Research Needs to Support Management and Conservation of Cavity-Dependant Birds and Bats on Forested Landscapes in the Pacific Northwest

Andrew J. Kroll, Michael J. Lacki, and Edward B. Arnett

ABSTRACT

Snags provide habitat for numerous vertebrates and invertebrates. We review how current regulatory guidelines and forest management practices influence snag populations on intensively managed landscapes in the Pacific Northwest. We identify ecological relationships that require investigation to assess alternative practices that optimize ecological and economic goals. Functional and numerical relationships among snag type, abundance, and distribution and demographic responses of both vertebrates and invertebrates are poorly understood. Relatively little is known about temporal and spatial distributions of snags required to maintain viable populations of cavity-dependent taxa or how landscape-scale features (e.g., proximity and amount of mature and late-successional forest) interact with snag types and distributions at the stand level to influence wildlife responses. Regulations for snag retention have been developed and implemented with a substantial degree of uncertainty about their ecological effectiveness. Current regulations, designed to protect forest workers from injury, typically limit retention of snags of large size and advanced decay classes that are often the most limited snag types on intensively managed landscapes. We describe current findings and future research needs that can be used to evaluate operational and ecological effectiveness of current regulations that influence snag management. We identify questions of interest and frame these within the appropriate ecological context of intensively managed landscapes.

Keywords: bats, birds, cavity nesters, commercial forests, forest management, habitat, nest-sites, research outcomes, roost trees, snags, viability

> We emphasize that the complete ecological role of snags in the forest is still unknown; therefore, management strategies involving the snag resource must be flexible. (Cline et al. (1980, p. 785)

The importance of retaining a range of snag species, sizes, and decay classes has long been recognized because of studies that described the substantial number of vertebrates and invertebrates that rely on snags to fulfill their life history requirements (Thomas et al. 1979, Neitro et al. 1985, Hayes 2003). Significant reductions of late-successional forest area, intensification of management on commercial forests, and increasing urbanization have reduced abundance and distribution of snags in the Pacific Northwest (PNW) of the United States (Blewett and Marzluff 2005, Hayes et al. 2005). As a result, contemporary temporal and spatial distributions of snags are likely to be reduced compared with when naturally regenerated second-growth and late-successional stands were more prevalent across the landscape (Cline et al. 1980, Mannan et al. 1980, Zarnowitz and Manuwal 1985, Schreiber and DeCalesta 1992).

Population-level consequences of these changes for snag-dependent organisms are largely unknown. For example, a significant volume of literature reports species, size, decay class, and environmental setting (e.g., forest interior or edge) of snags used by different bird and bat species (Mariani and Manuwal 1990, Aubry and Raley 2002a, Hayes 2003, Walter and Maguire 2005, Barclay and Kurta 2007). However, few studies have examined how animal abundance or vital rates (e.g., clutch or litter size, fecundity, and survival) vary as a result of these or other factors (Bunnell and Huggard 1999). Also, little is known about how snag selection and use vary due to local density of cavity-dependent species. Moreover, how territorial dynamics and seasonal movements of bark- and cavity-dependent species (Kunz and Lumsden 2003, Barclay and Kurta 2007) interact with landscape composition (Jaberg and Guisan 2001, Erickson and West 2003, Gorresen et al. 2005, Arnett and Hayes 2009) of intensively managed forests is poorly understood. Information about these responses is expensive data to gather, especially for species that roost communally (e.g., Vaux's swift, *Chaetura vauxi* and California myotis, and *Myotis californicus*), are difficult to locate and monitor (e.g., brown creeper, *Certhia americana*; fringed myotis, *Myotis thysanodes*), or have large home ranges (e.g., long-legged myotis, *Myotis volans*; pileated woodpecker, *Dryocopus pileatus*; Mariani and Manuwal 1990, Brigham et al. 1997, Bull 2003, Hunter and Mazurek 2003, Johnson et al. 2007). As a result, significant uncertainty exists with regard to how past and current snag management practices influence populations and communities of snag-dependent organisms.

Purpose and Structure of Review

Conservation and management programs require a clear understanding about how regulatory prescriptions and operational practices influence population responses of native cavity-dependent

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This article uses metric units; the applicable conversion factors are centimeters (cm), 1 cm = 0.39 in.; meters (m), 1 m = 3.3 ft; hectares (ha), 1 ha = 2.47 ac.

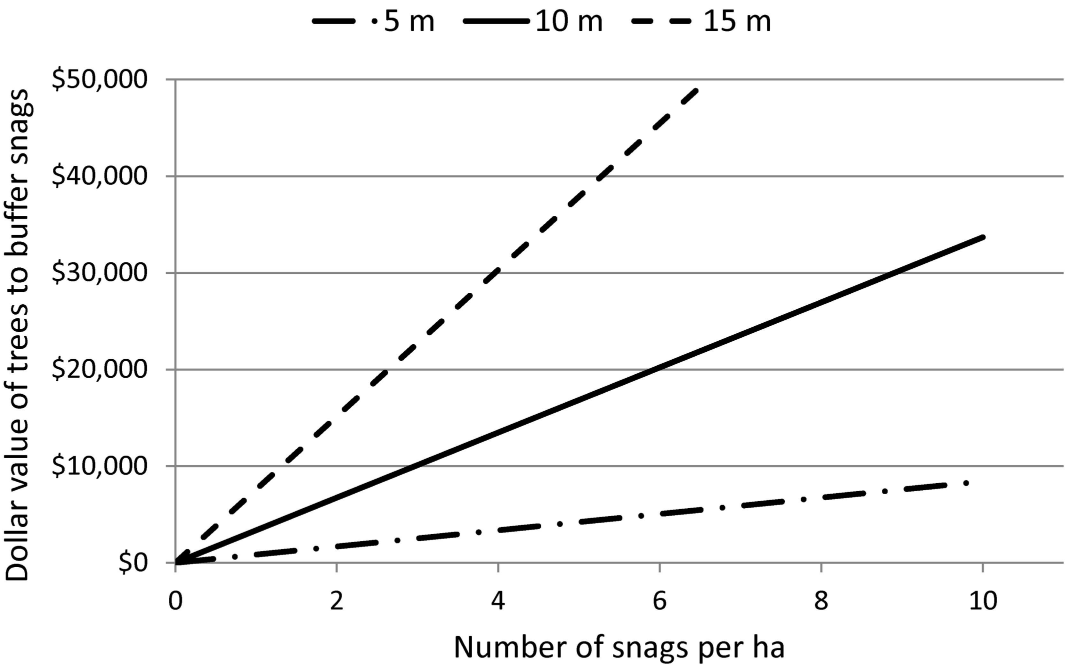

Figure 1. Dollar value of live Douglas-fir left in safety buffers (radius equals 2 * snag height) required by OSHA (OSHA 2010) for snags 5, 10, and 15 m tall retained at densities ranging from 0 to 10 trees/ha, PNW.

wildlife species (Bunnell and Huggard 1999, Hayes and Loeb 2007). Our goals in this study are to (1) describe how forest management influences current and future snag populations and (2) suggest critical research that is needed to support effective conservation and management regulations and practices for cavity-dependent birds and bats. We focus our review on the Coast Ranges and western Cascades of the PNW and make recommendations for specific issues prevalent on intensively managed landscapes in that region. We contend that many of our basic conclusions are true for snag management in forested ecosystems throughout the world and are relevant for conservation of many cavity-dependent bird and bat species.

Methods

We reviewed studies that examined associations between abundance, reproductive success, survival, and habitat use of snag-dependent bird and bat species. We conducted a literature review of studies that focused on individual snag characteristics, spatial distribution and dispersion of snags and snag clusters, density or abundance of snags at harvest unit and landscape-level scales, within harvested and unharvested forests, and within different ecological settings (e.g., upland or riparian and hardwood or conifer-dominated stand). We electronically searched *Biological Abstracts* and reviewed reports and theses cited in published articles but not contained within the *Biological Abstracts* database. In addition, we supplemented the search with individual databases developed during the course of other research efforts on this topic. We included literature from the Coast and Cascade Ranges, with most studies occurring in the latter area. We included research results from studies outside of the PNW region to elucidate general patterns in behavior and habitat use of snag-dependent birds and bats associated with forest management or to identify critical conservation issues related to cavity-dependent species in intensively managed landscapes.

Forest Management Impacts on Snag Populations

Forest Practice Impacts on Snag Retention

Effective snag management faces two challenges, retention and development, both of which are manifested at stand and landscape scales and involve interrelated operational and economic issues of forest commodity production (Eklund et al. 2009). As a result, volume of deadwood in managed forests is typically lower than unmanaged forests and snag numbers and distribution typically decline with successive management actions (Spies and Franklin 1991, Bunnell et al. 2002, Ohmann and Waddell 2002, Kennedy et al. 2010).

Forest practice regulations in Oregon require retention of five green trees (green trees are live, merchantable trees that are retained on a per hectare basis in clearcut units) or snags >10 m in height and 27 cm in diameter/ha (Anonymous 2008). Washington regulations stipulate retention of 7.4 wildlife trees (defective trees) and 5 green trees/ha (Anonymous 2001). Often, snags are not retained between harvest rotations because of safety concerns (Neitro et al. 1985, Lewis 1998, Ohmann and Waddell 2002). In many instances, snag retention may be illegal under laws set forth by the US Department of Labor (Occupational Safety and Health Administration [OSHA] 2010). As a result, snags that interfere with harvest operations or pose direct risks to safety of forest workers are often felled, regardless of stand ownership (Hope and McComb 1994). If a landowner chooses to retain an unsafe snag, current OSHA regulations define an inoperable safety buffer that represents approximately two times the total height of the snag (OSHA 2010). This practice represents an opportunity cost because commercially valuable trees are not harvested (Figure 1). For example, leaving two 10-m tall snags/ha would cost approximately $6,700 to buffer with Douglas-fir *Pseudotsuga menziesii* (based on an average volume of 67 thousand board feet [mbf]/ha at $400/mbf, Anonymous 2010). Pairing these costs with recommendations for snag retention of 2–3 snags >50-cm dbh/ha (Bunnell et al. 2002) indicates that buffering of snags with unharvested, merchantable trees to meet OSHA regulations is prohibitively expensive for landowners.

Information about species-specific fall rates can guide management targets for snag retention. For example, data from forests west of the Cascade Range showed declines in snag density with increasing stand age for old-growth stands and managed and unmanaged stands (Cline et al. 1980). Densities of snags of >9-cm dbh varied by stand type, with densities of snags in unmanaged stands declining from 815/ha at age 41 years to 212/ha by age 62 years, and to 35/ha at 120 years in age. Managed stands contained 20.3, 57.3, and 17.8 snags/ha in stands aged 35, 55, and 105 years, respectively (Cline et al. 1980). In the western Oregon Cascade Range, Arnett (2007) found that densities of snags increased with stand age and were highest in stands >80 years old. Arnett (2007) also found that densities of small and large and all snags were higher in 21- to 40-year-old and 41- to 80-year-old stands on federal lands compared with those stands on private lands, but were similar in older stands sampled from the two different ownerships. Parish et al. (2010) found that snag longevity in southwestern British Columbia was positively associated with dbh for Douglas-fir, western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). For all three species, snags <20-cm dbh had <40% probability of standing after 20 years. However, large Douglas-fir snags (>80-cm dbh) had an 80% probability of standing after 50 years, indicating the importance of retaining these types of snags during harvest operations. Studies east of the Cascade Range suggest highly variable fall rates among tree species for smaller-diameter snags (i.e., <41 cm dbh), but showed large-diameter Douglas-fir snags persisted longer than other species, with >40% snags remaining for >80 years (Everett et al. 1999). In general, these data indicated that large trees (>50-cm dbh) are more likely to remain standing and serve as important biological legacies as the clearcut stand regenerates.

Forest Practice Impacts on Snag Development

Current management of Douglas-fir plantations on private lands includes stand harvests at approximately 50 years, a practice that does not mimic natural regeneration periods (Tappeiner et al. 1997). This rotation length precludes development of large snags (i.e., from trees >80 years old) on commercial forest landscapes outside of riparian management zones or other nonoperational areas (Wilhere 2003). Green tree retention (i.e., the retention of live, merchantable trees in clearcut units, rather than two-story or other harvest treatments), thinning prescriptions, and snag creation are three methods for promoting habitat complexity in regenerating forests at the stand scale (Franklin et al. 2002, Aubry et al. 2009). However, green tree retention strategies can generate additional costs to landowners by damaging trees and reducing growth rates (Zenner et al. 1998, Moore et al. 2002). The effectiveness of retention strategies for bird and bat species in the PNW has received little research attention with the exception of Vega (1993), who reported negative effects of this practice on shrub-nesting birds. Limited understanding persists concerning the magnitude, direction, and duration of effects on these and other taxa.

In contrast, thinning of young, dense stands is a long-standing practice to enhance growth of residual trees. In addition, this practice promotes understory establishment and growth and can lead to the development of multilayered stands possessing greater structural diversity, including a range of snag types and sizes (Carey and Curtis 1996, Barbour et al. 1997, Hayes et al. 1997, Bailey and Tappeiner 1998). For example, old-growth forests develop through a variety of initial densities and sequences of intermediate disturbances, but, when young, were far less dense than contemporary plantations (Tappeiner et al. 1997). In plantations, sapling competition caused by high stocking rates often leads to a preponderance of small snags (<15-cm dbh) of limited ecological value to cavity-dependent vertebrates.

Thinning prescriptions may conflict with other operational goals. For example, although stands may be thinned to accelerate development of multilayered stands with large trees that could become snags, tight spacing of conifer seedlings and saplings is desired to yield high-quality wood grades and generate high financial returns (Briggs and Smith 1986, Bailey and Tappeiner 1998). Also, selected research suggests that extended harvest rotations, paired with multiple thinning entries, may generate competitive returns (Latta and Montgomery 2007), whereas other studies report that uneven-aged management generates costs, such as reduced growth rates, that landowners are unlikely to bear (Kellogg et al. 1996, Lippke et al. 2007).

Finally, snag populations may be supplemented by creating snags from harvest-age green trees. Forest managers have created snags by a variety of methods for decades (Bull and Partridge 1986, Chambers et al. 1997, Ross and Nima 1997), although application of these methods has been limited because of safety concerns and costs. Several authors report use of created snags by wildlife. For example, Walter and Maguire (2005) reported an average of 4.8 nesting cavities and 10–23 foraging excavations per snag, depending on silvicultural treatment (i.e., group selection, two story, and clearcut), 10–12 years after snag creation by topping. Brandeis et al. (2002) found that percentage of snags with foraging excavations ranged from 15 to 70% and snags with nesting cavities ranged from 10 to 25% 4 years after treatment, depending on treatment type. Treatment types in this study included girdling, triclopyr application to tree, monosodium methanearsonate application to tree, topping at the base of the live crown, and topping at the middle of the live crown.

Snag creation methods that can be incorporated into harvest operations, such as mechanical topping of merchantable trees, are a promising alternative. Unfortunately, population responses to snags created from rotation-age trees (i.e., 45–65 years old) are poorly documented. Arnett et al. (2010) evaluated six treatment levels (three created snag densities in either dispersed or clumped retention) and determined that 5 years after snag creation by mechanical topping, the percentage of created snags with foraging excavations ranged from 60 to 80%. However, <5% of the snags were used for nesting, regardless of the treatment type.

These results suggest that snag creation from merchantable trees has approximately a 5- to 10-year time lag before substantial cavity-dependent wildlife use begins, most likely until wood decay fungi sufficiently weaken the bark and cambial layers (Wright and Harvey 1967, Harris 1983). Mechanical topping of trees to create snags may be an option for quickly producing a large number of shorter snags, but this method can not provide the tall snags used by several bird and bat species (Bull and Holthausen 1993, Campbell et al. 1996, Ormsbee and McComb 1998, Lacki and Baker 2007).

Patch Retention

Bird and bat responses to riparian buffers have been well studied in the PNW (e.g., Anthony et al. 1996, Hagar 1999, Pearson and

Table 1. Summary of key results and trends from previous snag research on forested landscapes in the PNW.

Topic (spatial scale)	Response	Research result
Snag types (within unit)	Snag use by cavity-dependent species	A broad range of snag types (i.e., from different tree species), sizes, and decay classes are required to meet the needs of snag-dependent invertebrates and vertebrates
Snag distribution (within unit)	Snag use by cavity-dependent species	Retention of ecological context (e.g., forest buffer around a bat roost tree) or retention of additional ecological legacies can be a critical aspect of snag retention
Snag types (within unit)	Snag longevity	Larger snags tend to persist longer; some species (e.g., Douglas-fir and ponderosa pine) tend to persist longer
Snag distribution (within unit)	Snag abundance	Retain 2–3 large snags (>50-cm dbh) per ha; retain >10–20 small snags (<50-cm dbh) per ha; target is an average distribution across numerous operational units
Snag distribution (within unit)	Snag distribution	Aggregated retention mimics natural distributions; aggregation will reduce snag loss to windthrow
Snag distribution (within unit)	Snag location	Snags should not be located exclusively in riparian zones or other nonoperational areas; some species may not use snags located in riparian areas due to temperature and/or moisture conditions

Manuwal 2001), although the linear structure of riparian stands and sampling methods (point-count stations) have limited inference that can be made about cavity-dependent bird responses to this management practice. Many species of management interest may include multiple riparian buffers within their home ranges (e.g., pileated woodpeckers) and different sampling programs, such as telemetry studies, will be required to evaluate their responses. The importance of riparian buffers to snag-dependent bats is well documented (Hayes and Adam 1996). Riparian buffers may provide necessary habitat conditions for forest-dwelling bats including flight corridors in fragmented forested landscapes (Hein et al. 2009), an abundant prey base of emergent aquatic insects (Fukui et al. 2006), structural variation in habitat that influences activity patterns (Ober and Hayes 2008), and roosting sites, especially for pregnant female bats (Baker and Lacki 2006).

Effectiveness of patch retention in upland areas, however, has received less research attention, despite the apparent importance of these areas for bats. For example, lactating female long-legged myotis are reported to roost in upland forest patches whereas pregnant females roost in snags in riparian and upland areas (Ormsbee and McComb 1998, Baker and Lacki 2006). Others have reported limited use of PNW riparian areas by bats for roosting and suggest that managers should provide snags in upland habitats (Campbell et al. 1996, Waldien et al. 2000, Arnett and Hayes 2009). Also, little information exists to guide managers in the size, position, and distribution of retained patches, because only a single study has estimated the size of a local roosting area (11.4 ha; Ormsbee 1996). Recent advances in the study of social networks of bats indicate the existence of nonrandom associations among bats in maternity colonies (Garroway and Broders 2007, Patriquin et al. 2010), including species known to occur in forests of the PNW (Willis and Brigham 2004). Improvements in our understanding of fission–fusion behavior in bats should help to determine the size and distribution of patches needed at the landscape scale to sustain the integrity of social interactions of bat species that form maternity colonies in snags.

Finally, the probability of reuse of snags is known to vary for both birds and bats (Mannan et al. 1980, Neitro et al. 1985, Hayes 2003, Barclay and Kurta 2007). For example, California myotis (*M. californicus*) showed infrequent reuse of the same roost trees in subsequent years, although big brown bats (*Eptesicus fuscus*) may frequently reuse roost trees in subsequent years. Also, both Barclay and Brigham (2001) and Willis et al. (2003) documented reuse of most snag roosts by some individuals of these two species for up to 5–10 years after discovery of the roost site, suggesting that roost snags were limited in the landscape and/or site fidelity may be an important aspect of snag selection. None of these studies evaluated associations between site fidelity and forest patch size or dispersion of forest patches at landscape levels. If site fidelity is a widespread phenomenon, retention of roost trees within patches of suitable forest habitat may be critical for maintenance of local populations.

Research Needs to Support Management and Conservation Targets

Current regulations are intended to provide snag types, densities, and spatial distributions within harvest units to support future viability of cavity-dependent populations. However, empirical results do not provide guidance about the effectiveness of these regulations. In addition, effectiveness of regulatory prescriptions can not be determined without long-term monitoring and research programs. We generally agree with Hutto's (2006) contention that snag retention requirements should be informed by factors such as successional stage and habitat type (ponderosa pine *Pinus ponderosa* versus Douglas-fir forest), and contend that uniform regulatory prescriptions can be onerous to landowners and may not optimize potential ecological benefits for cavity-dependent wildlife. For instance, if a large percentage of green retention trees blow down before they become snags, the result will be a deficit of large snags in an advanced stage of decay. In addition, even if adequate scientific data existed to suggest that more snags would always generate positive changes in wildlife survival or reproductive success (or other vital rates of interest), such a prescription is not likely to be implemented in every place and at every opportunity (Bunnell et al. 2002).

Empirical studies that link density of snags at different scales to cavity-dependent wildlife populations, evaluate effectiveness of snag and green tree retention prescriptions, and validate snag models (e.g., Wilhere 2003) are sorely lacking and would greatly improve forest management planning for wildlife. In the following section, we address selected research areas that are relevant to management and conservation of cavity-dependent birds and bats (i.e., our list is not exhaustive, and the literature review suggests many more avenues that merit exploration), especially because maintenance of biological diversity will continue to be a goal in managing forested landscapes in the PNW (Table 1; Bunnell and Huggard 1999, Harrington and Nicholas 2007, Odion and Sarr 2007, Suzuki and Olson 2007).

Table 2. Summary of potential research and monitoring topics and questions to inform snag management on intensively managed forest landscapes in the PNW.

Topic (spatial scale)	Response	Research question	Study difficulty
Snag distributions (within unit)	Snag use by cavity-dependent species	Is the proportional use of dispersed snags different from clumped snags? Does proportional use depend on snag position (e.g., riparian or upland)?	Moderate
Snag numbers (within unit)	Abundance of target species	How does the abundance of species of interest respond to snag abundance?	Difficult
Harvest unit context (within unit)	Use of snags by cavity-dependent species	How do species-specific responses to created snags left in clearcut harvest units differ from those documented for snags in young stands created by natural disturbances? What other features (e.g., remnant green trees) are required before species found in early successional stands will use snags in clearcut stands?	Moderate
Green tree retention (within unit)	Fall rates of green trees	Where should harvest age green trees be retained so that fall rates are similar to those found in unmanaged stands? What proportion of green trees is still standing at 5-, 10-, and 20-yr intervals?	Difficult
Patch use (within unit)	Nesting/roosting occupancy of patch	If some species will only use snags if they occur in a patch of green trees, how big must retention patches be to promote nesting/roosting occupancy of cavity-dependent species of interest?	Difficult
Harvest unit context (landscape)	Occupancy of harvest unit; proportion of snags used for nesting, foraging, and roosting in unit	Does the amount/proportion of older forest (>80 yr old) in the landscape influence the use of snags in harvest units? Do snags in harvest units receive more use when the amount/proportion of older forest (>80 yr old) in the landscape is low?	Moderate

Broad-Scale Research Designs

Investigators should expand the scale of their efforts, both spatially and temporally, to provide data relevant to intensively managed forest landscapes that dominate lower elevations in the PNW. For example, although an effort has been made to describe the conditions under which snags develop and fall in both commercial and unmanaged stands (Cline et al. 1980, Wilhere 2003), we know very little about how wildlife populations respond to these changes in part because populations are not restricted to individual stands. In some cases, cavity-dependent birds can respond quickly to changes in temporal and spatial distribution of resources across the landscape (Kotliar et al. 2002, Hutto 2006). However, a positive response may represent a "true" increase in population abundance, simply an increase in activity in altered habitats, or a mixture of both (Hayes and Loeb 2007, Russell et al. 2009). Development of appropriate methodologies to discern differences between the three responses is required. Examining whether selection and use of snags by marked individuals change under different management scenarios (e.g., harvesting adjacent stands), and measuring the potential fitness consequences of these changes, is a critical research need (Miller et al. 2003).

Evaluations of the effects of different snag management prescriptions on bird and bat species that vary in size of home range and dispersal capability (e.g., brown creeper to pileated woodpecker; western long-eared myotis [*Myotis evotis*] to long-legged myotis) would help to address stand and landscape management. Selecting appropriate species of birds and bats for investigating population-level responses to snag management prescriptions requires identification of species that are common, sufficiently abundant to detect measured responses when they occur (Lundquist and Mariani 1991, Hayes and Loeb 2007), and that rely on snags to satisfy life history requirements. Our tentative recommendations for focal species to be investigated are pileated woodpecker and long-legged myotis. Both species are common throughout the PNW (Lundquist and Mariani 1991, Aubry and Raley 2002b, Baker and Lacki 2004) and their association with snags has been well studied, with baseline data available for each in both west- and east-side forests (Ormsbee and McComb 1998, Martin and Eadie 1999, Baker and Lacki 2006, Raley and Aubry 2006, Arnett and Hayes 2009). Additionally, pileated woodpeckers are keystone habitat modifiers and their presence will provide positive benefits to other snag-dependent wildlife populations (Bonar 2000). Potential cascading effects from reductions in abundance of pileated woodpeckers and other primary cavity nesters merit research attention (Martin and Eadie 1999, Bednarz et al. 2004). For example, do other populations (e.g., small mammals besides bats) and ecological functions (decay processes) change if abundance of primary cavity nesters declines significantly?

The Context of Snag Retention

We suggest that the response of snag-dependent birds and bats to alternative distributions of snags and/or green trees on intensively managed, forested landscapes is a research topic that needs immediate attention (Table 2). Other researchers have argued that a uniform distribution of snags and green trees is unlikely to be a successful strategy (Bunnell et al. 2002). In particular, the landscape context of individual stands should be considered when designing stand-level prescriptions. For example, the percentage of old-growth forest in the historically forested landscape of western Oregon and Washington has been estimated as high as 60–70% (Spies and Franklin 1988). Twenty percent of the historic amount of old-growth likely remains and most of these forests reside on public lands, primarily US Forest Service and Bureau of Land Management

(Bolsinger and Waddell 1993). Landscapes where intensively managed forests are intermixed with public forests (called "checkerboarding"; this pattern is most prominent in the Oregon and Washington Cascades and southern Oregon Coast Range) may contain substantial amounts of late-successional forests and sufficient habitat for cavity-dependent birds and bats without regulatory snag prescriptions that stipulate uniform distributions of snags across the landscape.

In contrast, significant portions of the forested landscape in the PNW (i.e., the Coast Ranges of Oregon and Washington) have only small patches of remnant old-growth forest, because the majority of these areas are intensively managed for wood production. Although uniform regulations likely play an important role in maintaining populations of cavity-dependent wildlife in these areas, such prescriptions are unlikely to create stand and landscape-level conditions that mimic historic snag distributions, viz., clusters with high densities of various snag sizes and types, especially very large (>80 cm) snags. In these areas, we suggest that greater flexibility in regulatory implementation, paired with specific research questions (Table 2), may improve effectiveness at a broader spatial scale. For instance, rather than retaining snags and green trees on a per harvest unit basis, landowners could group snags and green trees from multiple units together, a practice that is operationally efficient. This specific practice may promote retention of patches that contain high densities of snags and wildlife trees as well as green tree patches that are more likely to be wind firm and develop into large trees and, eventually, snags.

In addition, research is required on species-specific responses to snag types, numbers, and distributions in clearcut harvest units managed for wood production. Comparisons between clearcut harvest units and unmanaged stands are clearly not appropriate, because of vast structural differences that exist between these two stand types (Bennett and Adams 2004). Although the closest natural analog to a clearcut harvest unit is a stand created by disturbance such as windthrow or fire, important differences exist even between these types (Swanson et al. 2011). For example, harvested stands are immediately replanted at uniform densities, rarely contain scattered live remnant trees of various ages within the unit, pass through truncated successional stages, and, depending on their geographic location, may be located in proximity to an extensive riparian buffer that was not disturbed during harvesting. In contrast, in young stands created by natural disturbances, seedling recruitment is irregular, extensive biological legacies often remain in the stand, the early successional stage can last for decades, and disturbances influence both upland and riparian areas (Hayes et al. 2005, Swanson et al. 2011). Furthermore, patch sizes on intensively managed landscapes are restricted by forest practice regulations (currently, 120 acres in Oregon and Washington, Anonymous 2001, 2008) although patches created by natural disturbances can range in size from less than an acre to tens of thousands of acres (Hayes et al. 2005, Odion and Sarr 2007, Turner 2010). Because of these critical differences, young stands created by natural disturbances can not serve as a template for snag management in clearcut harvest units. Research orchestrated in clearcut units, which can reach canopy closure within 20 years of stand establishment, is needed to address the issue of how within unit context influences snag use and species retention (Arnett et al. 2010 provides one example of context-specific research).

Snag Longevity

Effectiveness of current regulations for retention and development of snags to meet specific ecological objectives has not been tested (Wilhere 2003). In addition, these regulatory prescriptions have not been framed with reference to specific ecological questions or management targets. For example, what percentage of harvest-age green trees (approximately 50 years old) will survive to be large snags (>80-cm dbh; Spies and Franklin 1991, Gibbons et al. 2008)? How long are snags of different size classes retained in the following rotation? How do other activities change snag numbers, such as removal of leave trees after harvest activities have ended (e.g., Bate et al. 2007, Wisdom and Bate 2008)? How does the road network (i.e., accessibility) influence snag distributions?

Contribution of Buffers and Green Trees

Intensively managed landscapes are divided into two coarse classifications: operable and inoperable areas. Operable areas occur predominantly in upland areas and are dedicated to wood production; inoperable areas included riparian zones, unstable slopes, cliffs, and similar areas where intensive wood production is not economically feasible. Given current silvicultural practices on intensively managed ownerships, as well as strong focus on safety issues related to snags, future snag distributions within operable areas are unlikely to resemble historical patterns (Kennedy et al. 2010). We see two primary avenues for addressing this problem. First, managers can consider maximizing snag retention and development (number and size) on inoperable areas of managed forest landscapes. Second, incentive programs can promote snag retention within operable areas. However, research that evaluates interest in, and effectiveness of, specific incentive programs is needed (e.g., Giampaoli and Bliss 2011). We think incentive programs may be unlikely to gain sufficient socioeconomic support for broad-scale implementation and contend that focusing snag resources in inoperable areas may be the most viable option.

To support retention efforts, additional research on temporal (i.e., seasonal) and spatial variation in habitat selection by cavity-dependent wildlife could elucidate the relative importance of buffers and set-asides in operational stands and suggest what proportion of a planning landscape should be allocated to different stand prescriptions. Although locating green trees (that may become snags) within riparian buffers might be logistically feasible (and likely preferred by many forest managers), the ecological suitability of this practice requires attention. For example, further study is needed to determine the relative quality of bat roosts located within riparian habitat versus those located in upland sites (Duchamp et al. 2007). In lieu of this research, it is reasonable to assume that maintaining roost structures and replacement trees for bats only in riparian areas, or only in upland areas, is not likely to meet the needs of a diverse species group of bats (Hayes 2003). Furthermore, if older trees and snags serve as night roosts and hibernacula, the appropriate landscape locations for these structures remain uncertain (Hayes 2003, Duchamp et al. 2007). Slope-stability areas offer unique opportunities, because they are the largest inoperable areas that occur in upland portions of the landscape. Slope-stability set-asides vary in shape and size because of underlying landforms that they are designed to stabilize. Supplementing these patches with green trees (that would otherwise be placed along riparian buffers) may provide additional benefits, such as reduction of nest predation rates because snags are not exposed or isolated. In addition, snags that are created in these areas are likely to be retained longer because they are sheltered within a larger patch of green trees.

Summary

- Snags serve a critical role in maintaining populations of bird and bat species in the PNW (Thomas 1979, Bunnell et al. 2002), but mechanisms that govern population and community responses to snag management remain poorly understood.
- Research programs that acknowledge critical differences in the ecological context of snags located in intensively managed young stands, young stands created by natural disturbances, and unmanaged stands are required to provide relevant biological results. Regenerating harvest units are unique biological systems, and cavity-dependent organisms may exhibit different responses than they would in early successional stands created by natural disturbances.
- Biologists, managers, and regulators should be willing to pursue spatially and temporally variable solutions for ecological and economic issues characterized by substantial uncertainty (Riley et al. 2002, Hayes and Loeb 2007). Regulations and management guidelines (amount, size classes, and spatial distribution of snags at the landscape scale) with explicit ecological outcomes (changes in abundance of focal species and maintenance of critical ecological processes) should be outlined before harvesting, structured as specific questions, and evaluated by research programs that provide feedback to restructure guidelines, i.e., adaptive management (Wilhere 2003, Hutto 2006). For example, how should large-diameter (>50-cm dbh) snags be distributed on intensively managed landscapes to facilitate roost-switching in snag-dependent bats, especially lactating female bats? Studies that address these types of questions are challenging and costly to implement but provide critical information to support effective management and conservation programs.

Literature Cited

Anonymous. 2001. *Chapter 222-30 WAC—Timber harvesting.* Washington Forest Practice Rules, Washington Department of Natural Resources, Olympia, WA. Available online at apps.leg.wa.gov/wac/default.aspx?cite=222-30; last accessed Mar. 21, 2012.

Anonymous. 2008. *Division 605—Planning forest operations.* Oregon Forest Practices Rules, Oregon Department of Forestry–Private Forests Program, Salem, OR. Available online at www.oregon.gov/ODF/privateforests/docs/guidance/OARDiv605.pdf?ga:t; last accessed Mar. 21, 2012.

Anonymous. 2010. Douglas fir log prices, Region 1. *Random Lengths* 20:9.

Anthony, R.G., G.A. Green, E.D. Forsman, and S.K. Nelson. 1996. Avian abundance in riparian zones of three forest types in the Cascade Mountains, Oregon. *Wilson Bull.* 108:280–291.

Arnett, E.B. 2007. *Presence, relative abundance, and resource selection of bats in managed forest landscapes in western Oregon.* Dissertation, Oregon State Univ., Corvallis, OR. 245 p.

Arnett, E.B., and J.P. Hayes. 2009. Use of conifer snags as roosts by female bats in western Oregon. *J. Wildl. Manag.* 73:214–225.

Arnett, E.B., A.J. Kroll, and S.D. Duke. 2010. Avian foraging and nesting use of created snags in intensively managed forests of western Oregon, USA. *For. Ecol. Manag.* 260:1773–1779.

Aubry, K.B., and C.M. Raley. 2002a. Selection of nest and roost trees by Pileated Woodpeckers in coastal forests of Washington. *J. Wildl. Manag.* 66:392–406.

Aubry, K.B., and C.M. Raley. 2002b. The pileated woodpecker as a keystone habitat modifier in the Pacific Northwest. P. 257–274 in *Proc. of the symp. on the Ecology and management of dead wood in western forests*, Laudenslayer, W.F. Jr., P.J. Shea, B.F. Valentine, C.P. Weatherspoon, and T.E. Lisle (eds.). US For. Serv. Pac. Southw. Res. Stn., Albany, CA.

Aubry, K.B., C.B. Halpern, and C.E. Peterson. 2009. Variable-retention harvests in the Pacific Northwest: A review of short-term findings from the DEMO study. *For. Ecol. Manag.* 258:398–408.

Bailey, J.D., and J. Tappeiner. 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. *For. Ecol. Manag.* 108:99–113.

Baker, M.D., and M.J. Lacki. 2004. Forest bat communities in the east Cascade Range, Washington. *Northw. Sci.* 78:234–241.

Baker, M.D., and M.J. Lacki. 2006. Day-roosting habitat of female long-legged myotis in ponderosa pine forests. *J. Wildl. Manag.* 70:207–215.

Barbour, R.J., S. Johnston, J.P. Hayes, and G.F. Tucker. 1997. Simulated stand characteristics and wood product yields of Douglas-fir forests managed for ecosystem objectives. *For. Ecol. Manag.* 91:215–219.

Barclay, R.M.R., and R.M. Brigham. 2001. Year-to-year reuse of tree-roosts by California bats (*Myotis californicus*) in southern British Columbia. *Am. Midl. Nat.* 146:80–85.

Barclay, R.M.R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. P. 17–59 in *Bats in forests: Conservation and management*, Lacki, M.J., J.P. Hayes, and A. Kurta (eds.). The Johns Hopkins University Press, Baltimore, MD.

Bate, L.J., M.J. Wisdom, and B.C. Wales. 2007. Snag densities in relation to human access and associated management factors in forests of northeastern Oregon, USA. *Landsc. Urban Plan.* 80:278–291.

Bednarz, J.C., D. Ripper, and P.M. Radley. 2004. Emerging concepts and research directions in the study of cavity-nesting birds: Keystone ecological processes. *Condor* 106:1–4.

Bennett, L.T., and M.A. Adams. 2004. Assessment of ecological effects due to forest harvesting: approaches and statistical issues. *J. Appl. Ecol.* 41:585–598.

Blewett, C.M., and J.M. Marzluff. 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. *Condor* 107:678–693.

Bolsinger, C.L., and K.L. Waddell. 1993. Area of old-growth forests in California, Oregon, and Washington. US For Serv. PNW-RB-197, Pac. Northw. Res. Stn., Portland, OR. 32 p.

Bonar, R.L. 2000. Availability of pileated woodpecker cavities and use by other species. *J. Wildl. Manag.* 64:52–59.

Brandeis, T.J., M. Newton, G. M. Filip, and E.C. Cole. 2002. Cavity-nester habitat development in artificially made Douglas-fir snags. *J. Wildl. Manag.* 66:625–633.

Briggs, D.G., and W.R. Smith. 1986. Effects of silvicultural practices on wood properties of conifers: a review. P. 108–117 in *Douglas-fir: Stand management for the future*, Oliver, C.D., D.P. Hanley, and J.A. Johnson (eds.). College of Forest Resources, Univ. of Washington, Seattle, WA.

Brigham, R.M., M.J. Vonhof, R.M.R. Barclay, and J.C. William. 1997. Roosting behavior and roost-site preference of forest-dwelling California bats (*Myotis californicus*). *J. Mammal* 78:1231–1239.

Bull, E.L. 2003. Declines in the breeding population of Vaux's swifts in northeastern Oregon. *West. Birds* 34:230–234.

Bull, E.L., and A.D. Partridge. 1986. Methods of killing trees for use by cavity nesters. *Wildl. Soc. Bull.* 14:142–146.

Bull, E.L., and R.S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in northeastern Oregon. *J. Wildl. Manag.* 57:335–345.

Bunnell, F.L., and D.J. Huggard. 1999. Biodiversity across spatial and temporal scales: problems and opportunities. *For. Ecol. Manag.* 115:113–126.

Bunnell, F.L., M. Boyland, and E. Wind. 2002. How should we spatially distribute dead and dying wood? P. 739–752 in *Proc. of the symp. on the Ecology and management of dead wood in western forests*, Laudenslayer, W.F. Jr., P.J. Shea, B.F. Valentine, C.P. Weatherspoon, and T.E. Lisle (eds.). US For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southw. Res. Stn., Albany, CA.

Campbell, L.A., J.G. Hallett, and M.A. O'Connell. 1996. Conservation of bats in managed forests: Use of roosts by *Lasionycteris noctivagans*. *J. Mammal* 77:976–984.

Carey, A.B., and R.O. Curtis. 1996. Conservation of biodiversity: A useful paradigm for forest ecosystem management. *Wildl. Soc. Bull.* 24:610–620.

Chambers, C.L., T. Carrigan, T.E. Sabin, J. Tappeiner, and W.C. McComb. 1997. Use of artificially created Douglas-fir snags by cavity-nesting birds. *West. J. Appl. For.* 12:93–97.

Cline, S.P., A.B. Berg, and H.M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manag.* 44:773–786.

Duchamp, J.E., E.B. Arnett, M.A. Larson, and R.K. Swihart. 2007. Ecological considerations for landscape-level management of bats. P. 237–261 in *Bats in forests: Conservation and management,* Lacki, M.J., J.P. Hayes, and A. Kurta (eds.). The Johns Hopkins University Press, Baltimore, MD.

Eklund, A., M.G. Wing, and J. Sessions. 2009. Evaluating economic and wildlife habitat considerations for snag retention policies in burned landscapes. *West. J. Appl. For.* 24:67–75.

Erickson, J.L., and S.D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biol. Conserv.* 109:95–102.

Everett, R., J. Lehmkuhl, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. *Int. J. Wildl. Fire* 9:223–234.

Franklin, J.F., T.A. Spies, R.V. Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manag.* 155:399–423.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *J. Animal Ecol.* 75:1252–1258.

Garroway, C.J., and H.G. Broders. 2007. Nonrandom association patterns at northern long-eared bat maternity roosts. *Can. J. Zool.* 85:956–964.

Giampaoli, P., and J.C. Bliss. 2011. Landowner perceptions of habitat protection policy and process in Oregon. *West. J. Appl. For.* 26:110–118.

Gibbons, P., R.B. Cunningham, and D.B. Lindenmayer. 2008. What factors influence the collapse of trees retained on logged sites? A case-control study. *For. Ecol. Manag.* 255:62–67.

Gorresen, P.M., M.R. Willig, and R.E. Strauss. 2005. Multivariate analysis of scale-dependent associations between bats and landscape structure. *Ecol. Applic.* 15:2126–2136.

Hagar, J.C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. *J. Wildl. Manag.* 63:484–496.

Harrington, T.B., and G.E. Nicholas (eds.). 2007. *Managing for wildlife habitat in west-side production forests.* US For. Serv. Gen. Tech. Rep. PNW-GTR 285, Portland, Oregon. 135 p.

Harris, R.D. 1983. Decay characteristics of pileated woodpecker nest trees. P. 125–129 in *Proc. of the symp. on Snag habitat management*, Davis, J.W., G.A. Goodwin, and R.A. Ockenfels (eds.). US For. Serv. RM-99, Rocky Mtn. For. and Range Exp. Stn., Fort Collins, CO.

Hayes, J.P. 2003. Habitat ecology and conservation of bats in western coniferous forest. P. 81–119 in *Mammal community dynamics in coniferous forests of western North America: Management and conservation*, Zabel, C.J., and R.G. Anthony (eds.). Cambridge University Press, New York.

Hayes, J.P., and M.D. Adam. 1996. The influence of logging riparian areas on habitat utilization by bats in western Oregon. P. 228–237 in *Bats in forests symp.*, Barclay, R.M.R., and R.M. Brigham (eds.). Research Branch, BC Min. of For., Victoria, BC, Canada.

Hayes, J.P., S. Chan, W.H. Emmingham, J. Tappeiner, L. Kellogg, and J.D. Bailey. 1997. Wildlife response to thinning young forests in the Pacific Northwest. *J. For.* 95:28–33.

Hayes, J.P., S.H. Schoenholtz., M.J. Hartley, G. Murphy, R.F. Powers, D. Berg, and S.R. Radosevich. 2005. Environmental consequences of intensively managed forest plantations in the Pacific Northwest. *J. For.* 103:83–87.

Hayes, J.P., and S.C. Loeb. 2007. The influences of forest management on bats in North America. P. 207–235 in *Bats in forests: Conservation and management*, Lacki, M.J., J.P. Hayes, and A. Kurta (eds.). The Johns Hopkins University Press, Baltimore, MD.

Hein, C.D., S.B. Castleberry, and K.V. Miller. 2009. Site-occupancy of bats in relation to forested corridors. *For. Ecol. Manag.* 257:1200–1207.

Hope, S., and W.C. McComb. 1994. Perceptions of implementing and monitoring wildlife tree prescriptions on national forests in western Washington and Oregon. *Wildl. Soc. Bull.* 22:383–392.

Hunter, J.E., and M.J. Mazurek. 2003. Characteristics of trees used by nesting and roosting Vaux's swifts in northwestern California. *West. Birds* 34:225–229.

Hutto, R.L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conserv. Biol.* 20:984–993.

Jaberg, C., and A. Guisan. 2001. Modeling the distribution of bats in relation to landscape structure in a temperate mountain environment. *J. Appl. Ecol.* 38:1169–1181.

Johnson, J.S., M.J. Lacki, and M.D. Baker. 2007. Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. *J. Mammal* 88:1261–1270.

Kellogg, L.D., P. Bettinger, and R.M. Edwards. 1996. A comparison of logging planning, felling, and skyline yarding costs between clearcutting and five group-selection methods. *West. J. Appl. For.* 11:90–96.

Kennedy, R.S.H., R.J. Pabst, K.A. Olsen, and T.A. Spies. 2010. Potential future dead wood dynamics in a multi-ownership region: The Coastal Province of Oregon, USA. *For. Ecol. Manag.* 259:312–322.

Kotliar, N.B., S. Hejl, R.L. Hutto, V.A. Saab, C.P. Melcher, and M.E. McFadzen. 2002. Effects of fire and post-fire salvage logging on avian communities in the conifer-dominated forests of the western United States. *Stud. Avian Biol.* 25:49–64.

Kunz, T.H., and L.F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. P. 3–89 in *Bat ecology*, Kunz, T.H., and M.B. Fenton (eds.).The University of Chicago Press, Chicago, IL.

Lacki, M.J., and M.D. Baker. 2007. Day roosts of female fringed myotis (*Myotis thysanodes*) in xeric forests of the Pacific Northwest. *J. Mammal* 88:967–973.

Latta, G., and C.A. Montgomery. 2007. Economic considerations in managing for older forest structure. P. 95–104 in *Managing for wildlife habitat in west-side production forests*, Harrington, T.B., and G.E. Nicholas (eds.). US For. Serv. Gen. Tech. Rep. PNW-GTR-695, Portland, OR.

Lewis, J.C. 1998. Creating snags and wildlife trees in commercial forest landscapes. *West. J. Appl. For.* 13:97–101.

Lippke, B., K.W. Zobrist, and K. Ceder. 2007. Issues and alternatives associated with private forest wildlife and riparian habitat management. P. 81–94 in *Managing for wildlife habitat in west-side production forests*, Harrington, T.B., and G.E. Nicholas (eds.). US For. Serv. Gen. Tech. Rep. PNW-GTR-695, Portland, OR.

Lundquist, R.W., and J.M. Mariani. 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range. P. 221–240 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (eds.). US For. Serv., Pac. Northw. Res. Stn., Portland, OR.

Mannan, R.W., E.C. Meslow, and H.M. Wight. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. *J. Wildl. Manag.* 44:787–797.

Mariani, J., and D.A. Manuwal. 1990. Factors influencing brown creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade Range. *Stud. Avian Biol.* 13:53–57.

Martin, K., and J.M. Eadie. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *For. Ecol. Manag.* 115:243–257.

Miller, D.A., E.B. Arnett, and M.J. Lacki. 2003. Habitat management for forest-roosting bats of North America: A critical review of habitat studies. *Wildl. Soc. Bull.* 31:30–44.

Moore, J.R., D.A. Maguire, D.L. Phillips, and C.B. Halpern. 2002. Effects of varying levels and patterns of green-tree retention on amount of harvesting damage. *West. J. Appl. For.* 17:202–206.

Neitro, W.A., V.W. Binkley, S.P. Cline, R.W. Mannan, B.G. Marcot, D. Taylor, and F.F. Wagner. 1985. Snags (wildlife trees). P. 129–169 in *Management of wildlife and fish habitats in western Oregon and Washington*, Brown, E.R. (ed.). R6-F&WL-192-1985, Portland, OR.

Ober, H.K., and J.P. Hayes. 2008. Influence of vegetation on bat use of riparian areas at multiple spatial scales. *J. Wildl. Manag.* 72:396–404.

Occupational Safety and Health Administration (OSHA). 2010. *Logging eTool.* US Department of Labor, Washington, DC. Available online at www.osha.gov/SLTC/etools/logging/manual/felling/hazards.html; last accessed Mar. 21, 2012.

Odion, D.C., and D.A. Sarr. 2007. Managing disturbance regimes to maintain biological diversity in forested ecosystems of the Pacific Northwest. *For. Ecol. Manag.* 246:57–65.

Ohmann, J.L., and K.L. Waddell. 2002. Regional patterns of dead wood in forested habitats of Oregon and Washington. P. 535–560 in *Proc. of the symp. on the Ecology and management of dead wood in western forests*, Laudenslayer, W.F. Jr., P J. Shea, B.E. Valentine, C.P. Weatherspoon, and T.E. Lisle (eds.). US For. Serv. PSW-GTR-181, Albany, CA.

Ormsbee, P.C. 1996. Characteristics, use, and distribution of day roosts selected by female *Myotis volans* (long-legged myotis) in forested habitat of the central Oregon Cascades. P. 124–131 in *Bats in forests symp*. Barclay, R.M.R., and R.M. Brigham (eds.). Research Branch, BC Min. of For., Victoria, BC, Canada.

Ormsbee, P.C., and W.C. McComb. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade range. *J. Wildl. Manag.* 62:596–603.

Parish, R., J.A. Antos, P.K. Ott, and C.M. Di Lucca. 2010. Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia. *For. Ecol. Manag.* 259:633–640.

Patriquin, K.J., M.L. Leonard, H.G. Broders, and C.J. Garroway. 2010. Do social networks of female northern long-eared bats vary with reproductive period and age? *Behav. Ecol. Sociobiol.* 64:899–913.

Pearson, S.F., and D.A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. *Ecol. Applic.* 11:840–853.

Raley, C.M., and K.B. Aubry. 2006. Foraging ecology of pileated woodpeckers in coastal forests of Washington. *J. Wildl. Manag.* 70:1266–1275.

Riley, S.J., D.J. Decker, L.H. Carpenter, J.F. Organ, W.F. Siemer, G.F. Mattfield, and G. Parsons. 2002. The essence of wildlife management. *Wildl. Soc. Bull.* 30:585–593.

Ross, D.W., and C.G. Nima. 1997. Using aggregation and antiaggregation pheromones of the Douglas-fir beetle to produce snags for wildlife habitat. *J. Appl. For.* 12:52–54.

Russell, R.E., J.A. Royle, V.A. Saab, J.F. Lehmkuhl, W.M. Block, and J.R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: Avian responses to prescribed fire. *Ecol. Applic.* 19:1253–1263.

Schreiber, B., and D.S. deCalesta. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. *For. Ecol. Manag.* 50:299–316.

Spies, T.A., and J.F. Franklin. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Nat. Areas J.* 8:190–201.

SPIES, T.A., AND J.F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. P. 91–109 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (eds.). US For. Serv. Gen. Tech. Rep. PNW-GTR-285, Portland, OR.

SUZUKI, N., AND D.H. OLSON. 2007. Options for biodiversity conservation in managed forest landscapes of multiple ownerships in Oregon and Washington, USA. *Biol. Conserv.* 16:3895–3917.

SWANSON, M.E., J.F. FRANKLIN, R.L. BESCHTA, C.M. CRISAFULLI, D.A. DELLASALA, R.L. HUTTO, D.B. LINDENMAYER, AND F.J. SWANSON. 2011. The forgotten stage of forest succession: Early successional ecosystems on forest sites. *Front. Ecol. Environ.* 9:117–125.

TAPPEINER, J.C., D.W. HUFFMAN, D. MARSHALL, T.A. SPIES, AND J.D. BAILEY. 1997. Density, ages and growth rates in old-growth and young-growth forests in western Oregon. *Can. J. For. Res.* 27:638–648.

THOMAS, J.W. (ED.). 1979. *Wildlife habitats in managed forests.* US For. Serv., Washington, DC. 512 p.

THOMAS, J.W., R.G. ANDERSON, C. MASER, AND E.L. BULL. 1979. Snags. P. 60–77 in *Wildlife habitat in managed forests*, Thomas, J.W. (ed.). US For. Serv., Washington, DC.

TURNER, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.

VEGA, R.M.S. 1993. Bird communities in managed conifer stands in the Oregon Cascades: Habitat associations and nest predation. Thesis, Oregon State Univ., Corvallis, OR. 93 p.

WALDIEN, D.L., J.P. HAYES, AND E.B. ARNETT. 2000. Day-roosts of female long-eared myotis in western Oregon. *J. Wildl. Manag.* 64:785–796.

WALTER, S.T., AND C.C. MAGUIRE. 2005. Snags, cavity-nesting birds, and silvicultural treatments in western Oregon. *J. Wildl. Manag.* 69:1578–1591.

WILHERE, G.F. 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. *For. Ecol. Manag.* 174:521–539.

WILLIS, C.K.R., K.A. KOLAR, A.L. KARST, M.C. KALCOUNIS-RÜPPELL, AND R.M. BRIGHAM. 2003. Medium- and long-term reuse of trembling aspen cavities as roosts by big brown bats (*Eptesicus fuscus*). *Acta Chiropterol.* 5:85–90.

WILLIS, C.K.R., AND R.M. BRIGHAM. 2004. Roost switching, roost sharing and social cohesion: Forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behav.* 68:495–505.

WISDOM, M.J., AND L.J. BATE. 2008. Snag density varies with intensity of timber harvest and human access. *For. Ecol. Manag.* 255:2085–2093.

WRIGHT, K.H. AND G.M. HARVEY. 1967. *The deterioration of beetle-killed Douglas-fir in western Oregon and Washington.* US For. Serv. PNW-50, Pac. Northw. Res. Stn., Portland, OR. 12 p.

ZARNCWITZ, J.E., AND D.A. MANUWAL. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. *J. Wildl. Manag.* 49: 255–263.

ZENNER, E.K., S.A. ACKER, AND W.H. EMMINGHAM. 1998. Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon. *For. Ecol. Manag.* 102:75–88.