Thinning Effects on Spotted Owl Prey and Other Forest-Dwelling Small Mammals

Todd M. Wilson and Eric D. Forsman

Abstract

Thinning has been promoted as a method for accelerating the development of late-seral habitat and improving the overall health and function of young forests in the Pacific Northwest. Population studies have shown early and positive responses to thinning by some small forest-floor mammals (primarily mice, terrestrial voles, and shrews). However, thinning reduces the abundance of some tree-dwelling rodents, especially Northern Flying Squirrels (*Glaucomys sabrinus*) and Red Tree Voles (*Arborimus longicaudus*), that are important prey species for Northern Spotted Owls (*Strix occidentalis caurina*). Recent studies suggest that reductions in Northern Flying Squirrel abundance following thinning may be driven by increased susceptibility to predation created by removal of critical above-ground cover. Predation, lack of canopy connectivity, and reduction in suitable nest substrates may all contribute to reduced Red Tree Vole abundance following thinning. The long-term benefits of some thinning treatments may be positive for both flying squirrels and Red Tree Voles, but may not be realized for several decades or more, as the development of a midstory layer of trees may be critical to the success of thinning in promoting habitat for these species. Additional research into the ecology of the two woodrat species (*Neotoma fuscipes* and *N. cinerea*) found in the Pacific Northwest is needed to provide a more complete understanding of the effects of forest management activities on spotted owls and their prey. It may be possible to design thinning prescriptions that lessen the short-term negative effects on arboreal rodents. Long-term goals should focus on creating more structurally and biologically complex forests across the landscape at scales and patterns compatible with the ecologies of spotted owl prey and other organisms. Joint research-management efforts to test new silvicultural prescriptions, expand current predictive models of high-quality prey habitat, and develop management strategies that consider the temporal effects of management on owl prey at the stand, landscape, and regional levels, could advance our understanding of owl prey ecology and help ensure that healthy populations of spotted owls and their prey persist on the landscape over the long term.

Keywords: Thinning, variable-density thinning, Northern Spotted Owl, Northern Flying Squirrel, Red Tree Vole, Northwest Forest Plan, old-growth forest.

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Introduction

The Pacific Northwest is rich in forest-dwelling small mammals, including mice, voles, shrews, tree squirrels, chipmunks, and woodrats. Collectively, these species serve as important prey for a wide variety of avian, mammalian, and reptilian predators. Small mammals also consume and disperse fungal spores essential for tree growth, help regulate invertebrate populations, disseminate vegetation through caching of seeds, nuts, and other fruiting bodies, and promote soil and carbon dynamics through excavation of down wood and soil (Carey and Harrington 2001). Thus, small mammal populations have been used as indices for the overall health and sustainability of forests in the region, including evaluation of the ecological effects of forest management activities like timber harvesting (Carey and Johnson 1995; Carey and Harrington 2001; Lehmkuhl et al. 1999; Suzuki and Hayes 2003). Four species, Northern Flying Squirrels (*Glaucomys sabrinus*), Red Tree Voles (*Arborimus longicaudus*), and Dusky-footed and Bushy-tailed Woodrats (*Neotoma fuscipes* and *N. cinerea*) dominate the diets of the federally threatened Northern Spotted Owl (*Strix occidentalis caurina*) (Forsman et al. 1984, 2004a,b; USFWS 1990). Spotted owl home-range size has been shown to decrease with increasing flying squirrel densities (Carey and Peeler 1995; Carey et al. 1992; Zabel et al. 1995), suggesting that understanding habitat needs for owl prey may be critical to the recovery of spotted owls and their habitat across the region (USFWS 2008).

One way to partition the small mammal community is by the relative degree to which each species uses the vertical strata of a forest (fig. 1). At one end of the continuum are forest-floor specialists like shrews and terrestrial voles that spend virtually all their time on or beneath the forest floor. At the other end of this continuum are arboreal (tree-dwelling) rodents like flying squirrels and Red Tree Voles that spend most of their time in the forest canopy (Maser et al. 1981, Wilson 2010). In addition, there are habitat generalists including deer mice (*Peromyscus* spp.), Trowbridge's Shrews (*Sorex trowbridgii*), and chipmunks (*Tamias* spp.) that spend considerable amounts of time on the forest floor but also regularly use forest canopies.

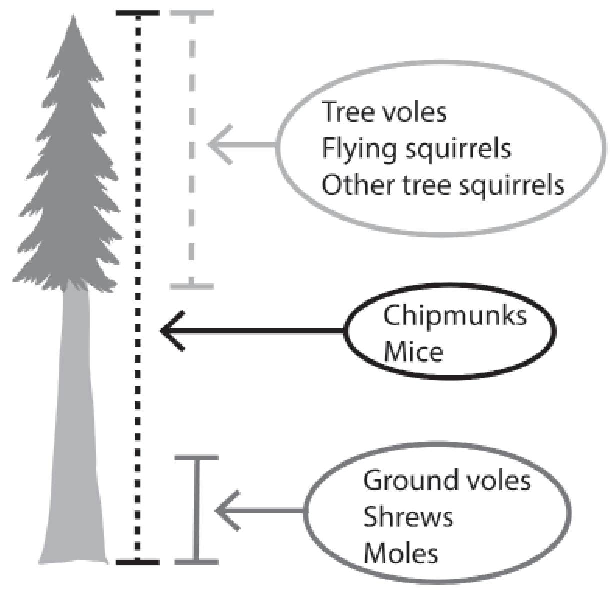

Figure 1—Illustration of the relative degree of use of the vertical component of a forest for several common rodent species in Pacific Northwest forests.

Thinning has become the management tool of choice for accelerating the development of late-seral wildlife habitat and improving the overall health and function of young forests in the Pacific Northwest. The effectiveness of thinning to either promote or maintain habitat has been demonstrated for a number of forest-floor specialists and generalists (Carey and Wilson 2001; Gitzen et al. 2007; Hayward et al. 1999; Klenner and Sullivan 2003; Suzuki and Hayes 2003; Wilson and Carey 2000). This is true in large part because the understory layer of a forest is usually the first and quickest to respond to the increase in growing space, light, and nutrients created by thinning. This understory response results in increased structure and plant diversity on the forest floor, providing food, shelter, and protective cover for small mammals. Positive responses have generally been strongest in forests that lacked substantial understory prior to thinning (e.g., young, even-aged, stem-exclusion forests with a primarily moss-dominated forest floor), but increases in abundance have also been noted for several small mammals in forests with a well-established understory prior to treatment (e.g., Carey and Wilson 2001). In this latter case, additional growth and maturation of a tall shrub and deciduous tree layer may provide additional habitat components important for some species.

In marked contrast, there is growing evidence that thinning can have negative effects on some arboreal rodent populations (Forsman 2004; Wilson 2010). For example, several studies have shown declines in flying squirrel abundance following thinning, empirically (but not necessarily statistically) higher numbers of squirrels in untreated stands compared to stands treated with thinning, or generally higher squirrel abundances in unthinned stands compared to thinned stands (Bull et al. 2004; Carey 2000, 2001; Gomez et al. 2005; Herbers and Klenner 2007; Holloway and Malcolm 2006, 2007; Holloway et al. 2012; Manning et al. 2012; Meyer et al. 2007a; Ransome et al. 2004; Waters and Zabel 1995; Waters et al. 2000; Wilson 2010). This includes arboreal rodent responses to the Forest Ecosystem Study (FES), a study specifically designed to test whether variable-density thinning (see Carey et al. 1999c) could accelerate the development of habitat for spotted owls and their prey in 50- to 60-year-old Douglas-fir (*Pseudotsuga menziesii*) forests of western Washington (Carey 2001, 2007; Wilson 2010).

The goals of this paper are to: (1) briefly highlight what is known about the ecology of each of the four major spotted owl prey species as it relates to thinning forests; (2) provide rationale for why thinning has negative consequences for some species in the near term; and (3) discuss possible management options and research directions that could benefit owls and their prey over the long term.

Flying Squirrels

Northern Flying Squirrels comprise 50 percent or more of the prey in spotted owl diets across much of Oregon and Washington (Forsman 1984; Forsman et al. 1991, 2004a), and most of the research into the ecology of owl prey in the Pacific Northwest has focused on this species. In general, two forest conditions can support relatively high numbers of flying squirrels—closed-canopy forest (old or young) with high stem density, and classic multi-layered old forest, with the latter generally providing the highest abundances (Wilson 2010).

Several habitat components have been associated with high-quality flying squirrel habitat, including understory cover, patch-level (40–80 m) changes in vegetation composition, large snags, large trees, ericaceous shrubs, high canopy cover, nearness to conifer forest, nearness to water, abundant down wood, large down wood, increased litter depth, and availability of fungi (Carey 1991, 1995; Carey et al. 1992, 1999a; Ford et al. 2004; Gomez et al. 2005; Holloway and Malcolm 2006, 2007; Hough and Dieter 2009; Lehmkuhl et al. 2004, 2006; Menzel et al. 2006; Meyer et al. 2007a, b; Payne et al. 1989; Pyare and Longland 2002; Rosenberg and Anthony 1992; Smith et al. 2004, 2005). However, these associations have not always held true across studies. For example, some forests that support high squirrel abundances have few large snags or little down wood (Wilson 2010). Likewise, some forests (including old forest) with relatively large quantities of snags, large live trees, or down wood have been found to support few squirrels (Carey 1995; Wilson 2010).

Part of the issue in associating squirrel abundance with habitat components is that most studies have only examined a limited number of forest conditions (e.g., comparing forest type A vs. B) or conducted analyzes based on broad categories (e.g., old forest vs. young forest). To help address this problem, Wilson (2010) used multivariate, structural equation models to

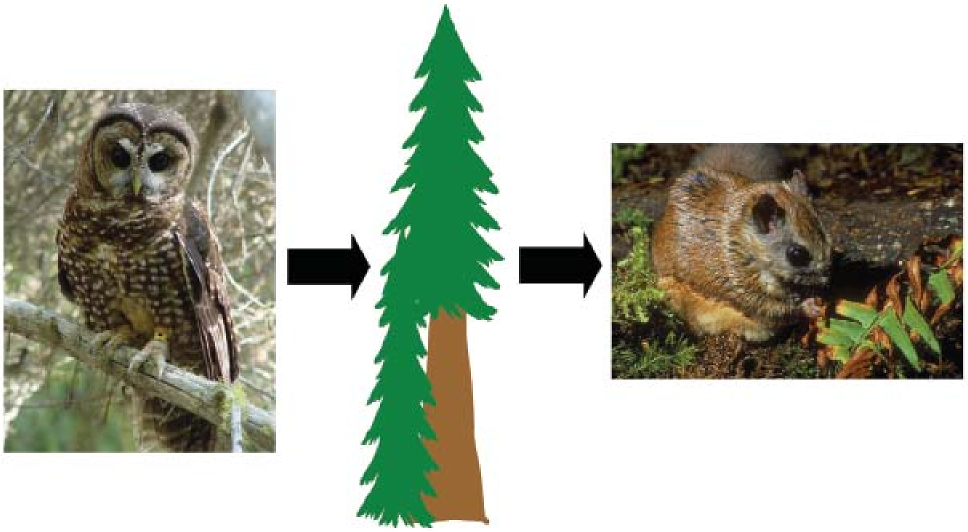

Figure 2—Forest structure, particularly in the midstory, provides the interface between predators like northern spotted owls and one of their major prey, northern flying squirrels. (Spotted owl photo by Stan Sovern; flying squirrel photo by Wes Colgan III.)

examine flying squirrel populations and habitat across 33 managed and unmanaged stands in the Puget Trough and Olympic Mountains physiographic provinces. Collectively, these stands were chosen to represent broad gradients in forest structural conditions found across low- and mid-elevation mesic forests west of the Cascade Range. Wilson (2010) found that important habitat components used in stand-level statistical models to predict flying squirrel abundance could all be associated with above-ground protective cover, and hypothesized that predation was a primary limiting factor regulating squirrels in these forests (Wilson 2010; fig. 2). Wilson suggested that structural occlusion (the degree to which physical structures inhibit detection of squirrels by predators and help squirrels escape direct attacks) was an important component of protective cover. When there is a high degree of occlusion in the midstory (e.g., high stem density, deep crowns, live crowns in the midstory layer, with few canopy gaps across the stand), it provides sufficient protection for squirrels to attain and sustain relatively high population levels (fig. 3). Even with relatively high predation rates (e.g., during spotted owl breeding years), enough female squirrels can survive each year in these forests to quickly restore populations to a relatively high level. In contrast, when there are too many gaps, too many large gaps, lack of a midstory canopy layer, or overall low stem density, squirrels succumb to predation pressure and few squirrels survive to reproduce.

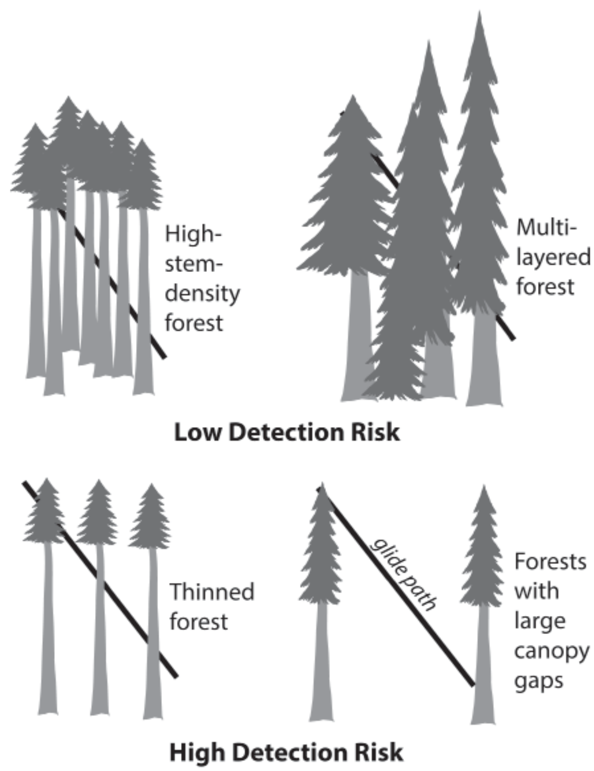

Figure 3—Black line illustrates a hypothetical glide path of a Northern Flying Squirrel and the structural occlusion created by different forest conditions that provide different levels of detection risk by avian and mammalian predators.

Most thinning prescriptions reduce occlusion in a way that appears to leave flying squirrels more vulnerable to predators than before thinning. This effect may be further compounded once the understory begins to develop in response to thinning, as abundance of forest-floor small mammals can quickly increase and, in turn, attract predators to the area that may opportunistically prey on vulnerable flying squirrels (e.g., spillover predation; Oksanen et al. 1992).

Red Tree Voles

Red Tree Voles are the most arboreal of all the rodents in the Pacific Northwest (Carey 1999). Similar to flying squirrels, the highest tree vole populations are found in old forests and forests with high stem density (Dunk and Hawley 2009). Tree voles also appear to be susceptible to increased predation brought on by reduced canopy density after thinning, as few are found in recently thinned forests (Forsman et al. 2004b). However, tree voles also have three additional ecological constraints that may make them especially susceptible to thinning. First, small trees in young forests generally have insufficient food resources (conifer needles) in a single tree to support breeding females, so individuals often forage in multiple trees surrounding their nests (Swingle and Forsman 2009). In closed-canopy forest, they can simply travel across interlocking branches to reach adjacent trees. Thinning breaks these connections, and voles must travel down (usually on bare, exposed boles) and across the ground to reach other trees. This not only increases their energetic demands, it also puts them at additional exposure to predation. Second, tree voles build nests composed of small twigs and conifer needles on platforms created by dwarf mistletoe (*Arceuthobium* spp.), epicormic branching, forked boles, and other irregularities in tree-branching patterns. Such nests need more support than the nests built of larger twigs and branches used by tree squirrels. If trees with complex limb structure, forked tops, broken boles, and dwarf mistletoe infections are removed during thinning, it may greatly restrict the ability of tree voles to find suitable nest substrates. Third, young tree voles have limited dispersal ability, and the absence of tree voles across much of northwest Oregon suggests that they may not be able to disperse across broad areas of intensively managed forest (Maser et al. 1981).

Woodrats

The Dusky-footed Woodrat and Bushy-tailed Woodrat are two of the most important species in the diet of Northern Spotted Owls, particularly in northwestern California, southwestern Oregon, and along the eastern slopes of the Olympic Mountains and eastern Cascades of Washington (Forsman 1975, 1991; Forsman et al. 2004a; Ward et al. 1998). The Dusky-footed Woodrat is a resident of California and southwestern Oregon, whereas the Bushy-tailed Woodrat occurs throughout much of the Pacific Northwest.

Sakai and Noon (1993) found that Dusky-footed Woodrats were most abundant in young (15- to 40-year-old) forests with brushy understories, with lower densities in seedling/shrub and old growth forests, and few or no woodrats in forests with merchantable timber but little understory. They hypothesized that young, brushy forest may provide important source areas for woodrats in adjacent old forests that are more suitable for spotted owls. Carey et al. (1999b) surveyed for woodrats in western Oregon and western Washington and suggested that the distribution of Dusky-footed Woodrats could be explained by a preference for dense shrub cover and the ability to consume plants toxic to other mammals. In contrast, Carey et al. (1999b) found that Bushy-tailed Woodrats were irregularly distributed, possibly as a result of their aggregated social structure (harems) that may allow predators to cue in and prey on family groups. In eastern Washington, Lehmkuhl et al. (2006b) found that large snags, dwarf mistletoe brooms, and partly decayed logs were good predictors of Bushy-tailed Woodrat abundance in dry forests. Lehmkuhl et al. (2006b) suggested that conventional fuels reduction prescriptions that reduced the amount of snags, dwarf mistletoe brooms, and logs would have a negative effect on Bushy-tailed Woodrat populations. However, there have been no subsequent studies conducted on woodrats in Washington or Oregon to further investigate these hypotheses.

Management Considerations

Thinning designed to create late-seral conditions in young forests has shown early success in promoting habitat for a number of vertebrate species. However, development of a midstory layer of trees appears important before species like flying squirrels and Red Tree Voles respond positively to thinning, and this will take time to develop. In fact, it may take several decades or longer for a midstory to develop to a point where it provides adequate protective cover and canopy connectivity. This is especially true when thinning young forests with small-crowned trees, sparse natural regeneration, and a large gap between the existing understory and the bottom of the tree canopy. The primary question, therefore, is how best to move landscape trajectories toward more complex forest while, at the same time, ensuring that the short-term negative effects on prey populations do not result in long-term negative effects for either spotted owls or their prey.

It is important to recognize that some arboreal rodents like flying squirrels have been found in fairly high numbers in forests that are relatively simple (e.g., high-stem-density young forest) or that lack habitat components often associated with flying squirrels (e.g., few snags, understory, or down wood; Wilson 2010). However, the ultimate goal when promoting owl prey habitat through thinning should be toward developing structurally and biologically complex forests that include multi-layered canopies including trees of varying sizes and species, snags, and down wood. Not only are these forests generally better habitat for spotted owls and their prey, they are the scarcest forest type on the landscape, they provide habitat for a wide array of other wildlife, and they help meet broader biodiversity goals including those outlined in the Northwest Forest Plan.

There are several specific management strategies that may help ameliorate some of the near-term negative effects of thinning on owl prey:

1. Accelerate and monitor mid-story development.

One of the primary objectives of variable-density thinning is to develop late-seral characteristics sooner by moving a forest through stages of forest development more quickly compared to leaving stands to develop as a result of natural stochastic events without management intervention (Carey et al. 1999c). However, without intentional focus on midstory tree growth, site-specific conditions can prevent or even forestall midstory development. For example, if a well-developed understory exists prior to thinning, it may outcompete new tree seedlings. If there is a limited shade-tolerant tree seed source, then midstory development may be patchy or sparse. In contrast, if the natural shade-tolerant seed source is too abundant, then regeneration competition may occur, slowing growth of the next layer of trees. Additionally, for a midstory to fully develop, new trees must grow tall enough to fill the structural void between the ground and the bottom of the existing overstory canopy. The larger this distance is, the longer it will take for a full midstory to develop.

There are a number of ways to promote a midstory. Underplanting can be considered for forests that lack a natural seed source of shade-tolerant trees. Patchy brush control could be used in conjunction with underplanting for thinning forests that have a well-established understory layer of aggressive shrub species like Salal (*Gaultheria shallon*). If shade-tolerant tree species regenerate aggressively on the forest floor, then early thinning of tree saplings can be considered. Because both thinning treatment and site-specific conditions affect development of a midstory, regular monitoring should occur to ensure that this critical forest layer continues along an accelerated path.

2. Include very young (<25-year-old) stands in the mix of stands targeted for creating late-seral forest.

High-quality habitat for spotted owl prey might be achieved most quickly by treating very young (<25-year-old) stands with pre-commercial thinning to stimulate midstory development, so that there is a much smaller vertical gap to fill with mid-story trees as compared to the gap that might develop if thinning is delayed until stands reach merchantable size. This does not preclude thinning older (25- to 80-year-old) stands, especially given their dominance on the landscape, but adding young stands could help fill a temporal niche in the presence of high-quality prey habitat across the landscape through time. Thinning at this early age is also not likely to affect existing flying squirrel populations, as they generally avoid highly-stocked Douglas-fir forests <25 years old.

3. Keep some young high-density forest on the landscape.

Although optimal spotted owl habitat is multi-layered older forest, high-stem-density forests do support owl prey and are used by owls as foraging habitat. High-stem-density forest can remain in a condition favorable for owl prey for several decades or more and could serve as a reservoir for abundant prey populations while thinned stands develop into suitable habitat over the long term. It is important to recognize, however, that high-stem-density forest can also quickly (<20 years) leave this stage, as suppression mortality and localized stochastic events (e.g., ice storms, wind, disease, insect outbreaks) remove existing trees (Wilson 2010).

4. Use defensible buffers to protect existing high-quality habitat.

Fire suppression in dry forests over the last century has created habitat that in some cases is favorable for owl prey, but such habitat is also vulnerable to stand-replacing fire events. It may be important to try to keep some of this habitat on the landscape until new suitable habitat becomes available. Strategically placed buffers with reduced fuel loads may help provide protection from catastrophic fire for these areas. Keeping such buffers as narrow as possible and with as much canopy cover as possible would be important to allow squirrels to travel and dispersal across the broader landscape and to prevent the buffers from possibly becoming predator traps.

5. Explore alternative thinning prescriptions.

It may be possible to develop new thinning prescriptions that keep moderately high populations of arboreal rodents in young forests while still achieving long-term management objectives for the stand. One such approach would be developing prescriptions that focus solely on skips (patches of trees left unthinned) and gaps (removal of patches of trees). This strategy is in marked contrast with most current prescriptions that typically thin throughout a stand (with or without delineated skips or gaps). Under such a strategy, it may be important to keep canopy-gap sizes small (100-400 m^2 per gap with <30 percent of the total stand area in gaps), and horizontal occlusion high, as there may be thresholds in the amount and extent of gaps distinguishing high- and low-quality habitat (Wilson 2010). A gap-skip-only approach may be most feasible in either young forests with sufficient bole density to provide structural occlusion at a relatively small scale (generally less than 20–40 meters), or in young mixed-conifer forest with a short, but existing multiple-layered canopy. Because there have been no demonstrated examples of the efficacy of such a strategy, this approach should be experimentally evaluated (testing size, patterning, and spatial distribution of canopy gaps) before any widespread application. A gap-skip-only approach may be particularly useful when the management goal is to reduce fuel loads as part of non-commercial restoration efforts in fire-prone forests, without necessarily wanting to accelerate tree regeneration or understory plant development. Rather than the common practice of removing the vertical component of a forest (e.g., ladder fuels) to reduce fuel loads, this approach focuses on creating horizontal patchiness to reduce fuel loads. Such a strategy may also have stronger ecological merit, in that it may more closely mimic natural fire events for some regions (Agee 1993; Harrod et al. 1999; White 1985). Depending on the size of canopy gaps, a skips-gaps-only strategy may also be suitable for developing late-seral conditions in more mesic forest, but only if gaps were large enough to accelerate mid- and understory development compared to leaving forests to develop on their own.

Future Direction

The need for sufficient structural occlusion to protect arboreal rodents from predators provides an explanation for why flying squirrels and tree voles decline in abundance following thinning, and provides a rationale for steps that might be taken to ameliorate this undesired effect. However, this hypothesis was developed from studying flying squirrels in mesic forests of western Washington, and may not reflect other limiting factors elsewhere within the range of the Northern Spotted Owl. For example, sufficient mid-story structure may be a critical component of xeric forests supporting high flying squirrel abundances in southwest Oregon, but there may also be minimum moisture thresholds needed for adequate year-round fungal production that restrict abundant populations to higher elevations, north-facing slopes, or near permanent water sources (T. Wilson, unpublished data). Likewise, predator load (predator species diversity and abundance) may also play a crucial role in regulating arboreal rodent populations for some forests. Thus there is need to further test the applicability of current empirical models using similar population and habitat analyses elsewhere. Of particular importance would be evaluating habitat in areas within and outside the range of the Northern Spotted Owl where there have been few or no population-level studies or where there are habitat conditions substantially different than those found in western Washington. For flying squirrels, these include mixed conifer forests in southwestern Oregon, high-elevation sites throughout the Oregon and Washington Cascades and Olympic Peninsula, dry forests on the eastern slopes of the Oregon Cascades and southern Washington Cascades, and throughout much of the forested area in eastern Oregon and Washington (e.g., Blue Mountain and Northern Rocky Mountain provinces; fig. 4).

For Red Tree Voles, empirical research is needed to better understand the effects of thinning on vole populations, and to determine if thinning prescriptions could be modified to allow tree voles to persist in thinned stands. There is also a basic need for understanding factors that influence the persistence of tree voles in young stands. Included in this is a better understanding of why tree voles are apparently slow to disperse through young stands, and whether or not specific management actions could improve dispersal rates.

There is also a need for further investigation into the habitat needs of both species of woodrats, given the lack of data on their distribution and habitat requirements. Recent controversy over the effects of broad-scale fire on distribution of spotted owls (e.g., Hansen et al. 2009; Spies et al. 2010) suggests that better understanding of woodrat ecology could be useful in informing such debates. For example, large stand-replacing fires would substantially reduce or eliminate flying squirrel populations, given the removal of above-ground predation cover. Such fires, however, may promote dense shrubs and early stages of forest development favorable to Dusky-

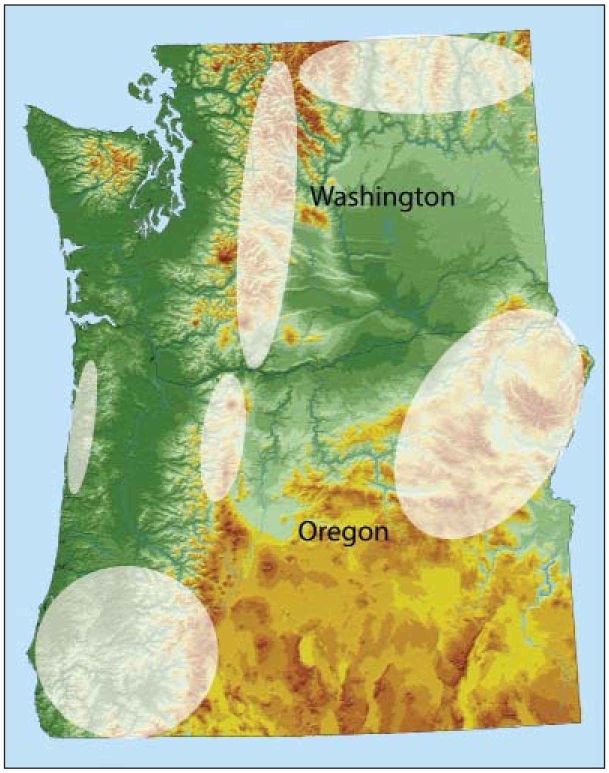

Figure 4—General areas (ovals shaded in white) of Oregon and Washington with forest types and conditions that could help strengthen an existing regional model defining high-quality habitat for flying squirrels and improve understanding of spotted owl prey ecology (Wilson 2010).

footed Woodrats, which could allow owls to persist in partially burned areas.

Finally, the continued decline in spotted owl populations throughout their range highlights the urgency of further understanding and appropriately managing for owl prey across a range of spatial scales. An important component of this is planning management activities at the landscape (e.g., fifth-field watershed or larger) and regional levels in a way that merges the spatial and temporal effects of thinning on spotted owl prey with the ecology and habitat needs of these species. Such efforts could include modeling of the: (1) current stand-level distribution of existing high-quality habitat for arboreal rodents across the region; (2) permeability of the landscape for arboreal rodents (e.g., capacity of the landscape to allow dispersal and colonization over time); and (3) projected changes in the amount and distribution of high-quality prey habitat over time under different management scenarios and stochastic events.

In summary, thinning has yet to be shown effective for promoting habitat for arboreal rodents like flying squirrels and Red Tree Voles. However, the importance of midstory cover and connectivity suggests that the trajectory of some thinned stands will eventually result in habitat conditions favorable for these species. Extra effort will be needed to ensure that the short-term negative effects of thinning on some owl prey species do not have long-term negative consequences for owls or their prey. One of the fastest and most efficient ways to move forward would be for researchers and forest managers to collaborate on projects such as testing novel silvicultural prescriptions, assessing habitat and prey abundance in different forest types, and developing landscape and regional management models and strategies for owl prey. A focused research-management effort over the next 10 years could greatly advance our understanding of owl prey ecology and hopefully result in management practices that support healthy populations of both owls and their prey in the Pacific Northwest over the long term.

Literature Cited

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press. 505 p.

Bull, E.L.; Heater, T.W.; Youngblood, A. 2004. Arboreal squirrel response to silvicultural treatments for dwarf mistletoe control in northeastern Oregon. Western Journal of Applied Forestry. 19: 133–141.

Carey, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-276. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 46 p.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications. 5: 648–661.

Carey, A.B. 1999. Red tree vole/*Arborimus longicaudus*. In: Wilson, D.E.; Ruff, S., eds., The Smithsonian book of North American mammals. Washington, DC: Smithsonian Institution Press: 620–622.

Carey, A.B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications. 10: 248–257.

Carey, A.B. 2001. Experimental manipulation of spatial heterogeneity in Douglas-fir forests: effects on squirrels. Forest Ecology and Management. 152: 13–30.

Carey, A.B. 2007. AIMing for healthy forests: active, intentional management for multiple values. Gen. Tech. Rep. PNW-GTR-721. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 447 p.

Carey, A.B.; Harrington, C.A. 2001. Small mammals in young forests: implications for management for sustainability. Forest Ecology and Management. 154: 289–309.

Carey, A.B.; Johnson, M.L. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological Applications. 5: 336–352.

Carey, A.B.; Peeler, K.C. 1995. Spotted owls: resource and space use in mosaic landscapes. Journal of Raptor Research. 29: 223–239.

Carey, A.B.; Wilson, S.M. 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. Journal of Wildlife Management. 65: 1014–1027.

Carey, A.B.; Horton, S.P.; Biswell, B.L. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs. 62: 223–250.

Carey, A.B.; Kershner, J.; Biswell, B.; de Toledo, L.D. 1999a. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs. 142: 1–71.

Carey, A.B.; MacGuire, C.C.; Biswell, B.L.; Wilson, T.M. 1999b. Distribution and abundance of *Neotoma* in western Oregon and Washington. Northwest Science. 73: 65–80.

Carey, A.B.; Thysell, D.R.; Brodie, A.W. 1999c. The Forest Ecosystem Study: background, rationale, implementation, baseline conditions, and silvicultural assessment. Gen. Tech. Rep. PNW-GTR-457. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 129 p.

Dunk, J.R.; Hawley, J.J.V.G. 2009. Red tree vole habitat suitability modeling: implications for conservation and management. Forest Ecology and Management. 258: 626–634.

Forsman, E. D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs. 87: 1–64.

Forsman, E.D.; Anthony, R.G.; Meslow, E.C.; Zabel, C.J. 2004a. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research. 38: 214–230.

Forsman, E.D.; Anthony, R.G.; Zabel, C.J. 2004b. Distribution and abundance of red tree voles in Oregon based on occurrence in pellets of northern spotted owls. Northwest Science. 78: 294–302.

Gitzen, R.A.; West, S.D.; Maquire, C.C.; Manning, T.; Halpern, C.B. 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. Forest Ecology and Management. 251: 142–155.

Gomez, D.M.; Anthony, R.G.; Hayes, J.P. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. Journal of Wildlife Management. 69: 1670–1682.

Hanson, C.T.; Odion, D.C.; DellaSala, D.A.; Baker, W.L. 2009. Overestimation of fire risk in the Northern Spotted Owl Recovery Plan. Conservation Biology. 23: 1314–1319.

Harrod, R.J.; McRae, B.H.; Hartl, W.E. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. Forest Ecology and Management. 114: 433–446.

Hayward, G.D.; Henry, S.H.; Ruggiero, L.F. 1999. Response of red-backed voles to recent patch cutting in subalpine forest. Conservation Biology. 13: 168–176.

Herbers, J.; Klenner, W. 2007. Effects of logging pattern and intensity on squirrel demography. Journal of Wildlife Management. 71: 2655–2663.

Holloway, G.L.; Malcolm, J.R. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. Journal of Wildlife Management. 70: 1735–1745.

Holloway, G.L.; Malcolm, J.R. 2007. Northern and southern flying squirrels use of space within home ranges in central Ontario. Forest Ecology and Management. 242: 747–755.

Holloway, G.L.; Smith, W.P.; Halpern, C.B.; Gitzen, R.A.; Maguire, C.C. 2012. Influence of forest structure and experimental green-tree retention on Northern Flying Squirrel (*Glaucomys sabrinus*) abundance. Forest Ecology and Management. 285: 187–194.

Klenner, W.; Sullivan, T.P. 2003. Partial and clear-cut harvesting of high elevation spruce-fir forests: implications for small mammal communities. Canadian Journal of Forest Research. 33: 2283–2296.

Lehmkuhl, J.F.; Gould, L.E.; Cazares, E.; Hosford, D.R. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management. 200: 49–65.

Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S.; Boulanger, J. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications. 16: 584–600.

Lehmkuhl, J.F.; Kistler, K.D.; Begley, J.S. 2006b. Bushy-tailed woodrat abundance in dry forests of eastern Washington. Journal of Mammalogy. 87: 371–379.

Lehmkuhl, J.F.; West, S.D.; Chambers, C.L.; McComb, W.C.; Manuwal, D.A.; Aubry, K.A.; Erickson, J.L.; Gitzen, R.A.; Leu, M. 1999. Assessing wildlife response to varying levels and patterns of green-tree retention in western Oregon and Washington. Northwest Science. 73: 45–63.

Manning, T.; Hagar, J.C.; McComb, B.C. 2012. Thinning of young Douglas-fir forests decreases density of northern flying squirrels in the Oregon Cascades. Forest Ecology and Management. 264: 115–124.

Maser, C.; Mate, B.C.; Franklin, J.F.; Dyrness, C.T. 1981. Natural history of Oregon Coast mammals. Gen. Tech. Rep. PNW-133. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Meyer, M.D.; Kelt, D.A.; North, M.P. 2007a. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. The American Midland Naturalist. 157: 202–211.

Meyer, M.D.; North, M.P.; Kelt, D.A. 2007b. Nest trees of northern flying squirrels in Yosemite National Park, California. Southwestern Naturalist. 52: 157–161.

Oksanen, T.; Oksanen, L.; Gyllenberg, M. 1992. Exploitation ecosystems in heterogeneous habitat complexes. II. Impact of small-scale heterogeneity on predator-prey dynamics. Evolutionary Ecology. 6: 383–398.

Pyare, S.; Longland, W.S. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old growth habitat. Canadian Journal of Forest Research. 32: 1016–1024.

Ransome, D.B.; Lindgren, P.M.F.; Sullivan, D.S.; Sullivan, T.P. 2004. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. I. Population dynamics of northern flying squirrel and red squirrel. Forest Ecology and Management. 202: 355–367.

Rosenberg, D.K.; Anthony, R.G. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology. 70: 161–166.

Sakai, H.F.; Noon, B.R. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. Journal of Wildlife Management. 57: 373–382.

Smith, W.P.; Gende, S.M.; Nichols, J.V. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rain forest of southeastern Alaska. Journal of Mammalogy. 85: 663–674.

Smith, W.P.; Gende, S.M.; Nichols, J.V. 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. Ecological Applications. 15: 689–700.

Spies, T.A.; Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggerio, L.F.; Aubrey, K.B.; Carey, A.B.; Huff, M.H., eds., Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 91–109.

Spies, T.A.; Miller, J.D.; Buchanan, J.B.; Lehmkuhl, J.F.; Franklin, J.F.; Healey, S.P.; Hessburg, P.F.; Safford, H.D.; Cohen, W.B.; Kennedy, R.S.H.; Knapp, E.E.; Agee, J.K.; Moeur, M. 2010. Underestimating risks to the northern spotted owl in fire-prone forests: response to Hanson et al. Conservation Biology. 24: 330–333.

Suzuki, N.; Hayes, J.P. 2003. Effects of thinning on small mammals in Oregon coastal forests. Journal of Wildlife Management. 6: 352–371.

Swingle, J.K.; Forsman, E.D. 2009. Home range areas and activity patterns of red tree voles (*Arborimus longicaudus*). Northwest Science. 83: 273–286.

U.S. Fish and Wildlife Service [USFWS]. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. Federal Register 55 FR 2611426194.

U.S. Fish and Wildlife Service [USFWS]. 2008. Recovery plan for the Northern Spotted Owl (*Strix occidentalis caurina*). Portland, OR: U.S. Department of the Interior, Fish and Wildlife Service.

Waters, J.R.; Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management. 59: 858–866.

Waters, J.W.; McKelvey, K.S.; Zabel, C.J.; Luoma, D. 2000. Northern flying squirrel mycophagy and truffle production in fir forests in northeastern California. In: Powers, R.F.; Hauxwell, D.L.; Nakamura, G.M., tech. coords., Proceedings of the California Forest Soils Council conference on forest soils biology and forest management; February 23–24, 1996; Sacramento, California. Gen. Tech. Rep. PSW-GTR-178. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 73–97.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology. 66: 589–594.

Wilson, S.M.; Carey, A.B. 2000. Legacy retention versus thinning: influences on small mammals. Northwest Science. 74: 131–145.

Wilson, T.M. 2010. Limiting factors for northern flying squirrels (*Glaucomys sabrinus*) in the Pacific Northwest: a spatio-temporal analysis. Ph.D. dissertation. Cincinnati, OH: Union Institute & University.

Wilson, T.M.; Carey, A.B. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Naturalist. 77: 35–39.

Zabel, C.J.; McKelvey, K.; Ward, J.P. Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). Canadian Journal of Zoology. 73: 433–439.

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