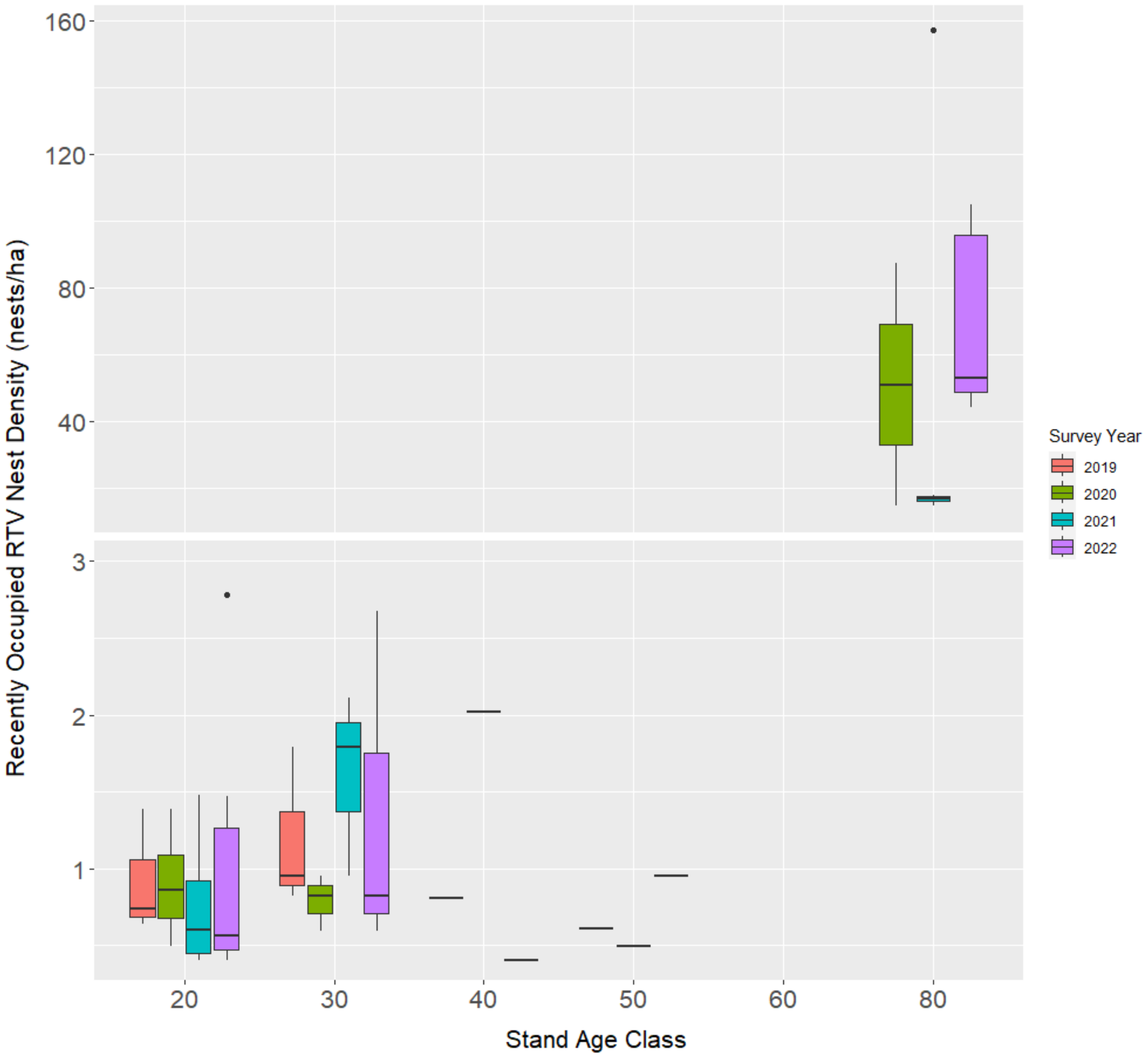

Figure 3.15. Estimated density of recently occupied tree vole nests for each age class in 2019 (red), 2020 (green), 2021 (teal), and 2022 (purple) using detection rates of 0.84 in young forests (<80) years and 0.055 in old forest (≥80 years) forest. All young forest stands were within an occupancy informed threshold of 1425m from the nearest patch of old forest.

Chapter 4: Conclusions and Recommendations

Jason T. Piasecki

Red tree voles *(Arborimus longicaudus*) are an elusive and highly canopy dependent species. I augmented current knowledge by quantifying nest survival and use in forests that differ in age, evaluating efficacy of multiple survey methods, and assessing occupancy and relative nest density in stands that varied in both age and distance from patches of old forest. In addition, I designed my study to provide a foundation for future evaluation of tree vole nesting dynamics as well as nesting habits and distribution of other canopy dependent mammals. My research is the first to examine trends in tree vole population metrics among age classes of young forest on intensively managed timber plantations in the Oregon Coast Range. Through this study, I inform landowners and managers on tree vole occurence, provide recommendations for management of the species, and identify future research needs for tree voles in managed forests.

Understanding survival of arboreal nests can play an important role in the conservation of canopy dwelling species such as tree voles. This is especially true in forests with limited structural complexity, where species may compete for nesting space. I determined that annual survival of both arboreal nests in general and specifically tree vole nests was largely dependent on nest size. Large nests were commonly supported in young forests by split trunks and broken tops and exhibited the highest probability of persisting over several years. Tree vole nest survival rates were estimated to be higher in forests >80 years old than in younger forests. I attribute this higher rate of survival to the highly cryptic nature of nests in old forests, which were commonly constructed under moss mats or deep in tree cavities. Management strategies that increase structural complexity in young forests and preserve structural complexity in old forests will likely serve to increase nesting space and nest survival for canopy dwelling species.

Detectability of arboreal nests continues to present a challenge to research and undoubtedly increases the difficulty in managing tree voles. I implemented novel, systematic, canopy-based surveys for tree voles in old forests. This method, while an improvement over ground-based survey techniques, still resulted in poor detection rates of individual arboreal nests (averaging 5.5%). In contrast, detection rates using ground-based survey techniques in young forests were high (averaging 84%) and although they were still imperfect, the bias on nest density estimation was relatively small. Based on these results, I maintain that ground-based surveys followed by tree climbing remain the most effective method to survey for tree voles in forests < 60yrs. In addition to my analysis of detection rates using various survey techniques, I suggest considering enough survey effort within a stand to have the confidence, or power, to accurately assign tree vole occupancy. Simulations from my comprehensive stand survey case study reveal the relationship between survey effort (in percent of area surveyed) and probability of detecting at least one recently occupied tree vole nest, given the site is occupied. In young forests, survey efforts greater than 38% of the stand area approach perfect detectability with near 100% likelihood of detecting at least one recently occupied tree vole nest when present. The spatial distribution of tree vole nests may not be homogenous and most prior and contemporary surveys, including our original design surveying only 10% of the stand, would have a high rate of false-negatives suggesting a stand was unoccupied when in fact, tree voles were present. Based on these results, I recommend a balanced approach between effectiveness and feasibility, where researchers and managers weigh the implications of low survey effort, uncertainty, and survey cost. Since these simulations were based on a single case study, I also recommend augmenting my simulation results with additional comprehensive stand surveys to provide a more accurate assessment of various survey efforts to detect recently occupied tree vole nests. I predict that stands with fewer nests would require additional effort to maintain the same power and confidence of detecting at least one tree vole nest.

Should the conservation of tree voles in managed forests be identified as a management priority, assessing the probability of stand-level occupancy will be an invaluable management tool for the species. I was able to provide the first predictions of tree vole occupancy probability across a range of forest age in young forests and along a gradient of distance from the nearest patch of old forest >20ha and >80yrs. Although my survey design using a ‘space for time’ approach introduced bias into the model, I adjusted my predictions based on simulations conducted by Guillera-Arroita (2011). My adjusted predictions of occupancy aligned with naïve stand level occupancy and suggested the likelihood of tree vole presence in young forests starting at 21 years of age was moderate (approximately 50%) declining to near-zero beyond 50 years of age. Simultaneously, occupancy likelihood was highest in young forest stands that were adjacent to patches of old forest (>20ha and ≥80 years) and declined to near-zero beyond 1425m from these patches. While my model aligned with my naïve data, future interpretation of tree vole occupancy should be considered within the limitations of survey effort, assumptions of old forest patch occupancy, and the imperfect detectability of arboreal nests. Although imperfect, I hope my estimates and extrapolations can serve as a tool in assessing potential habitat for tree voles across the dynamic and diverse checkerboard of management regimes of the Oregon coast range.

My data highlighted a relationship between stand age and arboreal nest density. In areas where tree voles were present, density estimates can provide insight to the capacity of young forests to support tree vole populations. I provided detectability informed estimates of recently occupied tree vole nest densities across stand age in young forests within 1425m of the nearest old forest patch (>20ha and ≥80yrs old). While density was high in forests between 25 and 35 years old, my data clearly reveals that old forests supported densities of recently occupied tree vole nests orders of magnitude higher than young forest stands.

Concurrently, I caution against the assumption that every nest that exhibits recent tree vole sign is indeed occupied. In young stands where I assessed the occupancy of tree vole nests with recent sign through photo verification using nest cameras, approximately 69% of nests were occupied. This aligns with results produced by Swingle and Forsman (2009) wherein a single tree vole can use multiple nests within its home range. Prior and ongoing research that implements live capture techniques to track tree vole movement and individual nest use can effectively contextualize the relationship between recently occupied tree vole nests and individual tree voles.

Should forest managers prioritize the conservation and management of tree voles in young forests in the Oregon Coast Range, I provide this research as a foundation to augment knowledge of the species and inform future conservation and management decisions on red tree voles. Although research is still needed to quantify reproductive rates and juvenile dispersal in young forests, I show that young forests can provide habitat for tree voles. Over the course of 4 years, I recorded tree vole persistence in multiple stands and, as part of a pilot study, captured reproductive adult females and juveniles suggesting that young forests within 1425m of old forest patches, often between 25-35 years old can support reproducing sub-populations of tree voles. While I maintain that old forests provided the highest quality habitat for tree voles, young forests near old forest refugia can serve as multi-generational habitat and could potentially facilitate connectivity across the highly fragmented landscape of the Oregon Coast Range.

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