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RETENTION AND FUNCTION OF LEAVE TREES IN MANAGED FORESTS: MODEL VALIDATION

Final Report

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Executive Summary

Retention and Function of Leave Trees in Managed Forests: Model Validation

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The importance of dead and decaying wood for both ecosystem function and maintenance of biodiversity is now well established. Snags (i.e., standing dead or partially dead trees) are recognized as critical habitat elements required by a diversity of wildlife species within forested landscapes. Depending on condition, snags may be used for feeding, resting, cover, reproduction, or other activities by both vertebrate and invertebrate species. The recruitment and loss of snags on unmanaged forested landscapes is a dynamic process and is tied to successional stage. Cycles of snag production are altered with conversion of forests to management for timber production. Although the importance of retaining deadwood in managed forest to maintain both important physical properties and biodiversity is broadly recognized, establishing comprehensive guidelines has proven difficult because of the complexity of the ecological relationships and the temporal changes in numbers and conditions of snags on managed landscapes. In this report, we first describe the models that are available for understanding the mechanisms that result in creation and loss of snags and for guiding forest management for retention of snags. Next, we evaluate predictions of models for snag retention based on population potentials for primary cavity-nesting birds. These models provide insufficient guidelines for management and we consider other factors important to distribution of cavity-nesting birds. Third, we consider the survival and use of leave trees in riparian managed forests of eastern and western of Washington. Finally, we examine the decay dynamics of artificially created snags and their use by cavity-nesting birds in northeastern Washington.

Given the importance of snags, the challenge for managers is to determine target numbers of snags under varying conditions. We review three general types of models that address the multi-faceted problem of retaining sufficient numbers of snags on managed-forest landscapes in the Pacific Northwest.

The first group of models is broadly based on the assumption that the retention of sufficient habitat for cavity-nesting birds will ensure adequate habitat for other snag dependent species. These models attempt to estimate the densities of snags required to support potential populations of cavity-nesting species. Initial *ad hoc* models developed in

the late 1970s and the 1980s estimate the maximum potential population of each cavity-nesting avian species by dividing the area of habitat by the species' territory size. Management objectives are then defined in terms of the proportion of the maximum potential population to be obtained (e.g., 30, 60, or 90%). Snag requirements per unit area are calculated as a function of the average number of cavities excavated by each species, the number of times a nesting pair will use a given tree, and the ratio of snags without cavities to those with cavities. Because of limited information available at the time, these initial models had to make several broad assumptions about factors underlying avian use of snags. Consequently, they have the potential to underestimate snag requirements for cavity-nesting species. Moreover, these earlier models provide only point estimates for snag sizes and densities, as well as, population response. More recent data-based models attempt to provide probabilistic statements that are applicable to risk assessment. These models extract information from the literature on two data elements, wildlife use of snags and estimates of dead wood across specific forested habitats of Washington and Oregon. To evaluate snag requirements of wildlife at watershed or larger scales, these models construct cumulative species richness curves for increasing snag densities for 3 statistical levels (the mean – 1 SE; the mean; the mean + 1 SE). These models also estimate types and quantities of dead wood based on vegetation surveys and forest inventories across Oregon and Washington. The goal is to provide management guidelines for balancing snag density and dbh, but these models remain in development. Prototype examples to illustrate application of the model point to several potential difficulties stemming from information gaps in the literature to scale of application. The importance of these data-based models is that they attempt to incorporate the biology of all species that use dead and down wood into a management tool.

We also include habitat suitability index (HSI) models developed individually for specific vertebrate taxa in this first group of models. These models were developed to provide managers with a simple tool for evaluating and mitigating the effects of habitat change on wildlife species due to human activities. Based on the underlying assumption that structural features of the habitat directly correlate with carrying capacity, these models attempt to quantify habitat quality for individual species by developing a 0-1 suitability index score. These scores incorporate variables that must be easy to measure, of importance to the species, predictable under future conditions, and responsive to anthropogenic activities. Although HSI models are appealing because of their simplicity, their use in making management decisions without local validation is risky. Procedures to test HSI models have been proposed but have not been widely implemented.

A second group of models addresses an issue that models for snag retention and for habitat suitability do not: maintaining snags over an extended period of time. More reliable projection of long-term snag availability requires additional consideration of patterns of snag creation and loss. Models in this second group are based on a life-table approach and incorporate estimates of recruitment and survival of snags into matrix projections. These matrix projections require accurate estimates of snag recruitment and survival for different tree species, decay classes, and environmental conditions. Failure to account for factors contributing to changing rates can lead to varying predictions in snag numbers. Nonetheless, these models are useful in projecting how snag populations will change with changes in model parameters.

The third group of models we consider can be used to evaluate the effects of management strategies on the population dynamics of specific cavity-nesting species. This issue becomes critically important for endangered species. These models are similar to those designed to model snag population dynamics, but the transition matrix contains information on fecundity, mortality, and, if necessary, development of the cavity-nesting species. Although such models can project the number of individuals in each age class at the next census interval, the important focus is on the sensitivity of population growth rates to changes in model parameters. The potential effects of different management options on various aspects of the species' life history (e.g., nesting success vs. adult survival) can be assessed.

Of the various models available to guide snag management, only potential population models have found their way into regulatory practice. These *ad hoc* models have recently been criticized, but little field evaluation of their utility is available. Such evaluation requires that the relationship between snag density and stand use by primary cavity-nesting species be determined. We examined this relationship for the eastside version of this model at the Turnbull National Wildlife Refuge, Cheney, WA. We selected 8 stands of ponderosa pine forest that covered the range of variation in density and distribution of snags at the refuge. Transects with from 6 to 12 point-count stations were established on each stand. We mapped all snags within 120 m of the transects using GPS, and recorded dbh, height, decay class on a 3-point scale, and evidence of foraging and cavity excavation. Live trees were mapped in 30-m radius circles centered on each point-count station and their diameter at breast height (dbh) was recorded. In 1998 and 1999, point-count surveys were conducted 7 times per stand from early May until mid-June. Nest surveys were also conducted throughout the same period. We examined the relationships between species richness and relative abundance of cavity-nesting species and distribution and density of snags using traditional stepwise and logistic regression models.

The snag requirements recommended by the model indicated that relatively low percentages of maximum population for Downy and Hairy Woodpeckers would be maintained, whereas Northern Flickers could be supported at much higher population levels. This result was more or less consistent with the trend in relative abundance observed. When model parameters were modified to better reflect conditions at the refuge, however, snag densities were expected to maintain high population levels of all 3 species of primary cavity nester. Other inconsistencies in the distributions of these species indicate that management based on snag density alone is likely to be insufficient.

Consequently, we examined other aspects of forest structure to better understand the resulting distributions of cavity-nesting species. Stand structure varied widely from heavily stocked (721 trees/ha) to more open overstory (32 trees/ha). Live trees and snags were more highly aggregated than expected by chance. Sizes of snags in the first two decay classes were skewed towards smaller diameter trees. Although these small-diameter snags were used for foraging, they do not remain standing long and are not suitable for cavity nests. Large diameter trees with more advanced decay were used most frequently for cavity excavation. Nearest-neighbor distances for trees with cavities were greater than those for all trees in the same decay class. We recorded 6,247 observations of 113 bird species over the 2 years. About 42% of these observations were primary cavity-nesting species including nuthatches (3 species), woodpeckers (4), and chickadees (2), and three secondary cavity-nesting species.

Species richness and relative abundance of cavity nesters was lower in heavily stocked stands and increased with more open canopy. Several species were associated with characteristics of snags including the number of cavities. Management activities that open the overstory and shift the size distribution of live tree towards larger diameters will directly benefit cavity-nesting species. This strategy will eventually allow recruitment of the large diameter snags needed to sustain cavity-nesting species.

Timber harvest prescriptions often vary between habitat types. For example, most state and federal agencies have different leave tree requirements in riparian as compared to upland habitats. The physical and biological features that characterize riparian areas might alter patterns of snag recruitment and loss observed in other habitats. We examined changes in the numbers of live and standing dead trees by resampling Riparian Management Zones (RMZs) in western and eastern Washington that had been surveyed after harvest from 4 to 10 years earlier in two studies using different protocols. First, the Washington Department of Fish and Wildlife characterized the vegetative and structural features of Riparian Management Zones following timber harvest to determine compliance with new state regulations in 1988-1990. Second, in 1991-1996, we conducted an experimental investigation of the effectiveness of Riparian Management Zones in providing habitat for terrestrial wildlife. We measured vegetative and structural features of riparian habitats on unharvested controls, sites harvested according to state mandated RMZs, and sites harvested according to a modified buffer prescription designed to protect key wildlife habitat features. In addition, we examined snags for presence of foraging holes and nesting cavities. We found that densities of standing dead trees of all size and decay classes declined on all RMZs harvested according to State guidelines. Densities of medium- and large-sized snags remained constant on sites with modified riparian buffers of the experimental study. Densities of live deciduous trees increased and densities of live coniferous trees did not change on western Washington RMZs. Densities of live coniferous trees decreased on RMZs harvested according to State guidelines for eastern Washington and the declines were more pronounced than on sites with modified riparian buffers. In western Washington the 9 tree species differed with respect to the frequency of foraging activity. Red alder was the only deciduous trees with either foraging or nesting sign. The proportion of Douglas-firs with foraging sign was greater than the proportion of either western hemlock or western red cedar. None of the smallest size class of trees had any sign of foraging or nesting. Frequency of sign of foraging activity increased between the smallest and next larger size classes, but then leveled off. In contrast, evidence of nesting activity was limited to larger snags. With respect to decay class, sign of nesting activity was limited to snags. In eastern Washington there were no differences between tree species with respect to frequency of foraging or nesting sign. Although frequency of nesting sign was greater in larger trees, foraging sign was observed on all size classes. Foraging sign was observed on snags of different decay classes, but nesting sign was only observed on the older snags.

Given local habitat conditions and past harvest histories, attaining targeted numbers of snags might prove difficult under certain managed forest conditions. To offset the loss of snags from logging, managers have implemented artificial creation of snags to help maintain cavity-nesting species. We compared two methods of snag creation: cutting tops and girdling. A total of 1,189 trees of 10 coniferous species was treated between 1991 and 1997 on timber sales in northeastern Washington. We monitored 1,108 trees at approximately 2-year intervals to determine degree of decay (on a nine-point scale), signs of foraging, and presence

of cavities. Nearly 7% of the girdled trees were still alive after 4 to 7 years, whereas all but one topped tree died. Initial decline (i.e., reaching decay class 2) was faster for ponderosa pine and western larch than for Douglas-fir. Western larch lost bark (decay class 4) earlier than other species. Topped trees declined more quickly than girdled trees, but girdled trees reached decay class 4 faster. The proportion of trees with evidence of foraging and cavities increased with decay class. Western larch was used more for foraging than other species, and there was no effect of treatment on foraging use. In contrast, topped Douglas-fir and grand fir were used more for foraging than girdled trees at later decay classes. Cavities were observed only in trees that were topped. Interspecific differences in presence of cavities were not observed before decay class 4; western larch had the lowest frequency of cavities, whereas grand fir had the highest. The use of specific treatments for creating snags and selection of species may make these habitat elements available over long time periods.

Chapter 1

Introduction to the Research

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The importance of dead and decaying wood for both ecosystem function and maintenance of biodiversity is now well established (Rose et al. 2001, Marcot in press). Snags (i.e., standing dead or partially dead trees) are recognized as critical habitat elements required by a diversity of wildlife species within forested landscapes (reviews in Thomas et al. 1979, Neitro et al. 1985, McComb and Lindenmayer 1999, Rose et al. 2001). Depending on condition, snags may be used for feeding, resting, cover, reproduction, or other activities by both vertebrate and invertebrate species. Based on studies in Oregon and Washington, 96 species of terrestrial vertebrates are known to use snags and 93 of these species occur in forested habitats (4 amphibian, 63 avian, and 26 mammalian species–Rose et al. 2001). Invertebrates, especially beetles, are important because they aid in the decomposition of snags by boring into the tree and introducing decay fungi (Müller et al. 2002), and because they provide an important food source to many vertebrate species. Terrestrial vertebrates differ in their degree of dependence on snags from obligate to opportunistic use. Many species require cavities in partially live or dead trees for nesting. Species that produce cavities (e.g., woodpeckers) are called primary cavity nesters, whereas species that use abandoned or natural cavities are called secondary cavity nesters. Because a large percentage of avian species (30-45%–Neitro et al. 1985) may use cavities, the loss or absence of snags may result in reduction or local extirpation of these species (Morrison and Meslow 1983). In managed forest landscapes, timber harvesting activities have the potential to greatly reduce numbers of snags. Consequently, guidelines for retaining snags and green recruitment trees have been developed by many resource agencies (e.g., Oregon Department of Forestry 1997, Washington State Department of Natural Resources 2000).

Establishing comprehensive guidelines is difficult because of the complexity of the ecological relationships and the temporal changes in numbers and conditions of snags on managed landscapes. The suitability of a snag will vary for different wildlife species depending on the diameter, height, degree and type of decay, and species of tree. The general changes that occur as a tree declines to death and ultimately decomposes have been described (Thomas et al. 1979, Cline et al. 1980, Neitro et al. 1985, Bull et al. 1997). Over time, deterioration is evidenced by loss of limbs, branches, and bark; breakage of top; reduction in height; sloughing of sapwood; and decay of heartwood. The rate of decay of a tree will depend on species and size, and local conditions also can affect this rate (Thomas et al. 1979, Harmon et al. 1986, Morrison and Raphael 1993). The cause of mortality also may affect the rate of decay (discussed further below). As decay progresses, snags change from "hard" to "soft." Hard snags consist largely of sound wood and may be marketable; some wildlife species (e.g., pileated woodpecker–Neitro et al. 1985) will only excavate in hard snags. The advanced decay of soft snags makes them unsuitable for commercial uses, but these snags are an essential resource because some snag-dependent species can excavate only soft wood (e.g., red-breasted nuthatch–Steeger and Hitchcock 1998).

The recruitment and loss of snags on forested landscapes is a dynamic process and is tied to the successional stage of a forest. In unmanaged stands, succession begins when catastrophic events such as fires kill a large number of trees (Hansen et al. 1991). For a mature forest (>100-200 years), the snags and remaining live trees will be of large size and will provide habitat for snag-dependent species many years into the future as the forest regenerates (Cline et al. 1980). Mortality in younger stands (<80 years) is due primarily to competition for resources and increases the density of snags, but their small diameter and high rate of decay make them of limited use for cavity nesters (Maser et al. 1988). As stands continue to age, snag densities fall, but both the mean size and size distribution of snags increase (Cline et al. 1980). Remnant snags are eventually replaced by mortality of trees in the replacement cohort. Because snag creation may be substantially greater than snag loss in late successional unmanaged forests, maximum abundance of primary cavity nesters may be obtained (Newton 1994).

These cycles of snag production have been altered with conversion of forests to management for timber production. Clearcutting, short rotation times (<80 years), removal of dead trees, and prescribed burns all act to limit the availability of large snags in managed forest landscapes (Cline et al. 1980). Managed forests in Washington State encompass about 17,305,000 acres (7,003,333 ha) of which about 63% are on State and private lands (Washington Department of Natural Resources 1992). Although remnant large snags occur at low density in many of these forests (Campbell et al. 1996), their availability in the future will require active management. This requires that biologically sound guidelines for maintaining a minimum number and size of snags be developed.

Several studies have shown a relationship between number of snags and abundance of wildlife species that utilize snags (Raphael and White 1984, Zarnowitz and Manuwal 1985, Lundquist and Manuwal 1990, Saab and Dudley 1998). Absence of snags has been related to loss of snag-dependent species (Scott 1979, Zarnowitz and Manuwal 1985). An objective of recent forest management has been to ensure that a minimum number of snags will be available to maintain some percentage of the maximum population of primary cavity nesters (Thomas et al. 1979, Neitro et al. 1985). Models that incorporate specific requirements of wildlife species have been developed (Thomas et al. 1979) and extended for management of multiple species (Neitro et al. 1985). These models require data on bird density, number of cavities excavated by a pair per year, number of snags used, and mean size of snags required. Consequently, their application requires good site-specific data, which often will not be available. These models assume that foraging requirements are unimportant, largely because of a lack of data. Because the models have been developed for primary cavity nesters, there is a need to know whether secondary cavity nesters are maintained as well. A new modeling approach is currently being developed that incorporates the growing body of knowledge on the ecology of deadwood (Decaid Advisory Model–Marcot et al. in press).

One component of snag management that is missing from the above models is consideration of the creation and loss of snags over time. Application of matrix population models (Caswell 1989) such as the Leslie matrix has been useful in understanding the temporal dynamics of snag populations (Raphael and Morrison 1987, Morrison and Raphael 1993). These models consider the recruitment of snags, the probability of transition from one decay class to the next, and snag mortality. The initial attempt to use such models to predict the numbers of snags in each decay class assumed that estimates of the model parameters remain constant (Raphael and Morrison 1987). Morrison and Raphael (1993), however, using data obtained over a longer time span, showed that this assumption was invalid. They showed that their matrix model predicted changes in snag density only if the specific environmental causes of mortality were incorporated. Their work indicates the need to better understand species-specific patterns of snag creation and the factors that result in tree mortality. Only a few such studies have been conducted (e.g., Harrington 1996, Huggard 1999).

Reduction of the loss of snags during harvesting operations can be achieved by preventing the loss of snags that are most likely to remain standing (Huggard 1999). Another approach is to buffer selected snags from harvesting. Buffering of snags may be particularly valuable in riparian areas, which may have the highest density of snags after adjacent upland harvest. Snags protected in this way might be less susceptible to blowdown, and allow maintenance of suitable snags in the system over a longer period of time.

In managed forests, the availability and creation of snags may be too low to provide sufficient habitat for snag-dependent species. One approach to this problem is to leave green reserve trees in harvest units and create snags artificially. For example, the Forest Plan for the Colville National Forest prescribes maintaining dead and defective tree habitat capable of supporting at least 60% of the potential population of primary cavity excavators over areas the size of harvest units (M. Borysewicz, USDA Forest Service, personal communication). To meet these requirements an average of 1.8 snags/acre must be provided. If there are insufficient trees in a unit to meet this goal, green trees are marked for snag creation. Trees are selected for marking based on size, species, and location in the unit. These trees are ultimately girdled or topped to produce snags. The value of snags produced in this way is not well documented. Franklin et al. (1987) indicated that a prolonged death from disease or insects would create snags that had long-term value to wildlife. Decay in girdled trees usually proceeds from the outside inwards, producing a snag with soft sapwood and hard heartwood. Miller and Miller (1980) consider this less desirable for cavity nesters than when decay softens the heartwood first. Bull and Partridge (1986) found that girdling was less effective than topping trees. Conner et al. (1983) reported that girdled southern red oaks became suitable for nesting and foraging by woodpeckers. Additional evaluation of the recruitment and survival of artificially created coniferous snags, and the use of these snags by wildlife species would be beneficial.

In the following chapters, we first describe the models that are available for understanding the mechanisms that result in creation and loss of snags and for guiding forest management for retention of snags (Chapter 2). Next, we document our attempts to relate distribution and use by primary cavity nesting birds to the density of snags, and to evaluate predictions of current models for snag retention (Chapter 3). We then consider the survival and use of leave trees in riparian managed forests east and west of the Cascade Crest (Chapter 4). Finally, we examine the decay dynamics of artificially created snags and their use by cavity-nesting birds

(Chapter 5). To ensure that the chapters are self-contained, we have allowed some redundancy. A bibliography containing over 1300 references to the literature on the biology and management of dead trees and cavity-nesting birds is available on the web (http://home.att.net/~tfwsnags) or from the authors.

Please note that the methods vary between studies, particularly for classification of snags. This is due primarily to our incorporation of data sets that were developed by other workers. For example, the program that the USDA Forest Service initiated for monitoring artificially created snags (Chapter 5) adopted the snag classification of Thomas et al. (1979), which uses 9 classes. The Washington Department of Wildlife used 6 condition classes to characterize trees and snags (Washington Department of Wildlife 1990) (Chapter 4).

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Literature Cited

Bull, E. L., C. G. Parks, and T. R. Torgerson. 1997. Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391. Pacific Northwest Research Station, Portland, Oregon.

Bull, E. L., and A. D. Partridge. 1986. Methods of killing trees used by cavity nesters. Wildlife Society Bulletin 14:142-146.

Campbell, L. A., J. G. Hallett, and M. A. O'Connell. 1996. Conservation of bats in managed forests: roost use by *Lasionycteris noctivagans*. Journal of Mammalogy 77:976-984.

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Massachusetts.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests. 44:773-786.

Conner, R. N., J. C. Kroll, and D. L. Kulhavy. 1983. The potential of girdled and 2,4-D injected southern red oaks as woodpecker nesting and foraging sites. Southern Journal of Applied Forestry 7:125-128.

Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1:5-18.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41:382-392.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Harrington, M. G. 1996. Fall rates of prescribed fire-killed ponderosa pine. USDA Forest Service Research Paper INT-RP-489. Intermountain Research Station, Ogden, Utah.

Huggard, D. J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9:1009-1016.

Lundquist, R., and D. A. Manuwal. 1990. Seasonal differences in foraging habitat by cavity-nesting birds in the southern Washington Cascades. Studies in Avian Biology 13:218-225.

Marcot, B. G. in press. An ecological functional basis for managing decaying wood for wildlife. in P. J. Shea, W. F. Laudenslayer, Jr., B. Valentine, and C. P. Weatherspoon, editors. Proceedings of the Symposium on The Ecology and Management of Dead Wood in Western Forests, Reno, Nevada, USDA Forest Service General Technical Report PSW-GTR-XXX. Pacific Southwest Research Station, Albany, California.

Marcot, B. G., K. Mellen, J. L. Ohmann, K. L. Waddell, E. A. Willhite, B. B. Hostetler, S. A. Livingston, C. Ogden, and T. Dreisbach. in press. DecAID -- work in progress on a decayed wood advisory model for Washington and Oregon forests. USDA Forest Service Research Note PNW-RN-XXX, Pacific Northwest Research Station, Portland Oregon.

Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin. 1988. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.

McComb, W. C., and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 in M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Miller, E., and D. R. Miller. 1980. Snag use by birds. Pages 337-354 in R. M. Degraff, technical coordinator. Management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86. Odgen, Utah.

Morrison, M. L., and E. C. Meslow. 1983. Avifauna associated with early growth vegetation on clearcuts in the Oregon Coast Ranges. USDA Forest Service Research Paper PNW-305. Pacific Northwest Research Station, Portland, Oregon.

Morrison, M. L., and M. G. Raphael. 1993. Modeling the dynamics of snags. Ecological Applications 3:322-330.

Müller, M. M., M. Varama, J. Heinonen, and A. Hallaksela. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. Forest Ecology and Management 166:165-181.

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). Pages 129-169 in E. R. Brown, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1 – Chapter Narratives. USDA Forest Service R6-F&WL-192-1985. Pacific Northwest Region, Portland, Oregon.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265-276.

Oregon Department of Forestry. 1997. Oregon Forest Practices Act - Selected Statutes: Section 9, Chapter 9, Special Session Oregon Laws 1996. Leaving snags and downed logs in harvest type 2 or type 3 units; green trees to be left near certain streams. http://www.odf.state.or.us/FP/RULES/fpa-statute.htm

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86:1-66.

Raphael, R. G., and M. L. Morrison. 1987. Decay and dynamics of snags in Sierra Nevada, California. Forest Science 33:774-783.

Rose, C. L., B. G. Marcot, T. K. Mellen, J. L. Ohmann, K. L. Waddell, D. L. Lindley, and B. Schreiber. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. Pages 580-623 in D. H. Johnson and T. A. O'Neil, editors. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Saab, V. A., and J. G. Dudley. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. USDA Forest Service Research Paper RMRS-11. Rocky Mountain Research Station, Fort Collins, Colorado.

Scott, V. E. 1979. Bird response to snag removal in ponderosa pine. Journal of Forestry 77:26-28.

Steeger, C., and C. L. Hitchcock. 1998. Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. Journal of Wildlife Management 62:1349-1358.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 in J. W. Thomas, editor. Wildlife habitats in managed forests; the Blue Mountains of Oregon and Washington, USDA Forest Service Agricultural Handbook No 553. Washington, D.C.

Washington Department of Natural Resources. 1992. Forest resource plan: policy plan. Washington Department of Natural Resources, Olympia, Washington.

Washington Department of Wildlife. 1990. Characterization of riparian management zones and upland management areas with respect to wildlife habitat: field procedures handbook, second edition. TFW-003-90-005, Washington Department of Wildlife, Habitat Management Division, Olympia, Washington.

Washington State Department of Natural Resources. 2000. Washington Forest Practices Rules, Chapter 222-30 WAC, Timber Harvesting. http://www.wa.gov/dnr/htdocs/fp/fpb/222-30.html

Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds of northwestern Washington. Journal of Wildlife Management 49:255-263.

Chapter 2

Models for Leave Tree Prescriptions in the Pacific Northwest: a Comparative Review

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Introduction

The importance of retaining deadwood in forest ecosystems to maintain both important physical properties and biodiversity is well established (Chapter 1, Rose et al. 2001). Until recently, most management strategies for retaining standing dead trees (i.e., snags) to achieve targets for biodiversity on managed forest landscapes have focused on cavity-nesting birds, particularly those that excavate cavities (i.e., primary cavity-nesting species including woodpeckers and nuthatches). The retention of sufficient habitat for these species has been assumed to ensure adequate habitat for other snag dependent species (Marcot in press).

Several general information needs must be met before developing appropriate management strategies based on cavity-nesting species. First, the local distributions of cavity-nesting species must be known, as well as their use of different forest types. Second, the resource requirements of individual species must be identified. These include differences in the characteristics of snags used for nesting and foraging, such as, species, physical condition (e.g., degree of decay and diameter), density, and distribution of snags. Other aspects of the ecology of cavity-nesting species including, for example, territory sizes and densities, may also be required.

Although this information may be sufficient to establish guidelines for the retention of snags directly following harvest, it may be insufficient for long-term success without additional consideration of patterns of snag creation and loss. Recruitment and longevity of snags may depend on the factors causing tree mortality (Morrison and Raphael 1993). The timeframe over which snags will be suitable for use by wildlife will depend on species-specific rates of (Hallett et al. 2001) and types of decay (Bull et al. 1997).

In this chapter we review the types of models that have been developed to address the multi-faceted problem of retaining sufficient numbers of snags on managed-forest landscapes in the Pacific Northwest. These models can be roughly divided into the three groups. First, we consider models that can be used to estimate the densities of snags required to support populations of cavity-nesting species. We include habitat suitability models developed individually for specific vertebrate taxa in this category. Second, we discuss models that consider the probability of recruitment and survival of snags. At this point in time, there has been little attempt to merge the two aspects of snag biology incorporated by these models (but see Marcot's (1992) Snag Recruitment Simulator). Third, we consider models for evaluating the effects of management strategies on the population dynamics of cavity-nesting species.

Snag retention

Ad hoc models

The first published attempt to provide a biological basis for determining the numbers and types of snags to retain on managed lands in the Pacific Northwest was by Thomas et al. (1979). Although their model can be adapted for other regions, they parameterized it with data from the Blue Mountains of Washington and Oregon. Their approach estimates the maximum potential population of each cavity-nesting avian species by dividing the area of habitat by the species' territory size (i.e., defended area around nest site). Management objectives are then defined in terms of the proportion of the maximum potential population to be obtained (e.g., 30, 60, or 90%). The snag requirement for each nesting pair is calculated as a function of (1) the average number of cavities excavated each year by each species, (2) the observation that an individual tree will usually be used only once by a nesting pair, and (3) the ratio of snags without cavities to snags with cavities.

Thomas et al. (1979) provide tables of estimated snag requirements based on their model for several plant communities representative of the Blue Mountains. Spreadsheets for calculating snag requirements and that allow changes in the assumptions are available from Marcot (1992). Data required for spreadsheets include (1) the cavity-nesting species and (2) the desired population level.

Neitro et al. (1985) modified the model of Thomas et al. (1979) for application in forests west of the Cascade Crest. As in the Thomas model, the west side model makes several important assumptions. First, providing habitat for woodpeckers during the breeding season will ensure that the requirements of other snag-dependent species will be met. Second, the snag requirements of all cavity-nesting species equal the sum of their individual requirements. Third, primary cavity nesters that have minimum snag diameter requirements will not use smaller diameter snags for nesting. However, larger snags can be substituted for smaller snags. Fourth, an individual snag will be used by only one pair of woodpeckers in a year, although snags may be reused in subsequent years.

The number of snags (S) necessary to be retained on 100 acres to support woodpeckers was calculated as:

$$S = (D) \times (C) \times (X),$$

where D is the maximum density (number of woodpecker pairs for 100 acres), C is the number of cavities excavated per pair per year, and X is a correction factor representing the total number of the snags including those used for cavities and those necessary to support the pair over the planning interval. Neitro et al. (1985) used estimates of maximum density, because Raphael and White (1984) indicated that minimum territory sizes, as used by Thomas et al. (1979), have rarely been determined. However, estimates of maximum densities are quite variable, and Neitro et al. (1985) selected values that were considered "reasonable." Species varied in the numbers of cavities excavated per pair per year from 1 to 5. The correction factor (X) was set to 4 based on Raphael and White (1984), who reported three potentially suitable snags without evidence of previous nesting for each snag that was excavated. Site-specific data, of course, would be preferable. Using this simple formula, Neitro et al. (1985) provided snag retention estimates for Douglas-fir forests.

These models have been criticized as additional information has become available in the subsequent 20 years (review in Rose et al. 2001). First, calculating the number of the snags based on their biological potential may underestimate the numbers that are required to retain primary cavity-nesting species. Second, if management objectives are set too low (e.g., 40 %), viable populations are unlikely to be maintained. Third, secondary cavity-nesting species may have requirements for numbers and sizes of snags that exceed those of primary cavity nesters. Fourth, recent evidence suggests that clumping of snags may be required by some species, and uniform distributions of snags may be inappropriate. Fifth, decaying wood including the parts of live trees, hollow trees, natural cavities, and peeling bark provide important resources for some species, and management of these structures should also be considered. Sixth, wildlife species associated with deadwood other then cavity nesters may play significant roles in maintaining biodiversity and in ecosystem function.

Data-based models

The DecAID advisory model, which its authors hope will supplant the models of Thomas et al. (1979) and Neitro et al. (1985), is still in development, but sufficient information is available to outline its structure (Marcot in press, Marcot et al. in press-a, Marcot et al. in press-b, Mellen et al. in press). In addition to potentially underestimating snag requirements for cavity-nesting species, earlier models provide only point estimates for snag sizes and densities, as well as, population response. The DecAID model attempts to provide probabilistic statements that are applicable to risk assessment. Although the next generation of models considers the roles of deadwood in ecological systems in a broader context (e.g., in the decomposition process and as downed wood), given the focus of this review we limit our consideration to standing dead trees and terrestrial vertebrates.

The DecAID model is a knowledge-based approach based on a literature review that incorporates most of the existing data on the relationships between wildlife and dead wood for Washington and Oregon. In contrast to the more general geographic framework of the earlier models (i.e., forests east and west of the Cascade Crest), the DecAID model considers both wildlife habitat type and forest structural stage across several geographic subregions. Data are available for 7 forest types as defined in the Oregon-Washington Species-Habitat Project (SHP–Johnson and O'Neil 2001). Because of limitations in the original data, only 2 structural stages are considered: post-disturbance (i.e., post-fire or post-harvest) and forested (Marcot et al. in press-a). The model incorporates two data elements: wildlife use of snags and estimates of dead wood. We consider both components in turn.

First, descriptions of snags (e.g., species, density, decay class, diameter, height, forest structure, habitat type, and geographic location) and their use by wildlife species (e.g., breeding, feeding, resting) were abstracted from each study. Data tables were then constructed for each wildlife taxon to summarize its use of each wildlife habitat and structural type in which it occurred (Marcot et al. in press-a). Mean values (± 1 SE) were determined for snag density and dbh for each taxon. Other relevant information about study design and analysis were also recorded so that values from similar studies could eventually be weighted by sample size. An outline of the statistical methods used to combine data from different sources is provided in Marcot et al. (in prep). The authors considered the mean – 1

SE, the mean, and the mean + 1 SE to represent values of low, moderate, and high statistical reliability for each variable. The species were then ranked by increasing values of each variable for each statistical level. Cumulative species richness curves were then generated for increasing values of snag density or dbh for each statistical level. These curves are the centerpiece for evaluation of the snag requirements of wildlife at watershed or larger scales. Because the curves are composites of studies conducted under varying conditions, they are meant to reflect potential relationships and not the specific patterns that may be found in a region.

Second, data from vegetation surveys and forest inventories on federal lands for 9 of the 31 major SHP habitat types were summarized to estimate types and quantities of dead wood on forested lands across all ownerships in Oregon and Washington (Ohmann and Waddell. in press). These data were also identified by forest structural stage. To estimate historic conditions for dead wood, areas assumed to be unharvested were used. This approach appears to be better suited for forests west of the Cascade crest where fire suppression has been less important than for drier forests east of the crest. This approach has further difficulties for estimating natural conditions in eastern forests because of the influence of insect outbreaks and salvage logging (Marcot et al. in press-a). This is unfortunate because, where possible, comparisons of wildlife use of snags between harvested and unharvested stands would provide insight into how the quantities and types of snags required by wildlife change with forest structure.

Marcot et al. (in press-a) argue that by comparing the data for wildlife use with the inventory data, they can derive "a reasonable set of potential management guidelines for balancing snag density and dbh." Until the DecAID model is actually available, it will not be possible to determine the veracity of this statement. However, Marcot et al. (in press-a) provide some illustrative examples of the application of their approach in developing and interpreting cumulative species curves. These examples consider both snag density and snag diameter for Eastside Mixed Conifer Forest and Westside Lowland Conifer/Hardwood Forest in Washington and Oregon. The examples in Marcot et al. (in press-a) illustrate the mechanics of extracting data from the original studies and developing average values for each species or group. Moreover, these examples indicate six types of difficulties that may be encountered.

First, although the authors attempted to incorporate all relevant studies in their review, treatment across geographical areas is uneven. Some forest types have been little studied, whereas others have received considerable attention. For example, data were unavailable for Eastside Mixed Conifer Forest. This necessitated that research from a single study in Idaho be used to develop cumulative species richness curves. For other forest types, multiple studies were available, but data on snag density and size were reported in different ways. More than one cumulative species curve for each variable may be necessary to account for these differences. Different managers may interpret the data in different ways. Second as the authors acknowledge, interpretation of these cumulative species curves to set management objectives will not be simple. Although the authors contend that the DecAID model is appropriate at scales of the watershed or greater, actual application will typically be at the stand level. Such management will require greater understanding of local conditions and requirements of snag-using species. A manager might select, for example, a level of snag density presumed to maintain a given subset of species. Similarly, an average value for snag dbh could be determined. These independent selections might inadequately represent the distributions of snag density and size required by a set of species that will differ in their specific requirements. Third, guidelines for selecting an appropriate significance level are vague. The authors suggest that statistical confidence may be appropriate for protected areas, whereas low levels of confidence may be appropriate for managed forests. Such carte blanche assessments are premature, however, given that the adequacy of these cumulative species curves has yet to be determined. Fourth, the issue of distribution degree of clumping of snags on landscape requires further consideration. Based on a single unpublished study, the authors contend that managers will not need to be concerned about the distribution of clumps of snags and can be opportunistic in locating snags according to site conditions. Fifth, the authors recognize that the DecAID model will be used for the management of individual stands, and that such stands may have inadequate numbers of snags. Consequently, they recommend that planning take place over broader areas, such as watersheds. This strategy may be hard to implement in areas of mixed ownership. Sixth, the model does not consider loss or recruitment of snags. Temporal dynamics will have to be considered by managers using the best information available for their geographic area.

The importance of the DecAID model is that it attempts to incorporate the biology of all species that use dead and down wood into a management tool. Clearly, this provides a broader view for management of dead wood. Adequacy of the model will depend on the validity of the underlying data and their interpretation. Application of the model will depend on the abilities of managers to formulate management plans using more complicated model outputs.

Habitat suitability index models

Habitat suitability index (HSI) models were developed to provide managers with a simple tool for evaluating and mitigating the effects of habitat change on wildlife species due to logging and other human activities (U. S. Fish and Wildlife Service 1981). The underlying assumption is that structural features of the habitat directly correlate with carrying capacity. These models attempt to quantify habitat quality for individual species by developing a 0-1 index (higher values indicate better habitat quality) that incorporates one or more suitability index scores for appropriate life requisites (e.g., reproduction and foraging). Each suitability index score also is estimated on a 0-1 scale and is based on habitat variables that are selected under several constraints. The variables must be easy to measure or estimate, of importance to the species, predictable under future conditions, likely to change from anthropogenic activities, and likely to be affected by management decisions (Schamberger and O'Neil 1986).

Consider, for example, the structure of the model developed for the Downy Woodpecker (Schroeder 1983b), which considers the entire geographic range of the species in North America. Food and reproduction were identified as the key life requisites for the model. Based entirely on work done in the eastern U.S., habitat suitability for food is assumed to initially increase with increasing basal area, level off, and then decline at high levels of basal area. Habitat suitability for reproduction is modeled as a linear function of snag availability. Forests lacking snags have a suitability of 0, whereas those with >5 snags (>15 cm dbh) per acre have a suitability of 1. The upper threshold was based on estimates in Thomas et al. (1979) and Evans and Conner (1979) calculated from territory size, as discussed above. The final suitability value is the lesser of the two values for food and reproduction.

The appeal of the HSI modeling approach is its simplicity, which is well illustrated by the above example. HSI models were promoted by the U.S. Fish and Wildlife Service in the early 1980s. Since that time, models have been prepared for a variety of the fish and wildlife species including several cavity-nesting species (Schroeder 1983a, c, b, Sousa 1983b, a, Sousa 1987). The original models have not been updated since their publication. While HSI models are appealing because of their simplicity, application of the original, generalized models in making specific management decisions without local validation is inappropriate. The primary problems with HSI models are of two types. First, the underlying assumptions of the models may be false. Measures of population performance (e.g., abundance or physiological condition) are assumed to be related to structural habitat characteristics, but this need not be the case (Van Horne 1983). Habitat relationships are assumed to be linear and univariate, and to be static over time and space and for all life-history stages of a species. Interspecific interactions (e.g., competition and predation) are assumed to be of minor importance. Second, models were typically developed using a variety of data sources that vary in quality, sample size, and geographic scope. Applicability to a particular habitat type or region is thus not assured. Clearly model testing and validation are necessary if such models are to be appropriately used.

Procedures for testing HSI models were presented by Schamberger and O'Neil (1986). Important model components that should be considered are (1) model assumptions, especially about the input variables, interrelationships of the input variables, and model outputs, (2) variability of input data, (3) statistical validity of tests, (4) spatial scale of the model, (5) range of HSI values, (6) the population index, and (7) the duration of data collection (Roloff and Kernohan 1999). Unfortunately, a review of attempts to evaluate HSI models by Roloff and Kernohan (1999) indicates that few studies have adequately addressed more than three of these components. In particular, examination of the effects of changes in input variables on model outputs was neglected in most studies.

A final consideration is the inadequacy of single-species models for addressing broader biodiversity concerns. Incorporation of single-species HSI models into multi-species models, however, presents further difficulties (Van Horne and Wiens 1991). Because HSI models use variables that are chosen to be simple and specific for each species, there may be little overlap in variables across species. There are also problems associated with geographical differences in forest habitats used by different species.

In sum, HSI models developed by the U.S. Fish and Wildlife Service are poorly suited to provide a basis for management of snags and deadwood in Pacific Northwest forests.

Survival and recruitment of snags

Models for snag retention and for habitat suitability do not address the issue of maintaining snags over an extended period of time (e.g., length of a rotation). We would like models that can project the number of snags at various time intervals into the future. Such models require 2 components. Both the rate that snags will be lost and the rate that trees will die and create new snags must be estimated. These loss (i.e., death) and recruitment (i.e., birth) rates, of course, are the basis for matrix population models that project population size into the future (Caswell 1989).

Two approaches have been used for estimating the rate of loss or fall rate of snags. First, a group of snags may be marked and their fate followed over time (i.e., a cohort approach). For example, Raphael and Morrison (1987) determined the fate and decay class of snags that had been marked 5 years earlier in the Sierra Nevada of California. The probability of a snag remaining in the same decay class, advancing to a later decay class, or falling was then calculated. Raphael and Morrison (1987) found results were similar within genera (i.e., *Pinus* or *Abies*), but differed between genera (i.e., pines decayed faster than firs). Second, fall rates may be estimated by examining the current age distribution of the population (i.e., a time-specific approach). Huggard (1999) demonstrated this approach in a study of subalpine fir. He first determined relative abundance of live trees and snags in three decay classes. A cross-dating method that correlates ring widths of a snag to those of known age trees was used to determine the year each snag died. These data allowed calculation of the age of each snag. Plots of the cumulative age distributions for each decay class were used to determine the average age of a snag at the transition from one decay class to the next. The relative abundances and time intervals in each decay class were used to estimate fall rates for each class. The relative abundance per year is the relative abundance of a decay class divided by the time interval in that class. By plotting the logarithm of the relative abundance against the midpoint of the age distribution for the class, Huggard (1999) calculated the rate of fall between classes by estimating the slope of the line drawn between adjacent classes.

Recruitment of snags has been determined by counting the number of new snags in each decay class within a previously marked population after a specified time interval. This method was used by Raphael and Morrison (1987). Mortality rates of trees can be calculated as exponential decay rates (Runkle 2000) as follows:

$$\text{average annual mortality rate} = 1 - (S/N_0)^{(1/y)},$$

where S = number of survivors, N_0 = original number of trees, and y = number of years between samples.

Once rates of loss and recruitment of snags have been determined, matrix projection models can be developed. For example, Raphael and Morrison (1987) presented a modified Leslie matrix model. In their model, the transition matrix consists only of the probabilities of snags changing from one decay class to another. This matrix, of course, incorporates both the likelihood that snags change decay class or fall. Typical matrix models would also include recruitment rates in the transition matrix. Because recruitment is not dependent on procreation of standing snags, however, Raphael and Morrison (1987) added the number of recruits in each decay class at each iteration. Their model is $\mathbf{Dn}_t + R = \mathbf{n}_{t+1}$, where **D** is the transition matrix consisting of the probability of decaying to the next decay class, **n** is the vector of the number of standing snags in each decay class at time t, and R is the vector of the number of snags recruited into each decay class between time t and t+1.

Assuming that the transition matrix and recruitment vector remain constant, this model can project the numbers of snags and their distribution across decay classes at successive time intervals into the future. Under this assumption, the proportion of trees in each decay class will reach a stable distribution after some number of iterations. Unfortunately, the assumption of constant decay rates and recruitment is unlikely to be true

(Morrison and Raphael 1993). To examine this issue, Morrison and Raphael (1993) resurveyed snags after a second 5-year interval at their site in the Sierra Nevada. Population projections from matrix models constructed from the first 5 years and the second 5 years of** data gave different predictions for changes in snag numbers. The earlier projection indicated an increase in snag numbers over time (Raphael and Morrison 1987), whereas the later suggested declining snag numbers. This disparity was attributed to changes in the environmental conditions (e.g., drought, fire, and disease) that affected mortality rates of trees. Consequently, projections of matrix models will be flawed unless such factors are taken into account.

Although the assumption that model parameters will remain constant is unlikely to be true, the models can still be useful in projecting how snag populations will change with changes in the parameters. The standard methods of examining the sensitivity and elasticity of the projection matrix (Caswell 1989) cannot be used because recruitment is not included in the transition matrix. Consequently, it will be necessary to alter the parameters themselves. Such exercises could be conducted as computer simulations where the parameter values are randomly altered within ±1 SD and the projections are graphed over several iterations.

A similar life-table approach for simulating the population dynamics of snags is available from Marcot (1992). His model is presented in spreadsheet format and requires initial densities of snags for each age and size class considered, densities of trees killed during stand growth, and densities of snags by size class recruited over 10-year intervals. The latter values can be obtained from an appropriate growth and yield simulator for suppression mortality. Marcot's model is parameterized with data from Cline et al. (1980) for both decay and fall rates of snags for forests west of the Cascade crest. Marcot (1992) recognized that the model parameters, especially tree mortality, are likely to be quite variable. He suggests using the model to develop hypotheses about snag population dynamics. We have found no published references applying this model.

Other modeling approaches for snag dynamics are available, but have not been applied to Pacific Northwest forests. For example, Runkle (2000) used a simple exponential model that assumed that snags are created at constant rate and that a constant fraction of snags is lost each year. This approach is most appropriate for consideration of snags of a particular size class. Fall rates for smaller diameter snags are greater than for larger diameter snags (Raphael and White 1984), but fall rates within a restricted size interval are likely to be similar (Harrington 1996).

Species-specific life-history models

The issue of habitat management for cavity-nesting species becomes critically important when these species are endangered (e.g., the Red-cockaded Woodpecker [Picoides borealis] in the southeastern U.S.–Heppell et al. 1994). In Washington, four cavity-nesting species are designated as state candidate species for listing, and another four are designated as state monitor species (Washington Department of Fish and Wildlife 2002). At some point in the future, the approaches used to develop management strategies for threatened and endangered species may be required.

Central to the problem is determining the population consequences of particular management actions on an endangered species. For example, population growth may be more sensitive to changes in fecundity or mortality at some life-history stages (e.g., reproductive adults) than at others (e.g., juveniles). Identification of these critical stages may allow targeted intervention that will be more likely to ensure population growth. One approach to identifying these critical life-history stages is development of a matrix projection model (Caswell 1989). This technique was first described by Lewis (1942) and Leslie (1945) for age-structured populations and extended by Lefkovitch (1965) to stage-structured populations. These models follow changes in the numbers of individuals in each age or stage class over a given time period due to reproduction, survival, and development.

These models are similar to that already discussed for modeling snag populations (Raphael and Morrison 1987), but the transition matrix contains information on fecundity, mortality, and if necessary, development. The latter is required if these models are generalized for various life-history stages that are reached after varying lengths of time (e.g., non-breeder to breeder). Such models project the number of individuals in each age or stage class at the next census interval. The general matrix model is

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

where $\mathbf{n}_t$ is the vector of the abundances in each stage at time t and **A** is the matrix of transition probabilities given by the survival, fecundity, and developmental rates for each age or stage class.

Thus if we can estimate the elements of **A**, we can predict how the numbers in each stage will change over time. The concern, however, is not with population projection, but with determining the elements of **A** that contribute most to population growth and how these contributions might change with management activities. First, the population finite rate of increase, λ, is determined by calculating the dominant eigenvalue of **A**. This value indicates how the population will grow once a stable stage distribution has been reached. λ is a function of the survival, fecundity, and developmental rates at each stage. Next, the contribution of each element of **A** to λ is examined by conducting a sensitivity analysis. Both overall sensitivity (S–Caswell 1989:130) and elasticity, which measures the proportional contribution of each nonzero matrix element to λ may be calculated (de Kroon et al. 1986). Elasticity accounts for differences in the magnitudes of the matrix elements resulting from their different scales of measurement.

Heppell et al. (1994) provide an example of the application of a stage-based model for the Red-Cockaded Woodpecker. Estimates of fecundity, mortality, and probability of transition to another developmental stage were obtained from several years of field observations. The authors considered several management techniques and predicted their potential effect on elements of the transition matrix. For example, they predicted that removal of cavity invaders (e.g., flying squirrels) would increase fecundity. Creation of artificial cavities was predicted to increase fecundity and increase the probability of transition between fledgling and helper, while decreasing that between fledgling and breeder. Heppell et al. (1994) found that increasing the number of cavities in unoccupied cavities would make the greatest contribution to population growth. The authors point out, however, that stochastic models will be more appropriate for small, isolated populations, and that spatially-explicit models would best incorporate the territorial behavior of this species.

Conclusions

Initial models for guiding snag management (Thomas et al. 1979, Neitro et al. 1985) were *ad hoc* and based on limited information. The advantages of these models are that they are easy to understand and to apply in the field. Unfortunately, little effort to test or extend these models was made until recently. Limited data suggest that snag management based on these models may not provide sufficient snag densities to maintain cavity-nesting species. The more recent DecAID model (Marcot et al. in press-b) attempts to remedy this situation by developing management prescriptions using the accumulated knowledge about species that use dead wood and the roles of dead wood in forest ecosystems. This approach will help us both broaden our consideration and better assess our knowledge of species reliant on dead wood in the Pacific Northwest. Because the DecAID model is data rich, there may be difficulties in using its outputs, if they are too complex, for directly managing forested landscapes. This can not be evaluated until the model is completed. This advisory model can continue to improve as additional information becomes available and is likely to be the best tool for snag management in the Pacific Northwest. From a regulatory standpoint, however, it will be important to continue to develop minimum standards for snag retention. The DecAID approach permits too much uncertainty in how its outputs are applied in actual management situations.

Habitat suitability index models for cavity-nesting species are of little value in directing snag management. The greatest problems with these models are their questionable assumptions and the inadequacy of their source data. Habitat models for cavity-nesting species could become useful if they were developed and parameterized with regionally specific data.

The population dynamics of snags in managed and unmanaged forests is an area that requires further attention. The models that are available for projecting snag recruitment and loss are parameterized for limited geographical areas. Management could benefit from a better understanding of these processes and how they are likely to vary with forest age, topography, and other factors.

Population declines for some species of cavity-nesting birds may require in depth assessment of demography on population behavior. This information can be used to provide an initial evaluation of the likely effects of different management strategies on population dynamics. Spatial models of habitat use will probably also be required and ideally could be melded with GIS information on forest condition. Despite great interest in maintaining wildlife species that require dead wood, development of models to guide management of snags has lagged behind. We hope that current efforts will continue and bear fruit.

Literature cited

Bull, E. L., C. G. Parks, and T. R. Torgerson. 1997. Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391. Pacific Northwest Research Station, Portland, Oregon.

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773-786.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427-1431.

Evans, K. E., and R. N. Conner. 1979. Snag management. Pages 215-225 in R. M. Degraff, editor. Management of north central and northeastern forests for nongame birds. USDA Forest Service General Technical Report NC-51. St. Paul, Minnesota.

Hallett, J. G., T. Lopez, M. A. O'Connell, and M. A. Borysewicz. 2001. Decay dynamics and avian use of artificially created snags. Northwest Science 75:378-386.

Harrington, M. G. 1996. Fall rates of prescribed fire-killed ponderosa pine. USDA Forest Service Research Paper INT-RP-489. Intermountain Research Station, Ogden, Utah.

Heppell, S. S., J. R. Walters, and L. B. Crowder. 1994. Evaluating management alternatives for red-cockaded woodpeckers: A modeling approach. Journal of Wildlife Management 58:479-487.

Huggard, D. J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9:1009-1016.

Johnson, D. H., and T. A. O'Neil, editors. 2001. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1-18.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Lewis, E. G. 1942. On the generation and growth of a population. Sankhya 6:93-96.

Marcot, B. G. 1992. SRS: snag recruitment simulator. http://www.spiritone.com/~brucem/whrtext.htm#What

_____. in press. An ecological functional basis for managing decaying wood for wildlife. in P. J. Shea, W. F. Laudenslayer, Jr., B. Valentine, and C. P. Weatherspoon, editors. Proceedings of the Symposium on The Ecology and Management of Dead Wood in Western Forests, Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-XXX. Pacific Southwest Research Station, Albany, California.

Marcot, B. G., K. Mellen, S. A. Livingston, and C. Ogden. in press-a. The DecAID advisory model: wildlife component. in P. J. Shea, W. F. Laudenslayer, Jr., B. Valentine, and C. P. Weatherspoon, editors. Proceedings of the Symposium on The Ecology and

Management of Dead Wood in Western Forests, Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-XXX. Pacific Southwest Research Station, Albany, California.

Marcot, B. G., K. Mellen, J. L. Ohmann, K. L. Waddell, E. A. Willhite, B. B. Hostetler, S. A. Livingston, C. Ogden, and T. Dreisbach. in press-b. DecAID – work in progress on a decayed wood advisory model for Washington and Oregon forests. USDA Forest Service Research Note PNW-RN-XXX, Pacific Northwest Region, Portland Oregon.

Marcot, B. G., J. L. Ohmann, and K. Mellen. in prep. The statistical basis for the DecAID decayed wood management advisory model. USDA Forest Service General Technical Report PNW-GTR-xxx. Pacific Northwest Research Station, Portland, Oregon.

Mellen, K., B. G. Marcot, J. L. Ohmann, K. L. Waddell, E. A. Willhite, B. B. Hostetler, S. A. Livingston, and C. Ogden. in press. DecAID: a decaying wood advisory model for Oregon and Washington. in P. J. Shea, W. F. Laudenslayer, Jr., B. Valentine, and C. P. Weatherspoon, editors. Proceedings of the Symposium on The Ecology and Management of Dead Wood in Western Forests, Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-XXX. Pacific Southwest Research Station, Albany, California.

Morrison, M. L., and M. G. Raphael. 1993. Modeling the dynamics of snags. Ecological Applications 3:322-330.

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). Pages 129-169 in E. R. Brown, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1 – Chapter Narratives. USDA Forest Service R6-F&WL-192-1985. Pacific Northwest Region, Portland, Oregon.

Ohmann, J. L., and K. L. Waddell. in press. Regional patterns of dead wood in forested habitats of Oregon and Washington. in P. J. Shea, W. F. Laudenslayer, Jr., B. Valentine, and C. P. Weatherspoon, editors. Proceedings of the Symposium on The Ecology and Management of Dead Wood in Western Forests, Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-XXX. Pacific Southwest Research Station, Albany, California.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86:1-66.

Raphael, R. G., and M. L. Morrison. 1987. Decay and dynamics of snags in Sierra Nevada, California. Forest Science 33:774-783.

Roloff, G. J., and B. J. Kernohan. 1999. Evaluating reliability of habitat suitability index models. Wildlife Society Bulletin 27:973-985.

Rose, C. L., B. G. Marcot, T. K. Mellen, J. L. Ohmann, K. L. Waddell, D. L. Lindley, and B. Schreiber. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. Pages 580-623 in D. H. Johnson and T. A. O'Neil, editors. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Runkle, J. R. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81:554-567.

Schamberger, M. L., and L. J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5-10 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin, Madison, Wisconsin.

Schroeder, R. L. 1983a. Habitat suitability index models: black-capped chickadee. U.S. Department of the Interior, Fish and Wildlife Service FWS/OBS-82/10.37. Fort Collins, Colorado.

_____. 1983b. Habitat suitability index models: downy woodpecker. U.S. Department of the Interior, Fish and Wildlife Service FWS/OBS-82/10.38. Fort Collins, Colorado.

_____. 1983c. Habitat suitability index models: pileated woodpecker. U.S. Department of the Interior, Fish and Wildlife Service FWS/OBS-82/10.39. Fort Collins, Colorado.

Sousa, P. J. 1983a. Habitat suitability index models: Lewis' woodpecker. U.S. Department of the Interior, Fish and Wildlife Service FWS/OBS-82/10.32. Fort Collins, Colorado.

_____. 1983b. Habitat suitability index models: Williamson's Sapsucker. U.S. Department of the Interior, Fish and Wildlife Service FSW/OBS 8.2/10.47. Fort Collins, Colorado.

_____. 1987. Habitat suitability index models: hairy woodpecker. US Department of the Interior, Fish and Wildlife Service Biological Report 82(10.146). Fort Collins, Colorado.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 in J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook No. 553, Washington, D.C.

U.S. Fish and Wildlife Service. 1981. Standards for the development of suitability index models. U.S. Department of the Interior, Fish and Wildlife Service, Ecological Services Manual 103. Washington, D.C.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Van Horne, B., and J. A. Wiens. 1991. Forest bird habitat suitability models and the development of general habitat models. U.S. Fish and Wildlife Service Research 8:1-31.

Washington Department of Fish and Wildlife. 2002. Species of concern. http://www.wa.gov/wdfw/wlm/diversty/soc/soc.htm

Chapter 3

Relationship of Cavity-Nesting Birds to Snag Abundance in Dry Forests: Test of a Management Model

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Introduction

Dying and dead trees (snags) are critical habitat components for many species of wildlife (reviews in McComb and Lindenmayer 1999, Rose et al. 2001). The relationship of cavity-nesting birds (e.g., woodpeckers, nuthatches) to these habitat elements is particularly strong (Lundquist and Mariani 1991, Bull et al. 1997), and the negative effects on cavity nesters from the loss of snags due to timber harvest is well documented (e.g., Cline et al. 1980, Zarnowitz and Manuwal 1985, Ohmann et al. 1994). Because of the importance of snags on forested landscapes, management prescriptions have been developed to ensure that some of these habitat elements are retained on harvested lands. The specifics of these prescriptions vary with the resource agency (i.e., state or federal) and geographical location, but generally call for leaving a given number of snags and green trees per hectare after harvest (e.g., WAC 222.30, Washington State Department of Natural Resources 2000, see also examples in Chapter 5).

In the Pacific Northwest, many prescriptions have been influenced by models formulated by Thomas et al. (1979) and modified by Neitro et al. (1985) for forests east and west of the Cascade crest, respectively. These models attempt to estimate the density of snags required to maintain some proportion (e.g., 30, 60, or 90%) of the maximum potential population of primary cavity-nesting bird species (i.e., species that excavate cavities). Model application requires information about the forest associations of each species of cavity excavator likely to be present, an estimate of the maximum density of each species based on territory size, and the ratio of snags without cavities to snags with cavities (Thomas et al. 1979). The minimum diameter at breast height (dbh) that can be used by each cavity-nesting species also must be known. Thomas et al. (1979) provide tables to estimate required snag densities for different bird species in several forest types based on data for the Blue Mountains of Oregon. The models were designed originally to be applied to different forest types and consequently to different species of primary cavity nesters. Their application has been generalized in regulatory practice because of the need to have consistent regulations across large geographical areas, and because site-specific data on the density, dynamics, and avian use of snags are rarely available to managers (Ganey 1999).

Population potential models were developed as *ad hoc* guides for snag management. Simplifying assumptions were necessary because of the limited data available and the need to make the models practical in application. Recent criticisms of these models reflect the increased understanding of the role of dead wood in forest ecosystems (review in Chapter 2, Rose et al. 2001). In particular, the models may underestimate the numbers of snags required to maintain cavity-nesting species. This will be exacerbated by selection of a low population threshold (e.g., 30%). Additionally, the needs of secondary cavity-nesting species may not be met by guidelines generated by these models. Population potential models do not address the distribution of snags on forested landscapes and provide only average values for snag retention.

Regulations usually allow substantial latitude in the spatial distribution of snags and leave trees left in a harvest unit as long as average densities are maintained. Raphael and White (1984) recommended that snags be left in dispersed clumps because the best predictors of nest trees in the Sierra Nevada was the number of snags >38 cm dbh and those between 23-38 cm dbh. Saab and Dudley (1998) also reported greater use of clumped snags by several cavity-nesting species in Idaho. However, clumping of snags without dispersing the clumps might limit the numbers of breeding pairs of birds because of territoriality (Thomas et al. 1979). There is an important need to better understand the effects of spatial distribution of snags on avian use.

In addition, the influence of spatial distribution on relative abundance of cavity-nesting species may depend on the degree of decay of the snags. Primary cavity-nesting species all excavate cavities in dead trees, but differ in their abilities to excavate in hard wood (Steeger and Hitchcock 1998). Woodpeckers are generally strong excavators, whereas nuthatches and chickadees are weak excavators and require wood that is more decayed.

In this study, we compare the predictions of population potential models with patterns of snag density and the relative abundance of primary cavity-nesting birds in dry ponderosa pine (*Pinus ponderosa*) forest. In addition, we consider the following questions: (1) How does availability of snags in different decay and size classes vary over the landscape? (2) How do the size and decay characteristics of snags affect foraging and nesting use by all cavity-nesting species? (3) How does spatial variation in snag availability affect the distribution and relative abundance of cavity-nesting birds?

Methods

Study Area

Turnbull National Wildlife Refuge (TNWR) encompasses about 5,000 ha of Channeled Scablands on the eastern edge of the Columbia Basin. The refuge is dissected by sloughs, lakes, and marshlands. Aspen (*Populus tremuloides*) is often abundant adjacent to the moist areas. About 2,800 ha of the drier upland area is ponderosa pine forest of three associations: ponderosa pine/snowberry (*Symphoricarpos alba*); ponderosa pine/pine grass (*Calamagrostis rubescens*); and ponderosa pine/Idaho fescue (*Festuca idahoensis*). Although the management objective of the refuge is to maintain biological diversity rather than timber production, the desired forest conditions and management practices that the refuge employs are not dissimilar to the desired conditions and practices of multiple-use state or federal agencies and private landowners. TNWR is managing its pine forests to reduce fuel loading and to move forests towards pre-settlement conditions using thinning and prescribed burns

(U. S. Fish and Wildlife Service 1998). Evidence suggests that pre-settlement forests in this region were open woodlands with trees of large dbh.

We selected 8 stands for study that varied over the range of snag densities and stocking conditions at TNWR. Stands were located throughout the refuge, and were generally separated from each other by distances >1 km and often by different habitats including sloughs, lakes, and marshland. We established transects for tree and bird surveys that bisected each stand and that were marked by 6-12 stations placed at >150 m intervals. Transects were buffered by >200 m from other habitat types.

Tree surveys

To determine densities and distributions, we mapped snags and live trees on each transect. A 240-m band, centered on each transect and extending in a semicircle of 120-m radius past the first and last stations, was searched for snags. Snags were uniquely tagged with an aluminum band to allow future monitoring of snag survival. Each snag was placed into one of three structural classes following Bull et al. (1997). The three classes were (1) recently dead, little decay, retention of bark, branches, and top, (2) evidence of decay, loss of some bark and branches and possibly part of the top, and (3) extensive decay, missing bark and most branches, and broken top. This classification scheme is easier to apply consistently in the field than other schemes that include as many as nine classes (e.g., Thomas et al. 1979). Moreover, because population potential models are concerned only with primary cavity-nesting species, the "hard" snags in decay class 2 are of central concern.

We used a Trimble Pro XR GPS receiver to record data and, with a laser level, to determine the location (to within 0.25 m) and height of snags. Number of cavities and dbh (cm) were recorded for each snag. The bark of each tree was examined for evidence of foraging by cavity nesters (i.e., presence of drill holes), which was recorded as present or absent. Additionally, live trees within a 30-m radius of each point-count station (0.28 ha) were mapped and their dbh recorded.

Breeding Bird Surveys

We used the point-count method for surveying bird populations (Verner 1985, Manuwal and Huff 1987). We estimated the distance to birds detected within 50 m, and then simply recorded birds seen or heard beyond 50 m. Counts began within 15 minutes of dawn and were completed within 2 hours. Upon arriving at a survey point, the observer remained stationary and quiet for a minimum of 1 minute to allow birds to settle down after initial disturbance by the observer. During the survey period, the observer recorded the birds heard or seen within an 8-minute period. During the survey, the observer slowly scanned the vegetation at all levels within the sampled zone. Birds not previously recorded were tallied if they were detected between count points to obtain a complete species list for each stand; these data were not used in calculating abundance indices. Observers were systematically rotated among the stands being sampled to help correct for any between-observer bias in ability to detect birds among the stands. Furthermore, within-stand bias of bird detectability was reduced by reversing the travel routes during successive visits to each stand.

Bird surveys were conducted in late April through June in 1998 and 1999. Each stand was surveyed 7 times during this period each year. Surveys were spaced throughout the breeding season to account for different breeding phenologies of bird species in this region.

Counts were conducted when winds were <15 km/hr and there was no significant precipitation, as these factors have been shown to significantly bias results. Every attempt was made to avoid counting individual birds more than once.

Each transect was searched for active nests during the bird survey sampling period. Nest surveys were conducted by carefully searching for any signs of cavity construction or activity at snags or by following individual birds.

Analysis

We examined live trees and snags and the responses of the avian community at both stand and point-count station scales. Location data obtained by GPS was differentially corrected and converted to ARC/INFO (ESRI, Redlands, CA) files using GPS Pathfinder Office 2.1 (Trimble Navigation Limited, Sunnyvale, CA). For each transect, we mapped the locations of snags and live trees using PC ARC/INFO 3.5. To examine stand level characteristics, we centered a 120-m buffer on each transect to determine stand area and perimeter. We determined density, mean dbh, and mean height for each of the three classes of snags on each transect.

To examine the Thomas et al. (1979) model, we also calculated densities for snags >17 cm dbh for the Downy Woodpecker, >27 cm dbh for the Hairy Woodpecker, and >32 cm for the Northern Flicker on each transect. We compared these densities to model recommendations for different potential population levels for the 3 species using values from Appendix 22 of Thomas et al. (1979).

To examine forest structure on the scale of the point-count station scale, buffers were centered on each point-count station. We used 30-m radius buffers for live trees and 75-m radius buffers for snags. We used the latter to ensure that sampling units were independent. For live trees, we calculated density, basal area, and mean dbh. For snags, we determined the number of trees, number of cavities, and mean dbh in each decay class.

To examine patterns of aggregation of trees, we used the SPACESTATPACK program (Pace and Barry 1999) to calculate nearest-neighbor distances for each decay class of snags on the transects and for live trees within the 30-m buffers. Using these values, we determined if the distribution of snags or live trees was more aggregated or more uniform than expected under a random distribution using Donnelly's (1978) correction to Clark and Evans' (1954) test. This test adjusts for edge effects and correlations among nearest-neighbor distances. Tests were conducted separately for all snags and for snags that had cavities in each decay class. Differences in $\log_e$-transformed nearest neighbor distances between all snags and those with cavities were determined by factorial ANOVA by decay class and transect.

For birds, we determined the following population parameters: species richness and a detection index (i.e., mean number of detections per station per day) as a relative measure of abundance for all species with an adequate numbers of detections. Both metrics were determined for detections within the 50-m radius point-count circles.

We examined correlations among cavity-nesting species in the detection index for the transects and point-count stations for both years. We next conducted stepwise regression analysis to determine if the habitat variables we measured were useful predictors of either species richness, or the detection index for cavity-nesting species individually or as a group of species (i.e., primary vs. secondary cavity nester). If a species was negatively correlated with another species, which might reflect interspecific competition, we included those species as additional independent variables.

Unless otherwise noted, statistical analyses were conducted with the Statistical Analysis System (SAS Institute 1988). Tests were considered significant at $P < 0.05$.

Results

Model analysis

To examine recommended snag densities for primary cavity-nesting species as generated by the Thomas et al. (1979) model, we first determined snag densities at TNWR. We mapped a total of 2184 snags in the three decay classes (1, $n = 1001$; 2, $n = 959$; 3, $n = 224$). Densities of snags varied with decay class and transect (Table 1). Decay classes 1 and 2 had higher mean densities and greater variance (decay class 1, $\bar{x} = 5.1 \pm 2.3$; decay class 2, $\bar{x} = 3.8 \pm 0.9$) than decay class 3 ($\bar{x} = 1.0 \pm 0.1$). There was no correlation between the densities of decay class 1 and 2 snags across transects ($r = -0.15$, $P = 0.7$). Three transects (C, H, and K) had densities 2-10 times higher in either decay class 1 or 2, suggesting that a mortality event affected the stand at one point in time (Table 1).

The densities of decay class 2 or "hard" snags also varied across transects and declined with an increase in minimum dbh size (Table 2). Comparison of these values with model recommendations (Appendix 1) indicate that only one transect (C) had sufficient snag density to support Downy Woodpeckers at 60% of maximum potential population size. For the Hairy Woodpecker, the highest snag density corresponds to 40% (transect K). The situation for Northern Flickers is better with 2 transects (C and K) at 100% and 6 transects >80% maximum potential population size.

Model values can be adjusted for the actual ratio of used to non-used trees. The ratio of 1:16 used in Thomas et al. (1979) model was based on a sample of 8000 snags, but decay condition was not specified. At TNWR, about 1 snag is used for every 6 unused snags in decay class 2 and with dbh >17 cm. Substituting 6 for 16 reduces the predicted snag requirements by 62% (Appendix 1). These lower snag requirements suggest that several areas at TNWR should support 100% of maximum potential population for all 3 species.

All 3 primary cavity-nesting species were observed during point-count sampling on all transects in at least 1 year (Table 2). Occurrence of nests on the transects was unpredictable for Downy and Hairy Woodpeckers, but was greater and more consistent for Northern Flicker. No relationship was observed between frequency of occurrence or nesting for any species and the corresponding densities for decay class 2 snags (Spearman rank correlation, $P > 0.25$). For the Northern Flicker, one transect (F) that was not expected to have any birds present had the greatest number of nests. The lack of correspondence between snag density and activity of these primary cavity nesters suggest that management based on number and size of snags alone will be insufficient.

Distribution of live trees

To further examine the factors affecting distribution of cavity-nesting birds, we mapped a total of 4047 live trees on 53 point-count stations. Considerable variation in tree density, mean dbh, and basal area was observed both within and between transects (Table 3).

Densities varied from 32 to 721 trees/ha and basal area from 3.9 to 35.5 m^2/ha (Table 3). Significant differences in tree densities and basal area among transects (F = 5.3, df = 7,45, *P* = 0.0002) largely reflected high values of these variables on three transects (C, I, and K) versus low values on another (F). Similarly, significant differences in mean dbh (F = 5.0, df = 7,45, *P* = 0.0003) were due to low values of mean dbh on most transects and high values one transect (F). Tree density was positively correlated with basal area (r = 0.78, $P < 0.0001$) and negatively correlated with mean dbh (r = -0.56, $P < 0.0001$). There was no relationship between mean dbh and basal area (r = -0.09, *P* = 0.51).

Spatial patterning of live trees and snags

Average nearest neighbor distances for live trees ranged between 1.8 and 7.9 m over the 53 sampling units (Table 4). Values of the modified Clark and Evans (1954) test statistic (MCE) calculated for each sampling unit indicated highly significant aggregation of live trees in all cases (data not shown). There were significant differences in nearest neighbor distances among transects (F = 15.4, df = 7,42, $P < 0.0001$) due to the greater values on two transects (F and H, Table 4).

Mean nearest-neighbor distances were quite variable for snags across all decay classes, transects, and for trees with cavities (Table 5). Tests of these means againstexpectations under a random distribution indicated strong aggregation for all transects in each decay class. After accounting for the variation due to transect, mean nearest neighbor distance was greater for decay class 3 than decay class 2 (F = 190.4, df 1,1262, $P < 0.0001$), and greater for trees with cavities than for all trees combined (F = 75.8, df 1,1262, $P <$ 0.0001; Table 6 and Fig. 1).

Tree Condition and Avian Use

Mean dbh differed significantly among the three decay classes of snags and live trees (F = 38.9, df = 3,6228, $P < 0.0001$). Means for live (28.6 ± 0.2 cm dbh, n = 3984) and decay class 3 (30.1 ± 0.8 cm dbh) trees did not differ, but both were significantly greater than for decay classes 1 (24.4 ± 0.4 cm dbh) and 2 (24.7 ± 0.4 cm dbh). The differences in mean dbh correspond to the significantly greater proportion of trees in the smaller dbh classes (i.e., <30 cm dbh; Fig. 2) for decay classes 1 (77.6%) and 2 (74.6%) than for decay class 3 (55.4%) and live trees (61.4%; overall—χ^2 = 139.7, df = 3, $P < 0.0001$; decay class 1 vs decay class 2—χ^2 = 2.6, df = 1, *P* = 0.11; decay class 3 vs. live trees—χ^2 = 3.3, df = 1, *P* = 0.07).

A high percentage of snags (78.6%) showed evidence of foraging. As expected, the percentage of snags with obvious signs of foraging increased significantly from decay class 1 (69.8%) to decay class 2 (82.9%; χ^2 = 46.6, df = 1, $P < 0.0001$) and from decay class 2 to decay class 3 (89.4%; χ^2 = 5.8, df = 1, $P < 0.02$). The latter percentage may be an underestimate because of the difficulty in evaluating foraging on snags that have sloughed bark.

The percentage of trees with cavities also increased with greater decay. The increases were from decay class 1 (2.2%) to decay class 2 (12.9%; χ^2 = 81.8, df = 1, $P < 0.0001$) and from decay class 2 to decay class 3 (60.0%; χ^2 = 235.6, df = 1, $P < 0.0001$). Of snags with cavities, the proportion of trees with >2 cavities was significantly higher for decay class 3 (60%, n = 135, χ^2 = 23.8, df = 2, $P < 0.0001$) than for decay class 1 (22.7%, n = 22) or 2 (31.1%, n = 124), which did not differ from each other (χ^2 = 0.9, df = 1, *P* = 0.34). Similarly, the mean number of cavities for snags with one or more cavities was greater for decay class 3 (4.7 ± 0.4) than for decay classes 1 (2.6 ± 0.7) or 2 (2.8 ± 0.3; F = 10.3, df = 3,277, $P < 0.0001$). Inclusion of dbh as a covariate was significant (F = 14.9, df = 1,277, $P < 0.0001$) and indicated that larger tree size, as well as decay class, is an important determinant of cavity use. In particular, for decay class 3, mean dbh of snags with cavities (32.9 ± 1.1 cm) was significantly greater than for snags without cavities (26.0 ± 1.2 cm; $F = 17.4$, df = 1,222, $P < 0.0001$). Mean height of decay class 3 snags did not differ for snags with (6.9 ± 0.4 m) and without cavities (6.6 ± 0.7 m; F = 0.7, df = 1,222, $P = 0.67$).

Patterns of Bird Distribution

We had totals of 3167 and 3080 observations of 63 and 93 species in 1998 and 1999, respectively. The species pool over both years was 105 species. We excluded species that were rare (observed <10 times) or associated with wetland and marsh habitats, and we considered a total of 33 species in our analyses (Table 7). We observed nine primary cavity-nesting species including two strong excavators (i.e., able to excavate in hard wood Steeger and Hitchcock 1998), Hairy Woodpecker, Downy Woodpecker, and Northern Flicker; and five weak excavators, Black-capped Chickadee, Mountain Chickadee, Red-breasted Nuthatch, White-breasted Nuthatch, and Pygmy Nuthatch. The latter species require trees with greater levels of decay for nesting. The Red-naped Sapsucker also requires soft wood for excavating and has been observed nesting exclusively in aspen (*Populus tremuloides*) at TNWR (Laura Nelson, Eastern Washington University, unpublished data). Secondary cavity-nesting species included the House Wren, European Starling, and Western Bluebird. As a group, cavity-nesting species accounted for about 42.0% of all observations from the 2 years.

The cavity-nesting species were broadly distributed on the refuge. The distributions of 6 of the 12 cavity-nesting species were positively correlated between the 2 years (Table 8). Few correlations were observed between primary cavity-nesting species considered in the population potential models and other primary or secondary nesting species. All secondary cavity-nesting species and two species of nuthatch had strong correlations between years. When correlations in the distribution of two species occurred, the relationships were usually positive and consistent between years (Table 9). Detection rates of Pygmy and Red-breasted Nuthatches, however, were negatively associated in both years.

Mean species richness observed at the point-count stations increased from 1998 to 1999 for weak primary cavity nesters and other passerines (Table 10). The mean rates of detection did not change between years for any species group (Table 10).

Species richness of all cavity-nesters at the point-count stations was positively related to the mean nearest-neighbor distance for live trees in both years, although this variable explained only a small proportion of the variance (1998: $r^2 = 24.4\%$, F = 15.2, df = 1,47, P = 0.0002; 1999: $r^2 = 8.2\%$, F = 4.2, df = 1,47, P = 0.05). Similarly, mean nearest-neighbor distance for live trees or a related variable, basal area of green trees, were consistent predictors of the detection index of both primary and secondary cavity nesters (Table 11). These results indicate that cavity nesters as a group are less abundant in more closed stands. Primary cavity-nesters also were positively associated with the number of cavities in decay class 2 snags (Table 11).

The results for individual species were less consistent between years and the overall R^2 values were low (Table 11). For four species, no habitat variables were significant in

1999. Examination of the variables that were significant across primary cavity-nesting species again point to their greater relative abundance in more open stands (i.e., positive associations with mean nearest-neighbor distance of green trees, mean dbh of green trees, and green tree density; negative associations with basal area of green trees and the number of green trees). Variables describing snag condition (i.e., the number of cavities present, and height and dbh of different classes of snags) were also significant predictors for individuals (Table 11).

Because the detection indices for Pygmy and Red-breasted Nuthatches were negatively correlated, we conducted two regression analyses for each species. In the first, we considered only the habitat descriptors. In the second, we allowed the other species to enter as an additional independent variable to determine if the reciprocal relationship could be explained by habitat selection alone or whether interspecific competition might be a factor (Hallett and Pimm 1979). For both species, the relative abundance of the other was a significant negative predictor after inclusion of habitat descriptors in both years (Table 11). For 1998, overall R^2 of these models increased substantially over models with habitat variables alone. The models for 1999 are limited by the lower number of observations for Red-breasted Nuthatches and did not exhibit similar improvement.

Discussion

Cavity-nesting species are an important component of the avifauna at TNWR. Management of these species using the Thomas et al. (1979) model presents several difficulties. Using model parameters presented by Thomas et al. (1979), there appears to be a good relationship between presence and nest use and the projected potential population size (Table 2). The ponderosa pine stands have fewer snags of appropriate size than required to maintain populations greater than 20-40% for Downy and Hairy Woodpeckers, and these species had a relatively low presence on these stands. Similar projections for the Northern Flicker indicate that sufficient snags are available to maintain populations at >90% over most stands. A corresponding greater number of observations and nest use was observed for this species. When the Thomas et al. (1979) model is modified to account for the actual ratio of unused to used snags at TNWR, predictions remain similar for the Northern Flicker, but Downy and Hairy Woodpeckers would be expected to have greater presence because ~100% of their snag requirements are met. Moreover, there was no relationship between occurrence or nest use with snag density. In particular, one transect with low snag density had amongst the highest nest production for the Northern Flicker. The additional lack of correspondence between the distributions of the modeled primary cavity producers and secondary cavity users suggests that the assumption that models built for primary nesters will ensure sufficient habitat for secondary nesters may be false.

Clearly factors other than snag density must be important in determining habitat suitability for cavity-nesting species. Our study demonstrates that forest structure (i.e., the spatial distribution and size characteristics of live trees), as well as the types and distributions of snags affect relative abundance of cavity nesters. These factors are not independent because forest structure ultimately affects the distribution and characteristics of snags.

The density and basal area of live ponderosa pine trees vary over an order of magnitude at TNWR. The high densities of small diameter trees at many locations are the result of suppression of periodic fires that previously had maintained a more open overstory

(Kinateder 1998). Our data indicate that species richness and relative abundance of cavity-nesting species increase as stands move from an overstocked condition to a more open overstory.

High levels of aggregation lead to natural suppression and the creation of large numbers of snags in many stands (Maser et al. 1988). This is supported by the higher proportion of decay class 1 and 2 snags in the smallest size classes than expected based on the distribution of live trees (Fig. 2). Mortality events appear to affect spatially separated stands at different times as reflected in the inverse numbers of decay class 1 and 2 snags on some stands (Table 3). These differences may result in shifts in relative abundances of cavity-nesters over time. Decay class 1 and 2 snags provide important foraging habitat due to the large numbers of trees in these classes. Because most of these snags are small in diameter, however, they are available for a limited time before falling over (compare decay class 1 and 2 versus decay class 3 in Fig. 2).

A small proportion of decay class 2 trees had cavities, but the absolute number of trees used was comparable to decay class 3, which had a much higher proportion of trees with cavities. Large decay class 3 trees, however, typically had multiple cavities and thus they provide a longer term resource. Snags that had cavities for both decay classes were further apart than the total population of trees in each class. This is consistent with territorial behavior in these species and a resulting dispersion of nest trees. This result confirms the need to ensure that snags are broadly distributed and not restricted to small pockets within a managed stand (Thomas et al. 1979, Raphael and White 1984). Laura Nelson (*in preparation*) examined nest site selection for cavity-nesting species in aspen and ponderosa pine stands at TNWR. She found that nest sites had greater snag densities than comparable random plots. Her work supports the recommendation by Raphael and White (1984) that clumps of snags be dispersed throughout a managed stand. These additional snags provide foraging habitat for cavity nesters and thus may reduce foraging costs. Such clusters occur naturally due to fire events or insect outbreaks (McClelland and Frissell 1975).

The importance of retaining large snags on the landscape is apparent from their greater use for excavation of cavities. At TNWR, patches of aspen provide additional opportunities for nesting that may be essential to maintaining cavity-nesting species on the refuge (L. Nelson, *in preparation*). This resource, however, is not available in many other ponderosa pine forests. In eastern Washington, most ponderosa pine stands have a size distribution similar to TNWR that is skewed towards heavily stocked, smaller diameter trees. Management prescriptions have been adopted at TNWR to return ponderosa stands to a more open overstory using mechanical thinning and fire (U. S. Fish and Wildlife Service 1998). This strategy should increase the species richness of cavity nesters as long as snags are not eliminated (Scott 1979). Equally important, it will begin to move the size distribution of trees towards larger diameter trees. This will be essential for maintaining nesting habitat over the long term.

Management practices may also benefit from additional understanding of the ecology of cavity-nesting species. The coexistence of several closely-related insectivorous cavity-nesting species has usually been explained by differences in foraging ecology (Murphy and Lehnhausen 1998), which may even be observed intersexually in some species (e.g., Downy Woodpecker--Matthysen et al. 1991). We found broad overlap in habitat use by the primary cavity-nesting species in our study with the exception of two nuthatch species. The negative association of the detection index for Red-breasted and Pygmy Nuthatches was consistent between years and was not explained by differences in habitat selection by either species. Pygmy Nuthatches are more closely associated with burned stands than are Red-breasted Nuthatches (Raphael and White 1984, Bateman 2000), but none of the stands in our study were recently burned. Although an important habitat variable may not have been included in our analyses, we cannot suggest one that is likely to be unrelated to those we measured. Our results suggest that interspecific competition underlies the observed pattern of distribution, but confirmatory experiments will be required to test this hypothesis.

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Literature Cited

Bateman, H. L. 2000. Effects of prescribed burns on wintering cavity-nesting birds. M.S. Thesis. Eastern Washington University, Cheney, Washington.

Bull, E. L., C. G. Parks, and T. R. Torgerson. 1997. Trees and logs important to wildlife in the interior Columbia River basin. General Technical Report PNW-GTR-391, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445-453.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773-786.

Donnelly, K. 1978. Simulations to determine the variance and edge-effect of total nearest neighbour distance. Pages 91-95 in I. Hodder, editor. Simulation methods in archeology. Cambridge University Press, London.

Ganey, J. L. 1999. Snag density and composition of snag populations on two National Forests in northern Arizona. Forest Ecology and Management 117:169-178.

Hallett, J. G., and S. L. Pimm. 1979. Direct estimation of competition. American Naturalist 113:593-600.

Kinateder, D. J. 1998. Fire history in eastern Washington and the impact of fire on snowberry, deer and elk. M.S. Thesis. Eastern Washington University.

Lundquist, R. W., and J. M. Mariani. 1991. Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range). Pages 221-240 in L. E. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests, USDA Forest Service General Technical Report PNW-GTR-285.

Manuwal, D. A., and M. Huff. 1987. Spring and winter bird populations in a Douglas-fir forest. Journal of Wildlife Management 51:586-595.

Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin. 1988. From the forest to the sea: a story of fallen trees. General Technical Report PNW-GTR-229, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Matthysen, E., T. C. Grubb, Jr, and D. Cimprich. 1991. Social control of sex-specific foraging behaviour in downy woodpeckers *Picoides pubescens*. Animal Behaviour 42:515-517.

McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. Journal of Forestry 73:414-417.

McComb, W. C., and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 in M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62:1359-1372.

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). Pages 129-169 in E. R. Brown, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington, USDA Forest Service R6-F&WL-192-1985.

Ohmann, J. L., W. C. McComb, and A. A. Zumrawi. 1994. Snag abundance for primary cavity-nesting birds on nonfederal forest lands in Oregon and Washington. Wildlife Society Bulletin 22:607-620.

Pace, R. K., and R. Barry. 1999. SPACESTATPACK: a spatial statistics package in Fortran 90 1.0.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86:1-66.

Rose, C. L., B. G. Marcot, T. K. Mellen, J. L. Ohmann, K. L. Waddell, D. L. Lindley, and B. Schreiber. 2001. Decaying wood in Pacific Northwest forests: concepts and tools for habitat management. Pages 580-623 in D. H. Johnson and T. A. O'Neil, editors. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, OR.

Saab, V. A., and J. G. Dudley. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. U.S. Forest Service Research Paper RMRS-11.

Scott, V. 1979. Bird response to snag removal in ponderosa pine. Journal of Forestry 77:26-28.

Steeger, C., and C. L. Hitchcock. 1998. Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. Journal of Wildlife Management 62:1349-1358.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 in J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553, USDA Forest Service, Washington, D.C.

U. S. Fish and Wildlife Service. 1998. Fire management at Turnbull National Wildlife Refuge. Draft Environmental Assessment. U.S. Fish and Wildlife Service, Spokane County, Washington.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247-302.

Washington State Department of Natural Resources. 2000. Washington Forest Practices Rules, Chapter 222-30 WAC, Timber Harvesting. http://www.wa.gov/dnr/htdocs/fp/fpb/222-30.html

Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management 49:255-263.

TABLE 1. Densities of ponderosa-pine snags (trees/ha) in three decay classes on 8 transects at the Turnbull National Wildlife Refuge.

Transect	Decay class 1		Decay class 2		Decay class 3		Total	
	Density	n	Density	n	Density	n	Density	n
C	4.1	99	8.4	204	1.2	30	13.8	333
F	0.6	17	0.1	3	0.3	9	1.0	29
G	5.8	157	4.4	120	1.3	35	11.5	312
H	20.4	391	2.0	38	0.6	11	23.0	440
I	3.6	118	3.4	112	1.1	37	8.1	267
J	1.1	30	2.5	70	1.3	35	4.8	135
K	1.8	71	5.7	222	1.1	44	8.6	337
M	3.7	56	3.5	53	0.8	12	8.0	121

TABLE 2. Densities of decay class 2 snags per 100 ha for 3 minimum dbh sizes for comparison with model values (in parentheses from Appendix 2) for Downy Woodpecker (>17 cm dbh, DOWO), Hairy Woodpecker (>27 cm dbh, HAWO), and Northern Flicker (>32 cm dbh, NOFL), and number of nests observed in 1998 and 1999 for each species.

	Snag densities per 100 ha			Number of observations						Number of nests					
Transect	>17 cm	>27 cm	>32 cm	DOWO		HAWO		NOFL		DOWO		HAWO		NOFL	
				98	99	98	99	98	99	98	99	98	99	98	99
C	472 (60)	174 (40)	116 (100)	1	2	6	8	5	9	0	0	0	1	0	1
F	11 (0)	4 (0)	4 (0)	1	4	5	2	18	12	0	0	0	0	1	2
G	299 (40)	103 (20)	77 (80)	7	3	2	8	12	9	0	1	0	0	1	1
H	146 (20)	89 (20)	84 (90)	0	2	7	11	24	10	0	0	0	1	0	1
I	228 (30)	104 (20)	82 (80)	3	4	4	4	23	7	0	0	0	0	0	1
J	233 (30)	122 (20)	90 (90)	2	4	1	0	26	11	0	0	0	0	2	1
K	409 (50)	184 (40)	102 (100)	3	1	3	3	20	17	0	0	0	0	0	1
M	138 (10)	46 (10)	33 (30)	0	1	4	2	18	14	0	0	0	0	1	0

TABLE 3. Mean (± SE) density of trees (trees/ha), DBH (cm), and basal area (m^2/ha) for live ponderosa pine on 8 transects at the Turnbull National Wildlife Refuge. The number of 0.28 ha sampling units (n) and the minimum and maximum values from these units are provided for each transect.

		Tree density				DBH				Basal area			
Transect	No. of samples	$\bar{x}$	SE	min	max	$\bar{x}$	SE	min	max	$\bar{x}$	SE	min	max
C	6	319	17	272	382	25.5	1.1	21.4	29.1	19.9	3.2	13.6	34.2
F	5	53	12	32	95	39.4	2.4	31.3	44.6	7.0	1.3	3.9	11.2
G	7	212	38	99	396	27.9	2.9	12.4	35.9	15.2	2.0	9.4	24.4
H	6	126	9	95	156	32.0	1.3	28.5	36.8	11.5	1.2	8.9	16.7
I	6	311	39	159	428	28.1	0.9	24.9	31.1	23.0	3.2	12.8	35.5
J	7	234	30	117	357	30.8	1.1	25.1	33.9	19.3	2.3	9.7	29.8
K	12	311	45	92	721	28.4	1.6	21.2	38.2	21.0	2.2	6.4	29.9
M	4	240	57	145	396	24.3	2.2	18.6	29.0	14.7	4.9	4.6	25.6

TABLE 4. Descriptive statistics for nearest-neighbor distances (m) of live ponderosa-pine trees on 8 transects at Turnbull National Wildlife Refuge. There was highly significant aggregation of trees for all 53 sampling units based on the modified Clark and Evans (1954) test statistic (data not presented). Means marked with a * were significantly greater than all other transects, but were not different from each other.

	Live trees					
Transect	n	$\bar{x}$	SE	CV	Minimum	Maximum
C	6	2.5	0.1	11.1	2.2	3.0
F	5	5.7*	0.7	26.0	4.3	7.9
G	7	2.8	0.3	28.8	1.9	4.1
H	6	5.0*	0.4	21.3	3.8	6.5
I	6	2.4	0.2	18.3	2.0	3.2
J	7	2.8	0.2	17.3	2.3	3.4
K	9	2.5	0.2	20.5	2.0	3.5
M	4	2.7	0.4	27.0	1.8	3.3

TABLE 5. Descriptive statistics for nearest-neighbor distances (m) of snags on 8 ponderosa-pine transects at Turnbull National Wildlife Refuge. Values are presented for all trees and for trees with cavities in each of three decay classes. The expected value of the mean, E($\bar{x}$), under a random distribution and the modified Clark and Evans (1954) test statistic (MCE) indicate highly significant aggregation of snags in all cases. The numbers of decay class 1 snags with cavities were too small for inclusion.

		All Trees						Trees with Cavities					
Decay class	Transect	n	$\bar{x}$	SE	CV	E($\bar{x}$)	MCE	n	$\bar{x}$	SE	CV	E($\bar{x}$)	MCE
1	C	99	14.3	1.2	85.4	37.1	-15.5						
	F	17	68.4	23.1	139.3	145.8	-7.3						
	G	157	9.4	0.9	120.1	29.4	-20.7						
	H	391	6.9	0.4	120.4	13.6	-21.5						
	I	118	15.3	1.7	118.5	39.9	-17.1						
	J	30	28.7	7.0	133.3	94.6	-11.6						
	K	71	25.2	2.7	91.3	63.5	-14.1						
	M	56	12.8	1.6	94.1	41.2	-13.5						
2	C	204	10.5	0.7	94.8	23.2	-18.4	16	42.4	8.0	75.1	139.2	-9.3
	F	3	12.4	6.4	88.9			0					
	G	120	8.9	1.2	141.6	35.0	-20.4	12	56.0	10.7	66.1	189.6	-8.7
	H	38	32.9	4.5	83.6	62.3	-8.2	4	156.8	48.0	61.2	370.6	-5.0
	I	112	13.8	1.7	130.7	41.4	-18.1	21	38.3	12.1	144.9	139.5	-11.0
	J	70	17.0	2.5	124.8	51.4	-15.0	11	74.6	18.1	80.5	207.5	-7.8
	K	222	13.2	0.9	106.7	29.4	-19.8	25	52.0	14.8	142.4	138.0	-10.2
	M	53	13.2	1.7	91.7	42.7	-13.3	53	13.2	1.7	91.7	42.7	-13.3
3	C	30	35.6	5.6	86.9	86.1	-9.6	15	43.2	10.4	93.0	146.4	-9.2
	F	9	31.8	8.4	79.3	243.6	-9.9	5	59.5	33.0	123.9		
	G	35	23.2	4.3	109.5	82.9	-12.6	26	25.1	5.3	108.1	103.5	-12.0
	H	11	41.5	8.5	67.9	159.5	-8.6	4	80.1	11.0	27.4	370.6	-6.8
	I	37	30.8	5.4	107.2	90.6	-12.0	23	36.2	6.0	79.1	130.0	-11.2
	J	35	34.8	5.5	93.4	84.4	-10.3	26	41.9	8.0	97.7	105.4	-9.6
	K	44	39.2	5.3	89.4	89.9	-11.1	23	80.5	12.1	72.3	147.3	-7.2
	M	12	49.2	12.1	85.5	127.7	-7.1	6	83.8	15.5	45.2	223.8	-5.9

TABLE 6. Mean nearest-neighbor distances (m) for snags in 2 decay classes for all trees and for trees with cavities on 8 transects at Turnbull National Wildlife Refuge.

Decay class	Group	n	Mean	SE	CV
2	All trees	819	13.2	0.6	119.7
2	With cavities	142	39.5	4.5	136.2
3	All trees	204	34.4	2.3	94.6
3	With cavities	108	53.4	4.8	93.3

TABLE 7. Number of observations of three groups of cavity-nesting and other passerine species encountered during surveys at Turnbull National Wildlife Refuge in 1998 and 1999 and included in analyses.

Type	Species	1998	1999
Strong primary	Downy Woodpecker (*Picoides pubescens*)	17	21
	Hairy Woodpecker (*Picoides villosus*)	32	38
	Northern Flicker (*Colaptes auratus*)	156	89
Weak primary	Red-naped Sapsucker (*Sphyrapicus nuchalis*)	23	20
	Red-breasted Nuthatch (*Sitta canadensis*)	228	82
	White-breasted Nuthatch (*Sitta carolinensis*)	170	133
	Pygmy Nuthatch (*Sitta pygmaea*)	209	195
	Black-capped Chickadee (*Parus atricapillus*)	50	55
	Mountain Chickadee (*Parus gambeli*)	173	103
Secondary	European Starling (*Sturnus vulgaris*)	23	38
	Western Bluebird (*Sialia mexicana*)	44	86
	House Wren (*Troglodytes aedon*)	488	205
Other passerine	American Goldfinch (*Carduelis tristis*)	10	32
	American Robin (*Turdus migratorius*)	238	299
	Black-billed Magpie (*Pica pica*)	24	20
	Black-headed Grosbeak (*Pheucticus melanocephalus*)	12	21
	Brown-headed Cowbird (*Molothrus ater*)	110	199
	Chipping Sparrow (*Spizella passerina*)	131	88
	Common Raven (*Corvus corax*)	12	25
	Dark-eyed Junco (*Junco hyemalis*)	86	158
	Eastern Kingbird (*Tyrannus tyrannus*)	10	26
	Evening Grosbeak (*Coccothraustes vespertinus*)	1	26
	Mourning Dove (*Zenaida macroura*)	57	64
	Red Crossbill (*Loxia curvirostra*)	146	32
	Song Sparrow (*Melospiza melodia*)	20	58
	Townsend's Solitaire (*Myadestes townsendi*)	32	62
	Townsend's Warbler (*Dendroica townsendi*)	1	9
	Tree Swallow (*Tachycineta bicolor*)	16	22
	Western Meadowlark (*Sturnella neglecta*)	55	59
	Western Wood Peewee (*Contopus sordidulus*)	82	153
	Willow Flycatcher (*Empidonax traillii*)	6	23
	Yellow Warbler (*Dendroica petechia*)	5	5
	Yellow-rumped Warbler (*Dendroica coronata*)	4	6

TABLE 8. Correlations in detection rates for cavity-nesting species between 1998 and 1999 across point-count stations at the Turnbull National Wildlife Refuge.

Species	r	*P*
Downy Woodpecker	-0.12	0.16
Hairy Woodpecker	0.18	0.05
Northern Flicker	0.14	0.12
Red-naped Sapsucker	0.10	0.26
Red-breasted Nuthatch	0.12	0.18
White-breasted Nuthatch	0.27	0.003
Pygmy Nuthatch	0.41	<0.0001
Black-capped Chickadee	0.005	0.95
Mountain Chickadee	0.06	0.51
European Starling	0.32	0.0003
Western Bluebird	0.51	<0.0001
House Wren	0.52	<0.0001

TABLE 9. Correlations between species across point-count stations at the Turnbull National Wildlife Refuge in 1998 and 1999 based on the detection index. Correlations are only presented if significant in at least 1 year.

	1998		1999	
Species pair	r	*P*	r	*P*
Black-capped Chickadee-Hairy Woodpecker	0.20	0.03	-0.05	0.32
Black-capped Chickadee-Northern Flicker	0.18	0.047	0.02	0.77
Black-capped Chickadee-Red-breasted Nuthatch	0.25	0.006	0.09	0.31
European Starling-House Wren	0.35	<0.0001	0.16	0.07
European Starling-Pygmy Nuthatch	0.35	<0.0001	0.25	0.005
European Starling-Western Bluebird	0.28	0.002	0.00	0.99
Hairy Woodpecker-Downy Woodpecker	0.18	0.054	-0.09	0.32
House Wren-White-breasted Nuthatch	0.18	0.048	0.17	0.06
Pygmy Nuthatch-Red-breasted Nuthatch	-0.28	0.0015	-0.19	0.035
Pygmy Nuthatch-House Wren	0.24	0.007	0.35	<0.0001
Western Bluebird-Northern Flicker	0.18	0.048	0.12	0.19
Western Bluebird-Pygmy Nuthatch	0.25	0.001	0.41	<0.0001
Western Bluebird-White-breasted Nuthatch	0.29	0.0013	0.164	0.07

TABLE 10. Means (± 1 SE) for species richness and the detection index (detections per station per day) for three groups of cavity-nesting species (listed in Table 6) and for other passerines. Means were calculated for observations within the 50-m radius point-count stations.

	Species richness				Detection index			
Cavity-nesting type	1998	1999	Test	P	1998	1999	Test	P
Strong primary	0.6 ± 0.1 (0 – 2)	0.6 ± 0.1 (0 – 3)	0.01	0.9	0.13 ± 0.02	0.15 ± 0.02	-0.88	0.39
Weak primary	2.1 ± 0.1 (0 – 5)	2.5 ± 0.1 (0 – 5)	5.8	0.02	0.74 ± 0.05	0.92 ± 0.11	-1.71	0.11
Secondary	1.2 ± 0.1 (0 – 3)	1.2 ± 0.1 (0 – 3)	0.6	0.4	0.52 ± 0.06	0.58 ± 0.09	-1.12	0.28
Other passerine	4.9 ± 0.2 (1 – 9)	5.4 ± 0.1 (2 – 10)	8.4	0.004	1.68 ± 0.11	1.94 ± 0.13	-1.83	0.09

TABLE 11. Habitat variables that were significant predictors ($P < 0.05$) of the combined detection index at the point-count stations for primary and secondary cavity nesters grouped together and individually. The sign of the relationship is given after the variable name. DC = decay class; NND = nearest neighbor distance.

	1998		1999	
Group or species	Variables	R^2	Variables	R^2
Primary	Green-tree basal area - DC2 cavities +	20.8	Mean NND of green trees + DC2 cavities + DC2 snags -	20.3
Secondary	Mean NND of green trees + DC1 snags +	22.1	Mean NND of green trees + Mean DBH of green trees +	24.8
Downy Woodpecker	Mean height DC1 +	8.7	Mean height DC2 + Mean DBH DC2 - DC3 snags -	34.5
Hairy Woodpecker	Mean DBH DC1 - Mean DBH DC2 - Mean NND of green trees + Mean height DC1 +	29.6	Mean height DC2 + Mean DBH DC2 -	12.4
Northern Flicker	DC1 snags + Mean height DC1 - Green-tree basal area - Mean DBH of green trees + Mean NND of green trees +	39.4	Mean height DC1 - Mean height DC2 + Mean DBH DC1 +	23.8
Red-naped Sapsucker	DC1 snags + Green-tree basal area - Mean DBH of green trees + Green tree density + Mean NND of green trees +	47.0	No model	
White-breasted Nuthatch	DC2 cavities + Green-tree basal area -	17.7	No model	
Red-breasted Nuthatch	DC2 cavities + Mean DBH of green trees +	18.5	No model	
Pygmy Nuthatch	Mean NND of green trees + Mean DBH DC1 -	22.9	Number of green trees - Mean height DC3 +	21.1
Red-breasted Nuthatch (including Pygmy Nuthatch)	DC2 cavities + Mean DBH of green trees + DC2 snags – Pygmy Nuthatch -	39.5	Mean DBH DC1 + Pygmy Nuthatch -	13.9

TABLE 11. Continued.

	1998		1999	
Cavity-nesting type	Variables	R^2	Variables	R^2
Pygmy Nuthatch (including Red-breasted Nuthatch)	Red-breasted Nuthatch – DC1 snags + Mean DBH DC1 - Mean DBH DC2 - DC2 cavities + DC3 cavities + Mean NND of green trees + Mean DBH DC1 -	56.7	Number of green trees - Mean height DC3 + Red-breasted Nuthatch -	25.2
Black-capped Chickadee	Mean DBH of green trees +	6.5	No model	
Mountain Chickadee	DC1 - Mean DBH DC3 + Green-tree basal area -	16.8	Mean height DC3 - DC3 cavities + DC2 cavities +	20.8
European Starling	DC1 + Mean DBH DC3 -	16.7	Number of green trees + Mean NND of green trees +	17.4
Western Bluebird	Mean DBH DC1 + Mean height DC2 + Number of green trees +	40.8	Mean DBH DC2 - Mean DBH of green trees + Mean NND of green trees + DC1 +	65.2
House Wren	DC1 + DC2 - DC3 cavities + Mean DBH of green trees +	22.9	Mean DBH of green trees +	6.7

APPENDIX 1. Snag required per 100 ha for three species of primary cavity-nesting birds at different percentages of maximum potential population size based on the Thomas et al. (1979) model (from Appendix 22 in Thomas et al. 1979) and values modified for Turnbull National Wildlife Refuge (TNWR) by substituting the actual ratio of non-used to used snags (see text).

Species		100%	90%	80%	70%	60%	50%	40%	30%	20%	10%
Downy Woodpecker	Thomas	741	667	593	519	445	371	296	222	148	74
	TNWR	282	253	225	197	169	141	112	84	56	28
Hairy Woodpecker	Thomas	446	401	356	312	267	223	178	134	89	45
	TNWR	169	152	135	119	101	85	68	51	34	17
Northern Flicker	Thomas	93	84	74	65	56	47	37	28	19	9
	TNWR	35	32	28	25	21	18	14	11	7	3

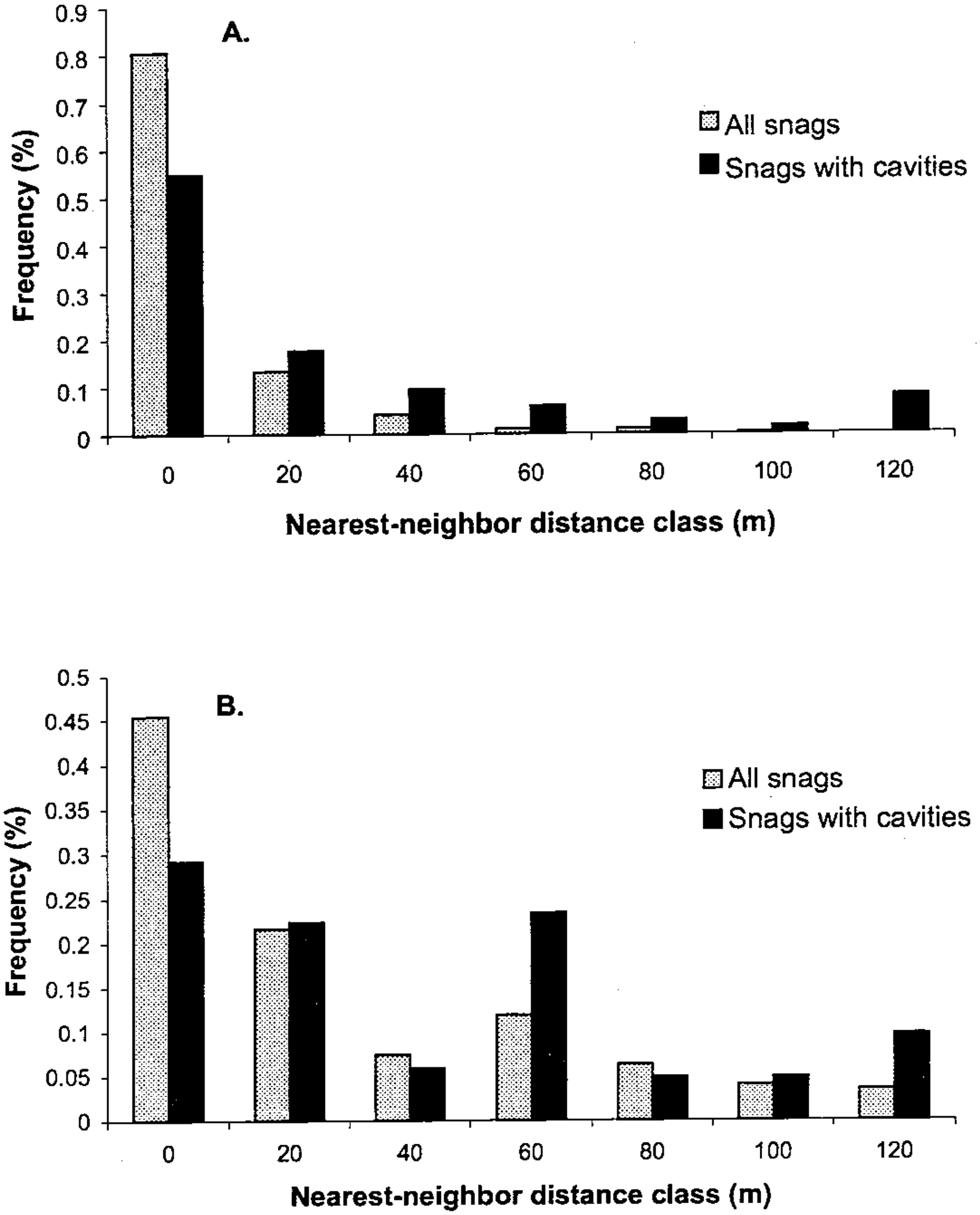

Figure 1. Frequency of nearest-neighbor distances in 20-m classes for all snags and for snags with cavities in (A) decay class 2 and (B) decay class 3.

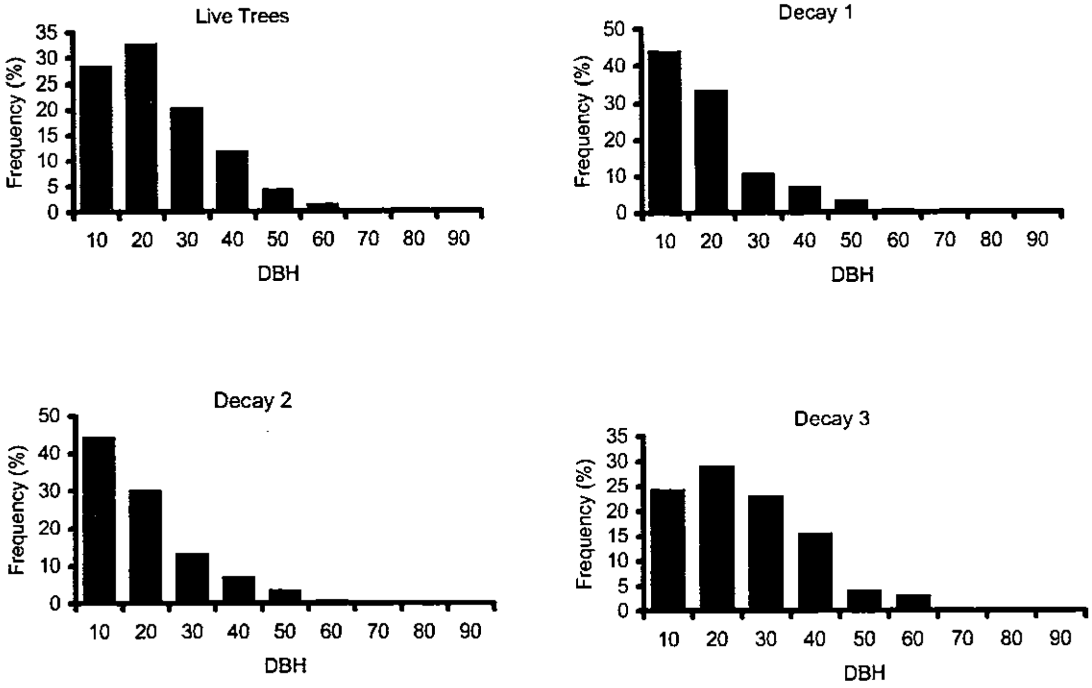

Figure 2. Size distributions of live trees and snags in three decay classes. The dbh classes indicate the minimum dbh (cm) for each size class.

Chapter 4

Persistence and Avian Use of Trees and Snags in Riparian Management Zones

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Introduction

Management of dying and dead trees in managed forests now focuses on promotion and active recruitment of such trees in recognition of their roles in forest dynamics, as sources of coarse woody debris, and as critical habitat for wildlife. Previously, elimination of snags was common because of lack of commercial value, safety concerns, and fire hazard. Several reviews document the importance of dying and dead trees of forests in general (e.g., McComb and Lindenmayer 1999) and in the forests of the Pacific Northwest in particular (e.g., Maser et al. 1988, Bull et al. 1997). When standing, dying and dead trees support a variety of fungi and invertebrates that are responsible for the progressive decomposition of the wood. Many vertebrates, including birds, mammals, amphibians, and reptiles, utilize snags or living trees with dead portions for foraging, roosting, and nesting. The length of time that snags remain standing is highly variable, but might be decades (McComb and Lindenmayer 1999), whereas live trees with dead portions typically remain standing for much longer (Bull et al. 1997). After these trees fall, or parts of these trees break off and fall, the logs continue to provide nesting and foraging habitat for many vertebrate species. In addition, these logs play important roles in ecosystem function such as nutrient recycling and as seedbeds for different plants. Logs falling into streams are one determinant of stream flows and sediment routing. The recognition of the roles that dead and dying trees play in forest dynamics has led to various guidelines for forest management to retain and recruit snags.

To provide adequate snag densities, prescriptive guidelines have been proposed for different forest types and by different regulatory agencies (e.g., Oregon Department of Forestry 1997, Washington State Department of Natural Resources 2000). Riparian forests, because of their critical importance, have received particular attention. Most management prescriptions require that areas adjacent to streams in harvested units have reduced or no logging to create a riparian buffer. Although the primary management objective of these riparian buffers is typically water and fish habitat quality and stream bank stabilization, the buffers often represent the highest concentration of snags and snag recruitment trees in the area after harvesting. The abiotic features that characterize riparian habitats, such as high soil moisture and flooding (Brinson and Verhoeven 1999), might result in differences in the persistence and recruitment of snags in riparian as compared to upland habitats.

Our objective was to assess temporal changes in tree and snag densities in previously logged riparian harvest units in managed forests of Washington State. We compared tree and snag densities to those recorded 4-10 years earlier in two projects that characterized the vegetational structure of riparian zones shortly after timber harvest (Washington Department of Wildlife 1991, O'Connell et al. 2000). In addition, we examined the proportion of trees and snags with signs of avian foraging and nesting activity.

Project Background

The managed forests of Washington State encompass approximately 15.9 million acres of which about 63% are owned by the State, various tribes, and private landowners (Washington Department of Natural Resources 1992). The Timber Fish and Wildlife (TFW) Agreement of 1987 introduced both a framework for management of Washington's state and private lands to protect natural and cultural resources within the context of the managed forest, and a mechanism to evaluate and modify management practices. A set of management goals for the different resources provided the starting point for participants to develop the TFW Agreement. For wildlife, the goal "... is to provide the greatest diversity of habitats (particularly riparian, wetlands, and old growth), and to assure the greatest diversity of species within those habitats for the survival and reproduction of enough individuals to maintain the native wildlife of Washington forest lands" (TFW Agreement 1987, *P*.2). Inherent in this statement was the recognition of the importance of maintaining habitat diversity to ensure wildlife species diversity and of the disproportionate importance of certain habitats, including riparian habitats. In an attempt to balance wildlife and economic goals, the TFW Agreement established Riparian Management Zones (RMZs) for the protection of riparian areas and recommended appropriate sizes, tree densities, and management practices for RMZs associated with several defined water types. These guidelines were incorporated into the Forest Practices Board Rules and Regulations (Washington State Forest Practices Board 1988). Definitions of the designated water types are as follows (Washington State Forest Practices Board 1988). Type 1 waters were defined as all waters, within their ordinary high-water mark, as inventoried as "shorelines of the state" under chapter 90.58 RCW. Type 2 waters were defined as natural waters not designated as Type 1; with a channel width >20 ft and a gradient of <4%; used by anadromous and resident fish for spawning, rearing or migration; and with a high use and importance from a water quality standpoint. Type 3 waters were defined as segments of natural waters which were not classified as Type 1 or 2 waters; with a channel width >5 ft and a gradient of <12%; used by anadromous and resident fish for spawning, rearing or migration; and highly significant for protection of downstream water quality. Type 4 waters were defined as segments of natural waters which were not classified as Type 1, 2, or 3 waters; perennial flow, with a channel width >2 ft. Type 5 waters were defined as segments of natural waters which were not classified as Type 1, 2, 3, or 4 waters including intermittent streams and ponds.

In western Washington, the 1988 RMZ guidelines (WAC 222) prescribed the maximum width of the RMZs on Type 1 and 2 streams to be 100 ft, on widest (>75 ft) streams and 75 ft on streams <75 ft. On Type 3 streams, the maximum width of RMZ was prescribed to be 50 ft on >5-ft wide streams and 25 ft on <5-ft wide streams. In eastern

Washington, the RMZ widths varied depending on the type of upland harvest. For partial cuts, the RMZ guidelines prescribed a minimum width of 30 ft and maximum width of 50 ft. For any other cut (e.g., regeneration, clearcut), the guidelines prescribed an average width of 50 ft and a maximum width of 300 ft. The RMZ guidelines mandated that a specified number and size of coniferous and deciduous trees be left within the RMZ buffers.

Several years after adoption of the RMZ guidelines, the Habitat Division of the Washington State Department of Fish and Wildlife, in conjunction with the Timber Fish and Wildlife Program, undertook a characterization of the Riparian Management Zones (Washington Department of Wildlife 1991). The physical and botanical features of the RMZs along water type 1, 2, and 3 streams on private and state owned forest sites on 155 west and 29 east side of the state were sampled during 1988, 1989, and 1990. We located and resampled 18 west side sites and 9 east side sites in 1998 and 1999. This project will be referred to as the WDFW RMZ Study in this report.

In 1991, the Timber Fish and Wildlife Program initiated a second project associated with the Riparian Management Zones (O'Connell et al. 2000). This project examined the effectiveness of RMZs in providing habitat for wildlife by monitoring population responses of selected wildlife species and species groups within riparian zones and adjacent upland habitats to different harvest prescriptions for the riparian buffer. Recognizing that variation is inherent to these forests, we selected 18 riparian forest stands that met the following criteria: mature, mixed-coniferous forest that had been previously harvested, similar elevation, and similar stream type. Because of the importance of both forest structure and composition to terrestrial vertebrates, we adapted standard vegetation sampling methods to examine structural as well as floristic components of the riparian and adjacent upland habitats on the 18 sites before and after timber harvest. Seven sites served as unharvested controls and the uplands of 11 were logged following a partial harvest prescription. The riparian zones of 6 of these 11 sites were harvested according to the Washington State guidelines for Riparian Management Zones (State) and those of 5 sites were harvested according to a modified riparian harvest that identified and protected habitat features such as seeps and snags (Modified). Trees and snags were counted in 1992 before logging, in 1995 or 1996 after logging, and in 1998 in conjunction with the present study. This project will be referred to as the TFW RMZ Study in this report.

Methods

WDFW RMZ Project 1988-1990

To characterize the physical and botanical features of Riparian Management Zones (RMZs), the Habitat Division of the Washington State Department of Fish and Wildlife surveyed RMZs along water type 1, 2, and 3 streams on private and state owned forest sites on 155 west and 29 east side of the state during 1988 and 1989 and 8 of these sites were resampled in 1990 (for convenience, we refer to this sampling period as 1990, Washington Department of Wildlife 1991). We located and resampled 18 west side sites in 1999 and 9 east side sites in 1998 (Table 1).

Study area.–This project was conducted on previously harvested areas on commercial, state, and private forests of Washington. Most western Washington sites were located in the Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) zones (Washington Department of Wildlife 1991). Sites on the east side of the state were in

Douglas-fir (*Pseudotsuga menziesii*), Pacific silver fir (*Abies amabilis*), and subalpine fir (*Abies lasiocarpa*) zones.

Field Sampling.–We followed the protocol in the procedures manual for the earlier study for sampling live and dead trees (Washington Department of Wildlife 1990). At each site, transects perpendicular to the stream were spaced 76.4 m (250 ft) apart for the length of the RMZ unit. Each transect extended from the high water mark of the stream to the RMZ harvest unit boundary. Consequently, individual transects varied in length. Trees and snags were sampled in plots that encompassed 7.62 m (25 ft) off both sides of the transect (Fig. 1A).

Trees and snags were recorded by species, diameter, condition of live trees, and decay class of snags. Diameters were categorized into 7 size classes: 1) >0 and <10 cm (0-3.9"); 2) ≥10 and <20 cm (4-7.9"); 3) ≥20 and <29 cm (8-11.9"); 4) ≥29 and <40 cm (12-15.9"); 5) ≥40 and <50 cm (16-19.9"); 6) ≥50 and <60 cm (20-23.9"); and 7) ≥60 cm (>24"). The 6 condition classes were: 1) live tree, undamaged; 2) recent snag; 3) live tree, broken top; 4) live tree, dead top; 5) older snag, bark intact; and 6) older snag, no bark. We recorded presence of foraging holes and nest cavities on trees and snags.

Data Analysis.–The total number of trees observed in each species, condition, and size category was tallied across all sites for each sampling period. We examined general trends by three approaches. First, we calculated descriptive statistics for the number of trees per hectare for each species and tree class category for each sampling period. We consolidated conditions classes as follows: 1) live tree; 2) recent snag; 3) live tree with dead or broken top; and 4) older snag. Second, we grouped tree species into coniferous and deciduous trees and determined the absolute number of each observed in each sampling period. Third, we calculated the number of sites at which the number of trees in each category increased or decreased between sampling periods.

To quantify differences between sampling periods, the numbers of deciduous and coniferous trees in each condition and size category were calculated for each transect at each site. A paired t-test was conducted on the differences between the mean number of trees in each category per transect in 1990 and 1998/1999 sampling periods. Because this was a paired t-test between individual transects, we express the tree means as number of trees per transect rather than as number of trees per hectare. Tests were considered significant at $P < 0.05$.

Because presence of foraging holes or nesting cavities was not determined during the initial WDFW RMZ Study, we could not conduct temporal analyses. For 1999 , we compared frequencies of foraging holes and nesting cavities between tree species, size classes, and decay classes using a χ^2 -analysis for small frequencies that incorporates a randomization procedure to determine probabilities (Zaykin and Pudovkin 1993). Tests were considered significant at $P < 0.05$.

TFW RMZ Project 1991-1996

Study Area.–Research was conducted in mixed-coniferous forests in the Selkirk Mountains of northeastern Washington (Stevens and Pend Oreille counties). Forest composition in this region is variable and is affected by slope, aspect, edaphic factors, fire history, and timber management practices. Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and alder (*Alnus incana* and *Alnus sinuata*). Shrubs included gooseberry (*Ribes* spp.), devil's club (*Oplopanax horridum*), Oregon grape (*Berberis* spp.), mountain boxwood (*Pachistima myrsinites*), red-osier dogwood (*Cornus stolonifera*), ninebark (*Physocarpus malvaceus*), spireae (*Spireae* spp.), serviceberry (*Amelanchier alnifolia*), rose (Rosa spp.), huckleberry (*Vaccinium* spp.).

We selected 18 sites that met the following criteria: 1) a minimum 800-m reach of Type 3 or permanent Type 4 stream; 2) >16.2 ha of previously harvested stands at harvestable age on either side of the 800-m reach; 3) ≥610 m and ≤1200 m elevation; 4) mixed coniferous forest; 5) landowners agreed to either leave sites unharvested for 10 yr (controls) or to harvest sites within timeframe and specifications of study design (cut sites). Seven sites were unharvested control sites. The upland areas of 11 sites were selectively harvested in 1994-1995 to yield a 6- to 12-m spacing of trees. The riparian zones of 6 of the 11 sites were harvested according to the Washington State Forest Practices RMZ guidelines (State sites) and 5 of the 11 sites were harvested according to a modified prescription designed for this project (Modified sites). The Modified RMZ incorporated site-specific guidelines. Within 33-m zone of the stream, habitat features such as seeps, snags, and deciduous trees, were identified and protected. For example, 1 snag per 2 acres was buffered by a no-entry zone equal to 1.5 times the height of the snag, and all seeps were buffered by a 10-m no-entry zone that extended to the stream. Following timber harvest, the mean width of the State RMZ buffers was 14.1 ± 3.0 m with a range from 8-22.6 m. and the mean width of the Modified RMZ buffers was 29.7 ± 17.4 m with a range from 12 to 144 m.

Field Sampling.–To compare tree and snag characteristics between recently logged sites with Washington State Riparian Management Zone buffers, sites with experimental buffers, and unharvested control sites, we established a 16 × 20-m plot at each 50-m interval along the riparian and upland transects for a total of 15 riparian plots and 15 upland plots per site (Fig. 1B). Sampling of control plots was conducted in August 1992. Post-harvest sampling of all State and two Modified sites was conducted in July 1995 and of the three remaining Modified sites in July 1996. All sites were resampled in July 1998. One site was only partially resampled in 1998 due to severe blowdown that made trails impassable.

Within each plot all trees were recorded by species and assigned to one of four DBH size classes: 1) 4-10 cm, 2) 11-25 cm, 3) 26-50 cm, 4) >50 cm. All snags within each plot were counted and designated as either Condition 1 (bark basically intact) or Condition 2 (bark peeling off to absent). Four average live trees and two snags were chosen at random and their heights were estimated using a clinometer.

Using a convex densiometer, percentage of overstory and understory cover were measured at the center of each plot and at the center of each quadrant. We averaged the five measurements per plot for each variable.

Data Analysis.–The mean overstory cover, number of coniferous and deciduous trees in each size class, and number of snags of each condition category and size class were compared between the two sampling years using a repeated measures Analysis of Variance (SAS Institute Inc. 1988). If there was a significant ($P < 0.05$) effect of time in this analysis, then the means for each habitat variable were compared between the 2 years using a univariate Analysis of Variance. In these univariate analyses, the significance level was set at $P < 0.025$ (Sokal and Rohlf 1995).

Results

WDFW RMZ Project 1988 -1990

West Side.– The density of live trees of the five predominant coniferous species varied between sites and years (Table 2). Western hemlock was the most common conifer with respect to both density of trees and number of sites at which the species were found (Table 2). Douglas-fir and western red cedar were widely distributed, but their densities varied between years (Table 2). Older coniferous snags were distributed across more sites than recent snags or broken/dead top trees (Table 2). Red alder was the most common of the five deciduous species with respect to both density and number of sites at which live trees and snags were found (Table 2). Some deciduous species, such as black cottonwood, and willow were common at only a few sites (Table 2).

The absolute number of small live deciduous and coniferous trees and largest coniferous trees increased between the two sampling periods (Fig. 2) and the number of sites on which these trees increased was greater than those on which the trees decreased (Table 3). However, the increase in the mean number of live trees per transect between sampling periods was significant only for the ≥50 to <60 cm sized deciduous trees (Table 4).

In contrast, the absolute number of coniferous snags and broken or dead top coniferous trees of all size classes and deciduous snags of half of size classes decreased between the two sampling periods (Figs. 3, 4). The number of sites on which snags decreased was greater than the number on which snags increased or remained the same (Table 4). The mean number of recent small coniferous snags, larger broken top and small deciduous snags significantly decreased between the two sampling periods (Table 4).

The percent of trees with foraging holes and nest cavities is presented for the different size and decay classes of each tree species in Table 5. The 9 tree species differed with respect to the frequency of foraging activity ($\chi^2 = 29.14$; df = 8; $P < 0.001$) but not of nesting cavities ($\chi^2 = 11.69$; df = 8; $P = 0.24$). Overall, there were no differences in the frequency of foraging ($P = 0.37$) or nesting ($P = 0.65$) between deciduous and coniferous trees. Red alder was the only deciduous species with either foraging or nesting sign (Table 5). There were significant differences between the four deciduous tree species with respect to frequency of foraging sign ($\chi^2 = 19.47$; df = 3; $P < 0.001$), but not, due to low sample size, with respect to nest cavities ($\chi^2 = 7.18$; df = 3; $P = 0.15$). Similarly, there were differences between the five coniferous trees with respect to frequency of foraging sign ($\chi^2 = 9.00$; df = 4; $P = 0.04$), but not nesting cavities ($\chi^2 = 4.42$; df = 3; $P = 0.27$). The proportion of Douglas-firs with foraging sign was greater than the proportion of either western hemlock ($P = 0.04$) or western red cedar ($P = 0.03$). There were no differences between the other conifers.

No trees <10 cm DBH, regardless of decay class, had any foraging or nesting cavity sign (Table 5). The frequency of foraging ($\chi^2 = 87.98$; df = 6; $P < 0.001$) and nesting ($\chi^2 = 44.90$; df = 6; $P < 0.001$) sign differed between the different size classes of red alder trees. The proportion of red alder trees with foraging holes increased between Size Class 1 and Size Class 2 trees ($P < 0.001$) and again between the latter size class and Size Class 3 trees ($P = 0.003$). Size Class 3 red alders had a higher frequency of cavity holes than Size Class 1 trees

($P < 0.001$). The frequency of trees with foraging sign and nest cavities did not differ between the remainder of the size classes of red alders. Larger Douglas-fir trees had a greater frequency of foraging ($\chi^2 = 32.05$; df = 6; $P = 0.002$) and cavity ($\chi^2 = 18.05$; df = 6; $P = 0.038$) holes than smaller trees. A higher proportion of Size Class 3 than Size Class 1 Douglas-fir trees had foraging holes ($P = 0.008$) and a higher proportion of Size Class 6 than Size Class 1 Douglas-fir trees had nest cavities ($P = 0.004$). Similarly, larger western hemlock trees had a greater frequency of both foraging ($\chi^2 = 35.93$; df = 5; $P <0.001$) and nesting ($\chi^2 = 43.03$; df = 5; $P = 0.003$). A higher proportion of Size Class 2 than Size Class 1 western hemlock trees had foraging holes ($P = 0.028$) and a higher proportion of Size Class 5 than Size Class 1 western hemlock trees had nest cavities ($P = 0.03$).

No live trees or broken top trees, regardless of size class had sign of either foraging or nesting activity (Table 5). The frequency of both foraging ($\chi^2 = 782.39$; df = 5; $P < 0.001$) and nesting ($\chi^2 = 434.74$; df = 5; $P = < 0.001$) sign differed between the different decay classes of red alder trees. The proportion of live and broken top red alder trees with foraging sign was lower than that of any condition of snag or dead top trees ($P < 0.001$). Only dead top red alder trees and older red alder snags that had no remaining bark had any cavity holes (Table 5). The frequency of both foraging ($\chi^2 = 127.54$; df = 4; $P < 0.001$; $\chi^2 = 161.47$; df = 4; $P < 0.001$) and nesting ($\chi^2 = 434.74$; df = 5; $P < 0.001$; $\chi^2 = 47.37$; df = 4; $P < 0.001$) sign differed between the different decay classes of Douglas-fir and western hemlock trees, respectively. The proportion of live and broken top Douglas-fir trees with foraging sign was lower than that of recent and older snags ($P = 0.007$). Older western hemlock snags had a greater proportion of foraging sign than live or broken top western hemlocks ($P < 0.001$). With respect to nest cavities, only older snags with no remaining bark of both Douglas-firs and western hemlocks had any sign of nest cavities (Table 5; $P < 0.001$).

East Side.– The distribution and abundance of tree species on the east side sites were highly variable, as evidenced by the high density, but low number of sites at which species such as lodgepole pine and grand fir were found (Table 6). Douglas-fir in all tree classes were found at more east side sites than other conifers (Table 6). Red alder was the most common deciduous tree (Table 6).

The absolute number of live, broken/dead top, and dead deciduous and coniferous trees of most size classes decreased between the two sampling periods (Figs. 5, 6, 7). In addition, for most size and condition classes, more sites exhibited a decrease rather than an increase in number of trees (Table 7). There were no significant differences in the mean number of deciduous trees per transect between the two sampling periods (Table 8). The mean number of live coniferous and older snags per transect decreased significantly between 1990 and 1998 (Table 8).

The frequency of foraging ($\chi^2 = 8.84$; df = 5; $P = 0.12$) or nesting ($\chi^2 = 9.51$; df = 5; $P = 0.08$) sign did not differ between different tree species (Table 9). Nor was there any difference in the frequency of foraging sign between trees of different size classes ($\chi^2 = 4.93$; df = 5; $P = 0.43$). There were differences in the frequency of nest cavities between trees of different size classes ($\chi^2 = 11.37$; df = 5; $P = 0.04$). No Size Class 1 trees had any sign of nest cavities (Table 9). There were differences between the trees of different decay classes with respect to the frequency of both foraging ($\chi^2 = 400.40$; df = 4; $P <0.001$) and nesting (χ^2

= 396.67; df = 4; $P < 0.001$) sign. No live or broken top trees had any sign of foraging ($P < 0.001$) and only older snags had any nest cavities ($P = 0.01$).

TFW RMZ Project 1991-1996

Riparian Habitats.–Of the 8 main coniferous trees found in the riparian habitats of the TFW RMZ Project sites, western red cedar, Englemann spruce, and western hemlock were the most common (Table 10). Although statistical analyses were performed on combined counts of all coniferous species, examination of Table 10 suggests that the mean number of most tree species and snags declined on the Modified and, especially the State sites, between the 2 sampling years (Table 10).

Percentage of overstory cover was lower on the control sites as compared to either Modified or State sites in 1992/5 (Table 11), but increased on Control sites between 1992 and 1998 (Table 11) so that overstory cover was greater on the controls compared to the two cut sites in 1998 (Table 11). Overstory cover declined on the State sites between 1995 and 1998 but remained unchanged on the Modified sites (Table 11).

The mean number of smaller, younger snags was greater in 1992/5 relative to 1998 across all sites. The same pattern was observed for larger, young snags on the State sites. In contrast, there were no differences in mean number of larger, young snags on either Control or Modified sites. Condition 1 snags of all sizes were greater on Control sites in 1998. With respect to Condition 2 snags, the mean number of snags of the smaller and largest size classes remained constant between 1992 and 1998, whereas the mean number of medium-large snags increased in 1998 on the Control sites. There were more smaller, older snags in 1995 than 1998 on the Modified and State sites. The number of larger, Condition 2 snags remained constant between years on the Modified sites but declined on the State sites.

The mean height of snags was greater in 1992/5 than 1998 on the Control and State sites, but remained constant on the Modified sites. Snag height was lower on State as compared to Control sites in both years (Table 11).

On Control sites, the mean number of small coniferous trees decreased between years, medium coniferous trees increased between years, and that of the larger sized coniferous trees did not change (Table 11). The mean number of coniferous trees of all size classes declined between 1995 and 1998 on the State sites (Table 11). On the Modified sites, the mean number of small and medium coniferous trees declined, whereas the number of the larger coniferous trees remained constant (Table 11). The mean number of larger deciduous trees was constant between years on all sites whereas the number of smaller deciduous trees declined between 1992/5 and 1998 across all sites (Table 11). The small size class coniferous trees tended to be more common on the State as compared to Control sites in both sampling years, whereas larger coniferous trees were more common on the Control sites. The number of larger coniferous trees was comparable between State and Modified sites in 1995 and 1998. The mean number of deciduous trees of all size classes was never greater on the State sites as compared to the Modified and Control sites.

Upland Habitats.–Of the 12 main coniferous trees found in the upland habitats of the TFW RMZ Project sites, western red cedar, lodgepole pine, and western hemlock were the most common (Table 12). Two species of trees, ponderosa pine and western white pine, that were very uncommon in the riparian habitats, were more common in the upland habitats (Table 12).

During both sampling years, percent overstory cover was greatest on the Control sites and lowest on the State sites (Table 13). Percent overstory cover increased from 1992 to 1998 on the Control sites, but remained the same between 1995 and 1998 on the Modified and State sites (Table 13).

The mean number of smaller, Condition 1 snags was greater in 1992/5 than 1998 across all sites (Table 13). There were no differences between years across all sites in mean number of larger, Condition 1 snags and Condition 2 snags of all size classes (Table 13). The number of Condition 1 snags was greater on the Control sites than the Modified and State sites during both sampling years. There were no differences between sites in the mean number of large Condition 2 snags in either 1992/5 and 1998. The mean number of smaller Condition 2 snags was lower on State sites relative to either the Modified or Control sites in 1992/5, whereas in 1998, the mean number of these snags was similar on the State and Modified sites and lower than on Control sites (Table 13). The mean height of snags was greater in 1992 than 1998 on Control sites, but remained constant on Modified and State sites between 1995 and 1998 (Table 13). Snag height was lowest on State sites in both sampling years (Table 13).

The mean number of coniferous trees of all sizes declined between 1995 and 1998 on both State and Modified sites (Table 13). Smaller coniferous trees also declined on Control sites, but the number of larger coniferous trees remained similar between 1992 and 1998 (Table 13). The mean number of larger deciduous trees was constant between years on all sites, whereas the mean number of smaller deciduous trees was more variable between sites and years. There was little variation in the number of deciduous trees between Control, Modified, and State sites (Table 13).

Discussion

The primary management objective of riparian buffers has been protection of the integrity of the aquatic environment. Additionally, riparian buffers can provide habitat for terrestrial wildlife. For terrestrial wildlife, buffers are initially stopgap devices to provide habitat during the post-harvest years before the young forest on the adjacent uplands develops a closed canopy. At canopy closure, the riparian zone is once more buffered by the surrounding forest and at lower risk from weather extremes and any potential negative biotic effects associated with high-contrast edges. The basic strategy is to design a riparian buffer that will maintain the biota of the riparian zone through these early post-harvest years. Maintenance of the habitat integrity of the riparian buffers is largely related to the ability of these buffers to retain their habitat complexity, generally in the form of trees and snags. Success for a buffer design can be variously measured.

One measure is to compare the forest composition of buffers established in harvest units to unharvested forest. For example, Hibbs and Bower (2001) compared several metrics of forest attributes between riparian buffers (50-m wide; 1-33 yr since harvest) and undisturbed riparian forests in the Oregon Coastal Range. They observed few botanical differences in forest composition and dynamics between the buffers and intact forest. They concluded that the forest communities observed on these buffers at this point in time were relatively insensitive to the types of microenvironmental edge effects previously observed in other studies (e.g. Brosofske et al. 1997). However, they also concluded that long-term succession models predict a relatively treeless community in many of the riparian buffers (Hibbs and Bower 2001). The composition of the forest on the west-side WDFW RMZ Project sites was characteristic of west-side forests with western hemlock and Douglas-fir dominating conifer stands and red alder predominating on hardwood sites (e.g., Hibbs and Bower 2001, Acker et al. 2002). However the density of trees on the buffers of the WDFW RMZ Project sites was much less than observed on other west-side riparian forests (e.g., Acker et al. 2002). In contrast, the density of recent and older snags was comparable to densities of "hard" and "soft" snags reported by Ohmann et al. (1994) for west-side forests. The density and distribution of snags in the coniferous forests of eastern Washington can be highly variable depending upon factors such as slope, aspect, and disturbance history (e.g., Flanagan et al. 1998) and our results support this observation. Snags of given species typically dominated at certain sites whereas those of different species dominated at other sites. Snag densities observed during the resampling years of our study were typically lower that those observed for other east-side forests (e.g., Flanagan et al. 1998, Everett et al. 2000).

Another measure of buffer design is the persistence of trees and snags in the buffer and their use by cavity-nesting wildlife. We observed a general decline in the number of snags on the riparian buffers sampled in both eastern and western Washington during this study and minimal recruitment of live coniferous trees. Fall rates of snags can be highly variable depending upon the species, size, decay class, cause of death, and timber management practices (e.g., Cline et al. 1980, Morrison and Raphael 1993, Harrington 1996, Huggard 1999). For example, Everett et al. (2000) observed that snags of thin barked trees (e.g., Engelmann spruce, subalpine fir, and lodgepole pine) <41 cm DBH persisted longer than thick barked trees (e.g., Douglas-fir and ponderosa pine) but that Douglas-fir snags >41 cm DBH persisted longer than thin-barked trees. Morrison and Raphael (1993) observed that fall rates of snags were greater with smaller snags, snags in advanced decay classes, snags created by fire, and in pine (*Pinus* spp.) versus fir (*Abies* sp.) stands. Although fall rates are best determined from a marked population of snags, our results suggest similar trends. On the western and eastern Washington WDFW RMZ Project sites sampled in 1990 and 1999, the number of smaller and older decay class snags declined significantly between the 2 sampling years, whereas no change occurred in the number of larger and younger snags. In contrast, an initial increase of small (<10 cm DBH) snags was observed on some of these sites (Washington Department of Wildlife 1991). The mean number of larger snags varied less than that of the smaller snags between sampling years in both the riparian and upland habitats of the control and logged sites of the eastern Washington TFW RMZ project.

Riparian habitats can have different microclimatic conditions compared to the surrounding uplands and these differences might extend up to 60 m from the stream (Brosofske et al. 1997). Of particular importance to the persistence of snags and live trees in these habitats is the effect of wind and the potential for loss due to windthrow. The linear structure and high amounts of induced edge of riparian buffers might make standing live and dead trees especially vulnerable to the effects of windthrow in these buffers. Hairston-Strang and Adams (1999) cited evidence that windthrow is the major factor contributing to the falling of trees in several Pacific Northwest forests. Windthrow was observed on 5 of the 6 resampled western Washington WDFW RMZ Project sites (Washington Department of Wildlife 1991). Patterns of wind speed in riparian habitats appear to be highly variable and very site-specific (e.g., Brosofske et al. 1997; Ruel 2000). For example, in Douglas-fir and western hemlock forests of western Washington, Brosofske et al. (1997) observed that before timber harvest, wind speed patterns varied greatly between riparian sites, reflecting topographic and vegetation differences between sites. Although wind speed generally increased after timber harvest, the high levels of inter site variation remained and were not directly related to buffer width. Ruel (2000) examined how the width and harvest prescription of riparian buffers affected windthrow in balsam fir forests of eastern Canada. Windthrow was highly variable and not dependent upon either buffer width or whether buffers had been thinned or not. Windthrow was greatest when heavy winds blew perpendicular to the buffer (Ruel 200).

Although we cannot attribute declines in snags on our 18 TFW RMZ Project solely to windthrow, we can compare declines in snag densities between the three treatments in eastern Washington. In general, the number of snags of both condition classes remained more constant in the riparian habitats of the unharvested Control sites than on the harvested sites. The number of larger snags remained more constant in the riparian habitats of the sites harvested following the Modified buffer prescription than in the riparian habitats of the sites harvested following the State prescription. The number of snags of all size and condition classes except the largest, oldest snags declined significantly between the sampling years on the State sites. The number of snags in the largest and oldest classes was very low across all sites. In contrast to studies by Brosofske et al. (1997) and Ruel (2000), our Modified and State buffers did not differ only with respect to buffer width. The prescription for the riparian harvest on the Modified sites was site-specific and designed to incorporate enhanced protection of important wildlife habitat features such as snags and seeps. Although the buffer widths of the Modified sites averaged wider than on the State sites, they were highly variable. Along any given stream on a Modified site, the buffer widths might equal the uniform width of the State Riparian Management Zone buffers in some places, but in others the buffer might extend more into the upland reflecting the unlogged buffer around a designated snag or seep. A combination of the prescribed protection of individual snags and the more variable buffer zone edge might explain the reduced interyear variation in snag density on these Modified sites. In contrast, the upland habitats of the Modified and State sites were logged following a similar prescription and, although Control sites had consistently greater snag densities, there were no differences with respect to interyear variation in snag densities between treatments.

Avian use of snags for foraging and nesting is mediated by a variety of factors including tree species, size, and decay condition (e.g., Weikel and Hayes 1999, Joy 2000, Haggard and Gaines 2001, Hallett et al. 2001), within tree variation in hardness (e.g., Schepps et al. 1999), the spatial distribution of snags (e.g., Haggard and Gaines 2001), and bird species (e.g., Weikel and Hayes 1999, Haggard and Gaines 2001). Observations from studies of snag use by cavity nesting birds in Pacific Northwest forests suggest that, in general, birds will forage on younger and smaller snags than they will use for cavity excavation. Our results support these observations. With the exception of a few tree species that had no evidence of foraging or nesting use (e.g., bigleaf maple, buckthorn), cavity holes were observed on older snags >29 cm DBH. Foraging activity was observed on smaller (>10 cm DBH) and recent snags of many tree species. In addition to size and decay condition, the species and spatial distribution of snags can influence their use by cavity nesting birds. Haggard and Gaines (2001) compared cavity-nesting bird use of snags in post-fire stands in the eastern Cascades with 3 different densities of snags (low: 0-12 snags/ha, medium: 15-35, and high: 37-80). They observed that primary cavity nesters selected ponderosa pines and that stands with larger (>35 cm DBH) snags at medium density had the highest use. Given that these medium snag density stands also had the greatest proportion of ponderosa pines, they were unable to separate the effects of tree species from snag density (Haggard and Gaines 2001). However, their results do highlight the need to pay attention to the species composition, size, and spatial distribution of leave trees when designing riparian buffers. For west-side forests, our results would suggest the importance of maintaining larger red alder and Douglas-fir snags. For east-side forests, our results also suggest the importance of maintaining large snags. Although low sample size precluded identification of selected species, other studies suggest the importance of ponderosa pine snags for a variety of species (e.g., Campbell et al. 1996, Haggard and Gaines 2001).

Although snag densities declined between sampling years on Riparian Management Zones of both western and eastern Washington WDFW RMZ Project sites, there was more variation in the densities of live trees between the two regions. Results from the WDFW RMZ Project suggest that recruitment of deciduous trees is greater on the western Washington sites than on the eastern Washington sites. On the western Washington sites, the significant increase in the densities of deciduous trees reflects a combination of the mesic climatic conditions and more open overstory after logging. An increase in small deciduous trees had been observed soon after harvest on the resampled western Washington sites (Washington Department of Wildlife 1991). In contrast, deciduous trees did not exhibit the same increases between 1990 and 1998 on the eastern Washington riparian management zone sites. Densities of coniferous trees remained similar between years on the western Washington sites, and on the eastern Washington sites, densities of several size classes of coniferous trees significantly declined. The apparent absence of recruitment and possible decline of coniferous trees on the sites raises the question of whether the design of the riparian management zone is a contributing factor. Wider riparian buffers have been associated with increasing densities of live trees in both southern pine forests (Burns et al. 1999) and Pacific Northwest coniferous forests (Hairston-Strang and Adams 1997). Examination of interyear variation of coniferous trees on Control, State, and Modified sites from the Riparian Management Zone study provides insight, but does not fully answer the question. Given that densities of coniferous trees were not equal across all treatments during the first sample, it is best to compare densities within rather than between treatments. Densities of the smallest size class of coniferous trees declined between the 2 sampling years across all treatments. The decline on the Control sites might reflect suppression of young trees in these closed-canopy forests. Densities of all other size classes either increased or remained constant between years on the Control sites. In contrast, densities of all size classes of coniferous trees were significantly less on the State sites during the 1998 sampling. Interyear variation on the Modified sites was intermediate between the Control and State sites; densities of the largest size class remained constant whereas densities of all other size classes declined. The timeframe between sampling years on these sites was comparatively short. Future sampling should provide stronger insight into how buffer design affects the recruitment and retention of coniferous trees.

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Literature Cited

Acker, S. A., S. V. Gregory, G. Lienkaemper, W. A. McKee, F. J. Swanson, and S. D. Miller. 2002. Composition, complexity, and tree mortality in riparian forests in the central Western Cascades of Oregon. Forest Ecology and Management *in press*.

Brinson, M. M., and J. Verhoeven. 1999. Riparian forests. Pages 265-299 in M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients for small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Bull, E. L., C. G. Parks, and T. R. Torgerson. 1997. Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391. Pacific Northwest Research Station, Portland, Oregon.

Burns, G. A., R. M. Whiting, Jr., G. M. LeGrande, and J. G. Dickson. 1999. Wildlife linkages: volumes and values of residual timber in riparian zones in eastern Texas. Forest Ecology and Management 114:321-327.

Campbell, L. A., J. G. Hallett, and M. A. O'Connell. 1996. Conservation of bats in managed forests: roost use by *Lasionycteris noctivagans*. Journal of Mammalogy 77:976-984.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773-786.

Everett, R., J. Lehnmkuhl, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2000. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. International Journal of Wildland Fire 9:223-234.

Flanagan, P. T., P. Morgan, and R. L. Everett. 1998. Snag recruitment in subalpine forests. Northwest Science 72:303-309.

Haggard, M., and W. L. Gaines. 2001. Effects of stand-replacement fire and salvage logging on a cavity-nesting bird community in Eastern Cascades, Washington. Northwest Science 75:387-396.

Hairston-Strang, A. B., and P. W. Adams. 1997. Oregon's stream-side rules: achieving public goals on private land. Journal of Forestry 95:14-18.

_____. 1999. Potential large woody debris sources in riparian buffers after harvesting in Oregon, U.S.A. Forest Ecology and Management 112:67-77.

Hallett, J. G., T. Lopez, M. A. O'Connell, and M. A. Borysewicz. 2001. Decay dynamics and avian use of artificially created snags. Northwest Science 75:378-386.

Harrington, M. G. 1996. Fall rates of prescribed fire-killed ponderosa pine. Research Paper INT-RP-489, USDA Forest Service, Intermountain Research Station, Ogden, UT.

Hibbs, D. E., and A. L. Bower. 2001. Riparian forests in the Oregon Coast Range. Forest Ecology and Management 154:201-213.

Huggard, D. J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecological Applications 9:1009-1016.

Joy, J. B. 2000. Characteristics of nest cavities and nest trees of the red-breasted sapsucker in coastal montane forests. Journal of Field Ornithology 7:525-530.

Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin. 1988. From the forest to the sea: a story of fallen trees. USDA Forest Service General Technical Report PNW-GTR-229. Pacific Northwest Research Station, Portland, Oregon.

McComb, W. C., and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 in M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge.

Morrison, M. L., and M. G. Raphael. 1993. Modeling the dynamics of snags. Ecological Applications 3:322-330.

O'Connell, M. A., J. G. Hallett, S. D. West, K. Kelsey, D. Manuwal, and S. Pearson. 2000. Effectiveness of riparian buffer strips in providing habitat for wildlife. TFW-LWAG-00-001, Washington Department of Natural Resources, Timber, Fish & Wildlife Program, Olympia, Washington.

Ohmann, J. L., W. C. McComb, and A. A. Zumrawi. 1994. Snag abundance for primary cavity-nesting birds on nonfederal forest lands in Oregon and Washington. Wildlife Society Bulletin 22:607-620.

Oregon Department of Forestry. 1997. Oregon Forest Practices Act - Selected Statutes: Section 9, Chapter 9, Special Session Oregon Laws 1996. Leaving snags and downed logs in harvest type 2 or type 3 units; green trees to be left near certain streams. http://www.odf.state.or.us/FP/RULES/fpa-statute.htm

Ruel, J. C. 2000. Factors influencing windthrow in balsam fir forests: from landscape to individual tree studies. Forest Ecology and Management 135:169-178.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition, SAS Institute, Inc., Cary, North Carolina.

Schepps, J., S. Lohr, and T. E. Martin. 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? The Auk 116:658-665.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research, Third edition. W. H. Freeman and Company, New York.

Washington Department of Natural Resources. 1992. Forest resource plan: policy plan. Washington Department of Natural Resources, Olympia, Washington.

Washington Department of Wildlife. 1990. Characterization of riparian management zones and upland management areas with respect to wildlife habitat: field procedures handbook, second edition. TFW-003-90-005, Washington Department of Wildlife, Habitat Management Division, Olympia, Washington.

_____. 1991. 1988-90 cumulative report: characterization of riparian management zones and upland management areas with respect to wildlife habitat. TFW-WLI-91-001, Washington Department of Wildlife, Habitat Management Division, Olympia, Washington.

Washington State Department of Natural Resources. 2000. Washington Forest Practices Rules, Chapter 222-30 WAC, Timber Harvesting. Olympia, Washington. http://www.wa.gov/dnr/htdocs/fp/fpb/222-30.html

Washington State Forest Practices Board. 1988. Washington State forest practices, rules, and regulations. Olympia, Washington.

Weikel, J. M., and J. P. Hayes. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern Coast Range of Oregon. Condor 101:58-66.

Zaykin, D. V., and A. I. Pudovkin. 1993. Two programs to estimate significance of Chi-square values using pseudo-probability test. Journal of Heredity 84:152.

TABLE 1. Locations of WDFW RMZ Project sites on the west side and east side of the Cascade Mountains of Washington.

Site Number	Owner	Township/Range/Section	Stream Name
WEST SIDE			
41	Simpson	13N/01W/22	Unknown
55	Champion	17N/05E/21	Ohop Creek
58	Champion	17N/05E/22	S. Fork Ohop Creek
73	Weyerhaeuser	17N/07W/34	W. Fork Vesta Creek
79	Weyerhaeuser	13N/01E/12	S. Fork Newau
91	Champion	18N/05E/25	Foster/Kings Creek
100	Weyerhaeuser	17N/07W/15	Elizabeth Creek
109	Weyerhaeuser	15N/05E/5	Trib. to Tilton River
110	Plum Creek	15N/06E/35	Big Creek
122	Champion	15/N05E/24	Bear Creek
124	Weyerhaeuser	18N/09W/3	Wyman Creek
145	Weyerhaeuser	14N/01E/18	Mitchell Creek
158	Manke Lumber	14N/05E/17	Roundtop Creek
160	Pacific Lumber	13N/04E/25	Heller
170	Weyerhaeuser	17N/09W/30	Chapin Creek
194	John Hancock	16N/11W/13	Barlow
206	Weyerhaeuser	14N/01E/32	Lucas Creek
217	John Hancock	15N/05E/28	Nisqually River
EAST SIDE			
22	Private	36N/42E/8	Deep Creek
84	Boise Cascade	30N/34E/33	Nine Mile Creek
86	Private	21N/33E/32	Lime Creek
87	Private	32N/38E/12	Stensgar Creek
166	Omak Wood	36N/38E/12	Aenas
176	Private	38N/41E/29	S. Deep Creek
177	Private	37N/44E/13	Harvey Creek
178	Private	37N/39E/28	S. Fork Clugston Creek
213	Private	12N/15E/18	N. Fork Ahtanum Creek

TABLE 2. Mean (± SE) density (trees per hectare), number of sites (*n*), minimum, and maximum number of trees by species and tree class (1 = live; 2 = recent snag; 3 = live with dead or broken top; 4 = older snag) on 18 western WDFW RMZ Project sites measured in 1990 and 1999.

Species	Year	Tree Class	*n*	$\bar{x}$	SE	Min	Max
Bigleaf Maple	1990	1	11	6.82	3.55	0.16	40.25
	1999	1	11	2.91	1.21	0.31	14.48
	1990	2	1	0.97		0.97	0.97
	1999	2	1	1.01		1.01	1.01
	1990	3	2	2.40	1.71	0.69	4.11
	1999	3	1	0.97		0.97	0.97
	1990	4	5	1.93	0.99	0.59	5.85
	1999	4	3	1.06	0.37	0.41	1.63
Bitter Cherry	1990	1	2	1.08	0.22	0.87	1.30
	1999	1	3	3.96	1.51	0.97	5.79
	1990	4	1	6.76		6.76	6.76
	1999	4	1	0.97		0.97	0.97
Black Cottonwood	1990	1	2	75.53	74.66	0.87	151.06
	1999	1	3	6.66	5.46	0.50	17.52
	1888	3	1	3.76		3.76	3.76
	1990	4	1	15.02		15.02	15.02
	1999	4	1	1.25		1.25	1.25
Douglas-fir	1990	1	12	6.52	4.64	0.17	56.64
	1999	1	17	1.87	0.47	0.12	6.85
	1999	2	1	2.83		2.83	2.83
	1990	3	2	0.43	0.00	0.43	0.43
	1999	3	1	0.79		0.79	0.79
	1990	4	9	0.55	0.18	0.18	1.83
	1999	4	6	0.47	0.13	0.26	1.04
Grand Fir	1990	1	3	12.82	12.17	0.65	37.19
	1999	1	2	0.48	0.00	0.48	0.48
	1990	2	1	7.51		7.51	7.51
	1999	2	1	1.01		1.01	1.01
	1990	3	1	2.50		2.50	2.50
	1990	4	1	1.25		5.01	5.01
Other Hardwood	1990	1	14	4.30	1.63	0.52	18.78
	1999	1	10	14.94	5.81	0.51	56.74
	1990	2	1	9.66		9.66	9.66

TABLE 2. Continued.

Species	Year	Tree Class	n	$\bar{x}$	SE	Min	Max
Other Hardwood	1999	2	2	17.83	17.17	0.66	35.00
	1990	3	2	1.66	0.83	0.83	2.49
	1999	3	1	4.63	0.00	4.63	4.63
	1990	4	3	5.24	0.92	3.56	6.62
	1999	4	4	0.64	0.11	0.37	0.73
Pacific Yew	1990	1	1	2.83		2.83	2.83
Red Alder	1990	1	17	22.99	6.83	0.83	113.79
	1999	1	17	17.93	4.75	1.30	62.68
	1990	2	7	0.91	0.41	0.25	3.04
	1999	2	4	1.09	0.33	0.33	1.98
	1990	3	10	0.91	0.22	0.18	1.81
	1999	3	11	0.56	0.19	0.19	2.33
	1990	4	16	2.82	1.08	0.12	17.81
	1999	4	16	1.06	0.24	0.12	3.60
Sitka Spruce	1990	1	8	2.82	1.11	0.34	9.40
	1999	1	7	2.74	1.14	0.36	9.24
	1990	2	1	4.22		4.22	4.22
	1990	4	3	1.09	0.25	0.84	1.68
	1999	4	1	8.44		8.44	8.44
Western Hemlock	1990	1	16	9.36	3.63	0.13	48.68
	1999	1	16	6.08	2.21	0.12	32.24
	1990	2	3	4.89	1.85	1.32	7.93
	1998	3	4	1.06	0.30	0.38	1.51
	1999	3	3	1.70		0.57	0.57
	1990	4	11	1.56	0.61	0.16	6.90
	1999	4	12	0.68	0.27	0.17	3.48
Western Red Cedar	1990	1	15	4.49	1.64	0.24	19.31
	1999	1	15	1.99	0.47	0.24	6.31
	1990	2	5	0.55	0.08	0.39	0.78
	1999	2	3	0.72	0.00	0.72	0.72
	1990	3	3	0.42	0.10	0.33	0.65
	1999	3	1	1.30		1.30	1.30
	1990	4	6	0.52	0.09	0.23	0.90
	1999	4	5	0.56	0.22	0.28	1.39
Willow	1990	1	1	366.73		366.73	366.73
	1999	1	1	116.89		116.89	116.89

TABLE 3. Number of western Washington WDFW RMZ Project sites at which trees increased, decreased, or remained the same between the 1990 and 1999 sampling periods.

Species	Tree Class	Size Class	Increased	Decreased	Same
Conifer	Live	1	8	2	0
Conifer	Live	2	3	6	0
Conifer	Live	3	5	4	0
Conifer	Live	4	4	4	0
Conifer	Live	5	4	2	3
Conifer	Live	6	2	2	5
Conifer	Live	7	2	3	5
Conifer	Recent Snag	1	0	5	0
Conifer	Recent Snag	2	0	2	0
Conifer	Recent Snag	3	1	1	0
Conifer	Recent Snag	4	0	1	0
Conifer	Recent Snag	6	1	0	0
Conifer	Recent Snag	7	1	0	0
Conifer	Dead Top	1	0	1	0
Conifer	Dead Top	2	0	2	0
Conifer	Dead Top	3	1	2	0
Conifer	Dead Top	4	0	1	0
Conifer	Dead Top	7	1	0	0
Conifer	Old Snag	1	1	7	0
Conifer	Old Snag	2	3	3	0
Conifer	Old Snag	3	2	2	2
Conifer	Old Snag	4	0	1	0
Conifer	Old Snag	5	1	1	0
Conifer	Old Snag	6	1	1	1
Conifer	Old Snag	7	0	4	0

TABLE 3. Continued.

Species	Tree Class	Size Class	Increased	Decreased	Same
Deciduous	Live	1	8	2	0
Deciduous	Live	2	3	7	0
Deciduous	Live	3	1	7	2
Deciduous	Live	4	4	6	0
Deciduous	Live	5	5	4	1
Deciduous	Live	6	6	1	0
Deciduous	Live	7	2	2	0
Deciduous	Dead Top	2	0	2	0
Deciduous	Dead Top	3	2	2	0
Deciduous	Dead Top	4	2	0	0
Deciduous	Dead Top	5	3	1	0
Deciduous	Dead Top	6	0	1	0
Deciduous	Old Snag	1	4	4	1
Deciduous	Old Snag	2	1	6	1
Deciduous	Old Snag	3	4	4	1
Deciduous	Old Snag	4	4	2	2
Deciduous	Old Snag	5	2	2	0
Deciduous	Old Snag	6	2	0	0
Deciduous	Old Snag	7	1	1	0

TABLE 4. Mean (± SE) number of coniferous and deciduous trees by tree class and size class per transect on 18 western Washington WDFW RMZ Project Sites in 1990 and 1999. Comparisons are based on differences in tree counts on each transect using a paired t-test.

Species	Tree Class	Size Class	1990		1999		Comparison		
			$\bar{x}$	SE	$\bar{x}$	SE	*n*	t-value	*P*
Conifer	Live	1	6.81	1.99	17.9	8.03	31	1.39	0.18
		2	5.13	1.22	4.83	1.17	24	0.23	0.82
		3	2.64	0.65	2.84	0.60	25	0.52	0.60
		4	2.43	0.50	2.19	0.39	21	0.69	0.50
		5	2.10	0.53	2.0	0.38	19	0.44	0.67
		6	1.29	0.22	1.29	0.27	14	0.00	1.00
		7	1.91	0.30	1.91	0.38	23	0.00	1.00
	Recent Snag	1	1.60	0.40	0.00	0.00	5	4.00	***0.016***
		2	2.50	0.50	0.00	0.00	2	5.00	0.13
		3	0.75	0.25	0.50	0.29	4	0.52	0.64
		4	1.00		0		1		
		6	0		1.0		1		
		7	0		1.0		1		
	Dead Top	1	1.0		0		1		
		2	1.0	0.00	0.00	0.00	2		
		3	0.67	.033	0.33	0.33	3	0.50	0.67
		4	1.00	0.00	0.50	0.50	2	1.00	0.50
		7	0		1.00		1		
	Old Snag	1	2.0	0.87	0.31	0.13	13	1.82	0.09
		2	1.23	0.39	1.0	0.25	13	0.51	0.62
		3	0.75	0.19	0.67	0.22	12	0.27	0.79
		4	0.67	0.33	0.33	0.33	3	0.50	0.67
		5	0.50	0.50	0.50	0.50	2	0	1.0
		6	0.50	0.29	0.50	0.29	4	0	1.0
		7	1.00	0.22	0.50	0.27	7	1.18	0.28
Deciduous	Live	1	20.35	4.28	67.5	19.1	30	2.49	***0.019***
		2	12.40	3.93	11.3	4.06	25	0.39	0.70
		3	17.12	6.00	11.7	3.47	17	1.72	0.10

TABLE 4. Continued.

Species	Tree Class	Size Class	1990		1999		Comparison		
			$\bar{x}$	SE	$\bar{x}$	SE	n	t-value	*P*
Deciduous	Live	4	18.64	6.60	16.4	6.48	14	1.79	0.09
		5	7.46	2.60	8.31	2.88	13	0.68	0.51
		6	4.11	1.89	5.33	2.10	9	2.82	***0.023***
		7	5.80	2.08	7.20	3.43	5	0.93	0.40
	Recent Snag	1	2.00	1.41	4.67	3.76	6	0.60	0.58
		2	0.87	0.40	4.37	3.69	8	0.91	0.39
		3	1.00	1.00	1.50	0.50	2	1.00	0.50
		4	1.00	0.00	0.00	0.00	2		
		5	0.00		3.00		1		
		7	0.00		1.00		1		
	Dead Top	1	1.25	0.63	0.25	0.25	4	1.22	0.31
		2	1.50	0.34	0.33	0.21	6	2.45	***0.05***
		3	1.00	1.45	0.80	0.37	5	0.25	0.81
		4	0.83	0.48	1.67	0.88	6	1.54	0.18
		5	0.25	0.25	1.00	0.41	4	1.19	0.32
		6	0.00		2.00		1		
	Old Snag	1	2.56	0.81	1.17	0.37	18	1.44	0.17
		2	3.62	0.86	1.00	0.24	20	3.09	***0.006***
		3	1.87	0.50	2.00	0.57	15	0.40	0.70
		4	1.07	0.34	1.29	0.24	14	0.61	0.55
		5	1.14	0.55	0.86	0.14	7	0.47	0.65
		6	0.00	0.00	1.5	0.5	2	3.00	0.20
		7	0.50	0.50	0.50	0.50	2	0.00	1.00

TABLE 5. Proportion of trees with foraging and nesting sign on 18 WDFW RMZ Project sites in western Washington in 1999.

Species	Tree Class	Size Class	Total	% Forage	% Nest
Bigleaf Maple	Live	1-7	205	0	0
	Live, Dead Top	2	1	0	0
	Recent Snag	7	1	0	0
	Old Snag w/Bark	3	1	0	0
	Old Snag no Bark	1-4	6	0	0
Bitter Cherry	Live	1-2	37	0	0
	Old Snag w/Bark	5	1	0	0
Black Cottonwood	Live	1-5	40	0	0
	Old Snag w/Bark	3	1	0	0
Buckthorn	Live	1-2	691	0	0
	Live, Dead Top	2	1	0	0
	Recent Snag	1-2	53	0	0
	Old Snag w/Bark	1	2	0	0
	Old Snag no Bark	1-2	2	0	0
Douglas-fir	Live	1-7	270	0	0
	Recent Snag	6	1	100	0
	Old Snag w/Bark	1	2	0	0
		2	2	100	0
		3	2	100	0
		4	1	100	0
	Old Snag no Bark	4	1	100	100
		6	2	100	100
		7	1	100	100
Grand Fir	Live	2	2	0	0
	Recent Snag	7	1	0	0
Red Alder	Live	1-7	2578	0	0
	Live, Dead Top	1-2	6	0	0
		3	2	50	0
		4	2	100	0
		5	1	100	100
		7	1	100	100
	Recent Snag	1	1	0	0
		2	4	75	0
		3	1	100	0
		5	3	67	0

Table 5. Continued.

Species	Tree Class	Size Class	Total	% Forage	% Nest
	Old Snag w/ Bark	1	12	0	0
		2	8	25	0
		3	8	50	0
		4	6	33	0
		5	2	50	0
Red Alder	Old Snag w/ Bark	6	1	100	0
	Old Snag no Bark	1	16	0	0
		2	14	36	7
		3	35	47	14
		4	19	58	32
		5	5	100	60
		6	4	100	100
		7	2	100	100
Sitka Spruce	Live	1	54	0	0
	Old Snag w/ Bark	3	1	0	0
	Old Snag no Bark	1	1	0	0
Western Hemlock	Live	1-7	813	0	0
	Old Snag w/ Bark	1	1	0	0
		2	6	33	0
		3	6	33	0
		7	1	100	0
	Old Snag no Bark	1	6	0	0
		2	11	0	0
		3	11	9	0
		4	1	100	
		5	1	100	100
		7	3	67	100
Western Red Cedar	Live	1-7	171	0	0
	Recent Snag	3	3	0	0
	Old Snag w/ Bark	1-4	4	0	0
	Old Snag no Bark	1-2	5	0	0
		7	1	0	100

TABLE 6. Mean (± SE) density (trees per hectare), number of sites (n), minimum, and maximum number of trees by species and tree class (1 = live; 2 = recent snag; 3 = live with dead or broken top; 4 = older snag) on 9 eastern WDFW RMZ Project sites measured in 1990 and 1999.

Species	Year	Tree Class	*n*	$\bar{x}$	SE	Min	Max
Black Cottonwood	1990	1	4	10.5	5.4	4.9	27.2
	1999	1	4	6.7	2.2	2.5	11.1
	1990	3	1	5.8		5.8	5.8
	1999	3	1	5.8		5.8	5.8
	1990	4	1	6.2		6.2	6.2
Douglas-fir	1990	1	5	82.5	59.6	4.0	318.5
	1999	1	3	71.0	50.5	10.4	271.7
	1990	2	2	4.9	3.0	2.0	7.9
	1999	2	2	6.2	20.7	4.1	8.3
	1990	3	1	6.2		6.2	6.2
	1990	4	3	10.6	1.9	6.9	13.7
	1999	4	2	2.3	0.5	1.8	3.5
Englemann Spruce	1990	1	2	123.2	34.4	88.8	157.6
	1999	1	2	89.9	3.3	86.6	93.2
	1990	3	1	2.9		5.8	5.8
	1999	3	2	5.5	1.1	4.4	6.7
	1990	4	2	8.9	4.4	4.4	13.3
Grand Fir	1990	1	1	596.6		596.6	596.6
	1999	1	1	215.3		215.3	215.3
	1990	2	1	9.0		9.0	9.0
	1999	2	1	40.4		40.4	40.4
	1990	4	1	62.8		62.8	62.8
	1999	4	1	4.5		4.5	4.5
Lodgepole Pine	1990	1	1	381.5		381.5	381.5
	1999	1	1	523.0		523.0	523.0
Ponderosa Pine	1990	1	4	24.4	9.9	7.8	51.6
	1999	1	4	20.7	8.5	3.4	37.0
	1990	2	1	12.3		12.3	12.3
	1990	4	4	2.8	0.7	1.1	4.5
	1999	4	3	2.4	0.5	1.8	3.6

Table 6. Continued.

Species	Year	Tree Class	n	$\bar{x}$	SE	Min	Max
Red Alder	1990	1	2	803.7	276.2	527.7	1080.1
	1999	1	5	102.5	33.3	1.1	190.2
	1990	2	1	43.6		43.6	43.6
	1999	2	1	4.5		4.5	4.5
	1999	3	1	25.3		25.3	25.3
	1990	4	1	128.0		128.0	128.0
	1999	4	2	10.2	1.5	8.7	11.6
Western Larch	1990	1	3	41.0	35.2	1.7	11
	1999	1	3	21.0	17.6	1.7	56.
	1990	2	1	29.1		29.1	29.
	1999	2	1	2.9		2.9	2.9
	1990	4	1	34.9		34.9	34.
	1999	4	1	2.9		2.9	2.9
Western Red Cedar	1990	1	2	471.6	430.6	41.0	90
	1999	1	2	194.8	123.0	71.8	31
	1999	2	1	592.0		592.0	59
	1990	4	1	538.2		538.2	53
Paper Birch	1990	1	3	4.5	0.0	4.5	4.5

TABLE 7. Number of eastern Washington WDFW RMZ Project sites at which trees increased, decreased, or remained the same between the 1990 and 1999 sampling periods.

Species	Tree Class	Size Class	Increased	Decreased	Same
Conifer	Live	1	2	4	1
Conifer	Live	2	3	4	0
Conifer	Live	3	1	5	1
Conifer	Live	4	2	1	2
Conifer	Live	5	1	2	2
Conifer	Live	6	0	3	1
Conifer	Live	7	0	1	1
Conifer	Recent Snag	1	1	2	0
Conifer	Recent Snag	2	2	2	0
Conifer	Recent Snag	3	2	0	0
Conifer	Recent Snag	4	1	0	0
Conifer	Dead Top	1	0	1	0
Conifer	Dead Top	2	1	0	0
Conifer	Dead Top	3	1	2	0
Conifer	Dead Top	5	1	0	0
Conifer	Old Snag	1	0	4	0
Conifer	Old Snag	2	0	3	0
Conifer	Old Snag	3	0	2	0
Conifer	Old Snag	4	1	1	0
Conifer	Old Snag	7	0	2	1
Deciduous	Live	1	2	2	1
Deciduous	Live	2	2	2	1
Deciduous	Live	3	1	1	1
Deciduous	Live	4	0	1	0
Deciduous	Live	5	1	2	0
Deciduous	Live	6	0	1	0
Deciduous	Live	7	0	3	1
Deciduous	Recent Snag	1	1	1	1
Deciduous	Recent Snag	3	0	1	0
Deciduous	Dead Top	1	1	0	0
Deciduous	Dead Top	6	0	1	0
Deciduous	Old Snag	1	1	2	0
Deciduous	Old Snag	2	0	1	0
Deciduous	Old Snag	3	1	0	0
Deciduous	Old Snag	4	0	1	0

TABLE 8. Mean (± SE) number of coniferous and deciduous trees by tree class and size class per transect on 9 eastern Washington WDFW RMZ Project Sites in 1990 and 1999. Comparisons are based on differences in tree counts on each transect using a paired t-test.

			1990		1999		Comparison		
Species	Condition Class	Size Class	$\bar{x}$	SE	$\bar{x}$	SE	n	t-value	*P*
Conifer	Live	1	27.41	8.04	18.23	5.81	17	2.19	***0.04***
		2	17.00	7.57	10.27	3.19	15	1.38	0.19
		3	9.62	4.26	4.94	1.98	16	1.98	0.06
		4	2.38	0.75	2.38	0.59	13	0.00	1.00
		5	4.11	1.07	2.00	0.50	9	2.33	***0.05***
		6	2.12	0.35	0.87	0.12	8	3.03	***0.02***
		7	2.25	0.63	0.75	0.25	4	2.32	0.10
	Recent Snag	1	3.50	2.21	1.75	1.11	4	0.61	0.58
		2	1.16	0.65	1.50	0.96	6	0.23	0.82
		3	0.00	0.00	1.67	0.67	3	2.50	0.13
		4	0.00		3.00		1		
	Dead Top	1	1.00		0.00		1		
		2	0.00		2.00		1		
		3	1.00	1.00	1.00	0.00	2	0.00	1.00
		5	0.00		1.00		1		
	Old Snag	1	4.07	0.66	0.23	0.17	13	6.32	***0.0001***
		2	1.87	0.52	0.37	0.26	8	3.00	***0.02***
		3	2.00	0.00	0.33	0.33	3	5.00	***0.04***
		4	1.00	1.00	1.00	0.00	2	0.00	1.00
		7	1.25	0.45	0.25	0.25	4	1.41	0.25
Deciduous	Live	1	99.44	62.47	45.25	19.4	8	0.79	0.45
		2	18.14	11.32	18.67	7.87	6	0.24	0.82
		3	0.67	0.33	0.67	0.33	3	0.00	1.00
		4	1.00		1.00		1		
		5	1.33	0.67	0.67	0.33	3	0.76	0.53
		6	6.00		4.00		1		
Deciduous	Live	7	5.00	2.38	2.25	0.75	4	1.31	0.28
	Recent Snag	1	13		0.5		1		
		3	2.0		0.00		1		
	Dead Top	1	0.00		2.00		1		
		6	2.00		1.00		1		
	Old Snag	1	9.75	6.06	1.67	0.88	3	1.41	0.29
		2	3.00	3.00	1.00	0.00	2	0.67	0.63
		3	1.00		0.00		1		
		4	2.00		0.00		1		

TABLE 9. Proportion of trees with foraging and nesting sign on 9 WDFW RMZ Project sites in eastern Washington in 1998.

Species	Tree Class	Size Class	Total	% Forage	% Nest
Black Cottonwood	Live	1-7	23	0	0
Douglas-fir	Live	1-7	239	0	0
	Recent Snag	2	1	100	0
		3	2	100	
	Old Snag w/Bark	1	1	100	0
		4	1	100	100
	Old Snag no Bark	1	2	100	0
		6	2	100	100
		7	1	100	100
Englemann Spruce	Live	1-7	91	0	0
Grand Fir	Live	1-5	48	0	0
	Recent Snag	1	2	0	0
		2	2	100	
		3	3	100	
		4	3	100	
	Old Snag no Bark	3	1	100	100
Lodgepole Pine	Live	1-4	85	0	0
Other Hardwood	Live	1-4	31	0	0
Ponderosa Pine	Live	1-7	74	0	0
	Old Snag w/Bark	2	3	100	33
		7	1	100	100
Red Alder	Live	1-7	472	0	0
	Recent Snag	1	1	0	0
	Old Snag w/ Bark	1	2	0	0
		2	81	100	0
	Old Snag no Bark	1	3	0	0
		2	1	100	
Western Larch	Live	1-5	37	0	0
	Recent Snag	1	1	0	0
	Old Snag no Bark	4	1	100	100
		5	1	100	100
Western Red Cedar	Live	1-6	37	0	0
	Recent Snag	1	5	0	0
		2	6		

TABLE 10. Mean (± SE), number of sites (*n*), minimum, and maximum number of main coniferous trees per hectare by species and size class (small = ≤25, large = >25 cm DBH) and of snags by size class on 7 Control Sites, 6 State Sites, and 5 Modified Sites in eastern Washington TFW RMZ Study sites measured in 1992(Control)/1994 (State and Modified) and 1998 (all sites).

Species	Treatment	Year	Size Class	*n*	$\bar{x}$	SE	Min	Max
Douglas-fir	Control	1992	Small	6	25.6	13.5	2.1	83.3
		1998	Small	6	11.9	3.5	2.1	20.8
	State	1994	Small	6	51.7	23.8	4.2	145.8
		1998	Small	2	17.7	11.5	6.3	29.2
	Modified	1994	Small	5	22.1	10.0	4.2	58.3
		1998	Small	4	14.6	6.9	2.1	33.3
	Control	1992	Large	6	19.4	5.0	8.3	39.6
		1998	Large	6	20.8	7.5	4.2	52.1
	State	1994	Large	6	36.5	12.1	6.3	85.4
		1998	Large	2	9.4	7.3	2.1	16.7
	Modified	1994	Large	5	34.6	20.0	10.4	114.6
		1998	Large	4	24.6	19.6	2.1	83.3
Englemann Spruce	Control	1992	Small	6	105.6	104.4	0.0	643.8
		1998	Small	7	53.5	32.3	0.0	233.3
	State	1994	Small	5	343.8	189.2	12.5	960.4
		1998	Small	2	100.0	97.9	2.1	197.9
	Modified	1994	Small	4	78.8	37.1	18.8	187.5
		1998	Small	3	15.2	3.8	8.3	20.8
	Control	1992	Large	6	21.5	15.0	2.1	95.8
		1998	Large	7	19.2	7.3	4.2	56.3
	State	1994	Large	5	95.0	52.3	8.3	260.4
		1998	Large	2	36.5	36.5	0.0	72.9
	Modified	1994	Large	4	55.8	28.8	25.0	141.7
		1998	Large	3	13.1	2.5	8.3	16.7
Grand Fir	Control	1992	Small	5	104.4	49.0	33.3	283.3
		1998	Small	7	75.6	14.2	2.1	93.8
	State	1994	Small	6	67.1	33.5	10.4	177.1
		1998	Small	1	4.2	0.0	4.2	4.2
	Modified	1994	Small	5	78.3	45.8	4.2	250.0
		1998	Small	3	40.2	25.6	12.5	91.7
	Control	1992	Large	5	32.5	14.2	2.1	79.2
		1998	Large	7	29.2	8.1	0.0	56.3

TABLE 10. Continued.

Species	Treatment	Year	Size Class	n	$\bar{x}$	SE	Min	Max
Grand Fir	State	1994	Large	6	30.4	21.3	0.0	133.3
		1998	Large	1	2.1	0.0	2.1	2.1
	Modified	1994	Large	5	30.4	11.7	6.3	58.3
		1998	Large	3	18.8	8.8	6.3	29.2
Lodgepole Pine	Control	1992	Small	3	43.1	36.9	2.1	116.7
		1998	Small	3	18.8	17.7	0.0	54.2
	State	1994	Small	5	29.6	15.6	4.2	89.6
		1998	Small	2	8.3	4.2	4.2	12.5
	Modified	1994	Small	4	2.7	0.5	2.1	4.2
		1998	Small					
	Control	1992	Large	3	18.8	16.7	2.1	52.1
		1998	Large	3	11.0	7.9	2.1	27.1
	State	1994	Large	5	29.2	18.8	0.0	102.1
		1998	Large	2	3.1	1.0	2.1	4.2
	Modified	1994	Large	4	6.9	2.9	2.1	14.6
		1998	Large	2	5.2	3.1	2.1	8.3
Subalpine Fir	Control	1992	Small	4	31.3	15.4	12.5	77.1
		1998	Small	5	27.1	13.3	2.1	75.0
	State	1994	Small	4	175.6	96.9	6.3	393.8
		1998	Small	2	156.3	147.9	8.3	304.2
	Modified	1994	Small	3	9.8	7.7	2.1	25.0
		1998	Small	2	1.0	1.0	0.0	2.1
	Control	1992	Large	4	11.3	2.9	6.3	22.9
		1998	Large	5	9.4	3.1	0.0	14.6
	State	1994	Large	4	52.7	24.4	6.3	110.4
		1998	Large	2	27.1	22.9	4.2	50.0
	Modified	1994	Large	3	3.5	1.5	2.1	6.3
		1998	Large	3	0.6	0.6	0.0	2.1
Western Hemlock	Control	1992	Small	6	323.3	139.6	10.4	762.5
		1998	Small	7	172.7	56.9	10.4	343.8
	State	1994	Small	6	511.0	267.9	27.1	1808.3
		1998	Small	2	481.3	418.8	62.5	900.0
	Modified	1994	Small	5	118.8	55.4	20.8	266.7
		1998	Small	5	59.2	24.6	10.4	122.9
	Control	1992	Large	6	31.3	16.3	0.0	106.3
		1998	Large	7	30.8	14.0	0.0	106.3
	State	1994	Large	6	29.8	10.8	2.1	75.0
		1998	Large	2	13.5	11.5	2.1	25.0
	Modified	1994	Large	5	37.1	19.8	6.3	112.5
		1998	Large	4	24.6	6.9	8.3	39.6

TABLE 10. Continued.

Species	Treatment	Year	Size Class	*n*	$\bar{x}$	SE	Min	Max
Western Larch	Control	1992	Small	6	15.2	12.3	0.0	77.1
		1998	Small	6	9.4	6.9	0.0	43.8
	State	1994	Small	6	55.8	21.9	2.1	141.7
		1998	Small	2	45.8	33.3	12.5	79.2
	Modified	1994	Small	5	9.6	5.2	0.0	29.2
		1998	Small	4	17.1	10.0	2.1	45.8
	Control	1992	Large	6	28.1	14.6	2.1	100.0
		1998	Large	6	24.6	7.5	10.4	60.4
	State	1994	Large	6	55.8	21.9	2.1	141.7
		1998	Large	2	49.0	5.2	43.8	54.2
	Modified	1994	Large	5	30.8	16.7	2.1	93.8
		1998	Large	3	18.5	9.0	2.1	33.3
Western Red Cedar	Control	1992	Small	6	412.5	103.8	164.6	764.6
		1998	Small	7	288.5	40.2	62.5	375.0
	State	1994	Small	6	227.1	45.4	127.1	429.2
		1998	Small	6	115.0	11.7	75.0	150.0
	Modified	1994	Small	5	404.2	77.5	164.6	641.7
		1998	Small	5	182.1	32.3	77.1	252.1
	Control	1992	Large	7	107.9	41.7	6.3	306.3
		1998	Large	7	109.4	27.7	4.2	218.8
	State	1994	Large	6	45.8	16.3	6.3	100.0
		1998	Large	6	25.4	10.6	4.2	68.8
	Modified	1994	Large	5	89.2	22.3	22.9	162.5
		1998	Large	5	57.1	13.8	12.5	95.8
Recent Snag	Control	1992	Small	7	122.7	37.5	70.8	320.8
		1998	Small	7	61.5	16.0	12.5	118.8
	State	1994	Small	6	177.5	47.7	52.1	358.3
		1998	Small	6	53.8	13.3	29.2	112.5
	Modified	1994	Small	5	90.8	16.5	66.7	152.1
		1998	Small	5	45.8	8.8	27.1	75.0
	Control	1992	Large	7	32.5	15.0	6.3	104.2
		1998	Large	7	20.8	6.7	6.3	50.0
	State	1994	Large	6	17.3	5.2	4.2	33.3
		1998	Large	6	6.9	2.1	0.0	12.5
	Modified	1994	Large	5	14.6	3.3	6.3	25.0
		1998	Large	5	12.9	1.9	4.2	16.7

TABLE 10. Continued.

Species	Treatment	Year	Size Class	n	$\bar{x}$	SE	Min	Max
Old Snag	Control	1992	Small	7	32.5	9.8	20.8	85.4
		1998	Small	7	35.2	5.6	16.7	58.3
	State	1994	Small	6	74.4	16.5	8.3	108.3
		1998	Small	6	28.5	7.3	12.5	62.5
	Modified	1994	Small	5	60.4	10.6	31.3	97.9
		1998	Small	5	29.6	8.5	14.6	62.5
	Control	1992	Large	6	15.2	4.0	4.2	29.2
		1998	Large	7	17.9	1.9	12.5	25.0
	State	1994	Large	6	20.8	4.4	10.4	35.4
		1998	Large	6	11.9	1.7	6.3	16.7
	Modified	1994	Large	5	30.0	6.0	12.5	43.8
		1998	Large	5	29.4	8.5	8.3	56.3

TABLE 11. Mean (± SE) values for canopy cover, snag height, and trees per hectare by type and size class measured on 15 riparian plots on the 7 Control, 5 Modified, and 6 State TFW RMZ Study sites in eastern Washington. Comparisons between treatment and times are based on ANOVA; <or >indicates $P < 0.05$; = indicates $P > 0.05$.

	Control				Modified				State				Treatment		**Time**		
	1992		1998		1995		1998		1995		1998						
Habitat Variable	$\overline{x}$	*SE*	$\overline{x}$	*SE*	$\overline{x}$	*SE*	$\overline{x}$	*SE*	$\overline{x}$	*SE*	$\overline{x}$	*SE*	1995	1998	Control	Modified	State
Overstory canopy cover (%)	84.2	0.7	91.4	0.8	89.5	1.3	85.5	1.3	87.7	1.1	80.4	1.7	C<M=S	C>M>S	1992>1998	1995=1998	1995>1998
Snag height	15.5	0.9	10.1	1.0	11.4	0.8	8.9	0.8	9.4	0.6	7.2	0.6	C>M=S	C=M>S	1992>1998	1995=1998	1995>1998
Deciduous trees																	
5-10 cm DBH	118.8	21.9	21.9	6.3	68.8	15.6	9.4	0.3	71.9	12.5	6.3	3.1	C=M=S	C=M=S	1992>1998	1995>1998	1995>1998
11-25 cm DBH	50.0	6.3	12.5	3.1	46.9	9.4	9.4	0.3	18.8	3.1	0.6	0.6	C=M>S	C=M>S	1992>1998	1995>1998	1995>1998
26-50 cm DBH	6.3	1.6	3.1	0.9	15.6	3.1	6.3	1.6	3.1	0.9	0.3	0.3	M>C=S	M>S	1992=1998	1995>1998	1995=1998
>50 cm DBH	3.1	0.9	3.1	0.9	3.1	0.9	0.3	0.3	0.0	0.0	0.0	0.0	C=M=S	C=M=S	1992=1998	1995=1998	1995=1998
Coniferous trees																	
5-10 cm DBH	640.6	56.3	250.0	21.9	378.1	40.6	156.3	12.5	709.4	75.0	371.9	75.0	C=M<S	C=M<S	1992>1998	1995>1998	1995>1998
11-25 cm DBH	315.6	21.9	487.5	37.5	328.1	21.9	237.5	18.8	615.6	40.6	434.4	28.1	C>S>M	C=M<S	1992<1998	1995>1998	1995>1998
26-50 cm DBH	221.9	21.9	203.1	12.5	240.6	15.6	200.0	9.4	287.5	12.5	162.5	12.5	C<M=S	C=M=S	1992=1998	1995>1998	1995>1998
>50 cm DBH	65.6	6.3	65.6	3.1	37.5	6.3	28.1	3.1	43.8	6.3	21.9	3.1	C>M=S	C>M=S	1992=1998	1995=1998	1995>1998
Snags, condition 1																	
5-10 cm DBH	90.6	12.5	25.0	3.1	40.6	6.3	12.5	3.1	112.5	18.8	6.3	0.3	C=S>M	C>M=S	1992>1998	1995>1998	1995>1998
11-25 cm DBH	50.5	6.3	28.1	3.1	50.0	6.3	15.6	3.1	59.4	6.3	9.4	3.1	C=M=S	C>M=S	1992>1998	1995>1998	1995>1998
26-50 cm DBH	28.1	3.1	15.6	3.1	9.4	3.1	6.3	1.6	12.5	3.1	3.1	0.9	C>M=S	C>M=S	1992=1998	1995=1998	1995>1998
>50 cm DBH	9.4	3.1	6.3	1.3	6.3	1.6	3.1	0.9	6.3	1.6	0.0	0.0	C=M=S	C>M=S	1992=1998	1995=1998	1995>1998
Snags, condition 2																	
5-10 cm DBH	12.5	3.1	15.6	0.3	28.1	3.1	9.4	3.1	37.5	6.3	3.1	1.6	C<M=S	C=M>S	1992=1998	1995>1998	1995>1998
11-25 cm DBH	18.8	3.1	21.9	3.1	31.3	3.1	9.4	3.1	31.3	6.3	6.3	3.1	C<M=S	C>M=S	1992=1998	1995>1998	1995>1998
26-50 cm DBH	9.4	3.1	18.8	3.1	2.2	3.1	18.8	3.1	15.6	3.1	3.1	1.6	C=M>S	C=M>S	1992<1998	1995=1998	1995>1998
>50 cm DBH	3.1	0.9	6.3	0.9	6.3	3.1	6.3	3.1	3.1	1.6	3.1	1.6	C=M=S	C=M=S	1992=1998	1995=1998	1995=1998

TABLE 12. Mean (± SE), minimum, and maximum number of main coniferous trees per hectare by species and size class (small = ≤ 25, large = >25 cm DBH) and snags by size class on 7 Control Sites, 6 State Sites, and 5 Modified TFW RMZ Study Sites in eastern Washington upland sites measured in 1992 (Control), 1994 (State and Modified), and 1998 (all sites).

Species	Treatment	Year	Size Class	*n*	$\bar{x}$	SE	Min	Max
Douglas-fir	Control	1992	Small	7	137.9	76.3	0.0	406.3
		1998	Small	7	57.5	18.3	2.1	133.3
	State	1994	Small	6	100.0	28.3	27.1	187.5
		1998	Small	5	73.3	25.2	18.8	139.6
	Modified	1994	Small	5	59.6	23.8	8.3	133.3
		1998	Small	5	33.3	10.0	8.3	56.3
	Control	1992	Large	6	24.6	10.8	0.0	60.4
		1998	Large	7	27.3	10.2	2.1	64.6
	State	1994	Large	6	21.9	8.8	0.0	56.3
		1998	Large	5	16.7	6.3	2.1	39.6
	Modified	1994	Large	5	27.1	10.0	4.2	58.3
		1998	Large	5	15.4	7.9	0.0	45.8
Englemann Spruce	Control	1992	Small	5	42.5	35.8	2.1	185.4
		1998	Small	3	23.5	18.3	4.2	60.4
	State	1994	Small	4	26.0	11.7	4.2	58.3
		1998	Small	5	11.7	7.5	2.1	41.7
	Modified	1994	Small	4	51.0	46.3	2.1	189.6
		1998	Small	4	43.8	37.7	2.1	187.5
	Control	1992	Large	5	2.1	1.0	0.0	6.3
		1998	Large	5	4.8	2.7	0.0	10.4
	State	1994	Large	4	0.6	0.6	0.0	2.1
		1998	Large	5	0.4	0.4	0.0	2.1
	Modified	1994	Large	4	2.1	1.5	0.0	6.3
		1998	Large	3	2.7	1.9	0.0	6.3
Grand Fir	Control	1992	Small	7	93.8	32.9	33.3	314.6
		1998	Small	7	87.5	17.5	2.1	135.4
	State	1994	Small	6	13.5	5.4	4.2	39.6
		1998	Small	5	18.8	4.4	10.4	33.3
	Modified	1994	Small	5	44.6	16.7	16.7	102.1
		1998	Small		0.0	0.0	0.0	0.0
	Control	1992	Large	7	17.9	4.6	2.1	27.1
		1998	Large	7	19.4	4.6	0.0	27.1
	State	1994	Large	6	3.5	1.7	0.0	8.3
		1998	Large	4	2.5	1.9	0.0	8.3
	Modified	1994	Large	5	7.1	1.3	4.2	10.4
		1998	Large	5	2.1	0.6	0.0	4.2

TABLE 12. Continued.

Species	Treatment	Year	Size Class	*n*	$\bar{x}$	SE	Min	Max
Lodgepole Pine	Control	1992	Small	4	208.8	136.3	2.1	575.0
		1998	Small	6	120.4	67.7	0.0	414.6
	State	1994	Small	6	114.6	58.5	2.1	366.7
		1998	Small	5	51.3	29.0	8.3	164.6
	Modified	1994	Small	4	21.9	6.9	10.4	41.7
		1998	Small	4	35.4	8.3	2.1	93.8
	Control	1992	Large	6	23.5	17.3	6.3	79.2
		1998	Large	6	19.4	8.5	0.0	56.3
	State	1994	Large	6	14.2	7.1	0.0	45.8
		1998	Large	5	6.3	4.4	0.0	22.9
	Modified	1994	Large	4	24.4	10.2	4.2	45.8
		1998	Large	4	8.3	5.2	0.0	22.9
Ponderosa Pine	Control	1992	Small	3	2.7	0.6	2.1	4.2
		1998	Small	3	4.2	3.1	0.0	10.4
	State	1994	Small	2	10.4	8.3	2.1	18.8
		1998	Small	2	22.9	22.9	0.0	45.8
	Modified	1994	Small	1	12.5	0.0	12.5	12.5
		1998	Small	1	2.1	0.0	2.1	2.1
	Control	1992	Large	3	5.6	3.1	0.0	10.4
		1998	Large	3	7.5	0.6	6.3	8.3
	State	1994	Large	2	24.0	5.2	18.8	29.2
		1998	Large	2	16.7	6.3	10.4	22.9
	Modified	1994	Large	1	27.1	0.0	27.1	27.1
		1998	Large	1	22.9	0.0	22.9	22.9
Subalpine Fir	Control	1992	Small	6	47.5	20.4	4.2	129.2
		1998	Small	4	34.8	14.8	2.1	68.8
	State	1994	Small	3	28.5	5.0	18.8	35.4
		1998	Small	5	15.0	5.6	4.2	31.3
	Modified	1994	Small	1	2.1	0.0	2.1	2.1
		1998	Small	2	10.4	6.3	4.2	0.0
	Control	1992	Large	6	7.9	4.8	0.0	31.3
		1998	Large	4	10.0	8.5	0.0	35.4
	State	1994	Large	3	4.2	4.2	0.0	12.5
		1998	Large	5	0.8	0.0	0.0	2.1
	Modified	1994	Large	0	0.0	0.0	0.0	0.0
		1998	Large	0	0.0	0.0	0.0	0.0
Western Hemlock	Control	1992	Small	7	136.9	85.0	0.0	560.4
		1998	Small	7	88.3	40.2	0.0	304.2
	State	1994	Small	4	434.8	254.4	4.2	1008.3
		1998	Small	5	23.8	98.1	8.3	462.5
	Modified	1994	Small	4	83.8	40.4	10.4	191.7
		1998	Small	5	50.6	32.9	2.1	147.9

TABLE 12. Continued.

Species	Treatment	Year	Size Class	*n*	$\bar{x}$	SE	Min	Max
Western Hemlock	Control	1992	Large	6	37.5	20.4	0.0	114.6
		1998	Large	7	39.8	23.3	0.0	133.3
	State	1994	Large	4	2.1	2.1	0.0	8.3
		1998	Large	5	0.8	0.4	0.0	2.1
	Modified	1994	Large	4	5.2	1.9	0.0	8.3
		1998	Large	4	4.2	1.5	0.0	6.3
Western Larch	Control	1992	Small	6	120.2	85.2	2.1	602.1
		1998	Small	7	57.1	50.6	2.1	360.4
	State	1994	Small	6	65.2	34.6	4.2	231.3
		1998	Small	6	40.2	14.2	2.1	79.2
	Modified	1994	Small	5	19.6	16.0	0.0	83.3
		1998	Small	5	31.7	28.1	0.0	143.8
	Control	1992	Large	7	41.7	10.6	10.4	66.7
		1998	Large	7	39.8	8.3	4.2	58.3
	State	1994	Large	6	45.4	19.4	0.0	129.2
		1998	Large	6	20.0	8.3	2.1	56.3
	Modified	1994	Large	5	29.2	17.1	2.1	95.8
		1998	Large	5	8.3	2.9	2.1	16.7
Western Red Cedar	Control	1992	Small	7	444.2	241.3	104.2	1302.1
		1998	Small	7	307.1	82.7	41.7	631.3
	State	1994	Small	5	73.8	19.4	10.4	114.6
		1998	Small	5	59.6	15.6	6.3	95.8
	Modified	1994	Small	5	259.6	87.1	12.5	466.7
		1998	Small	5	138.3	52.3	6.3	277.1
	Control	1992	Large	7	41.9	21.5	0.0	122.9
		1998	Large	7	52.3	12.3	0.0	87.5
	State	1994	Large	5	8.8	0.0	16.7	0.0
		1998	Large	5	7.5	2.5	0.0	14.6
	Modified	1994	Large	5	14.2	6.5	2.1	31.3
		1998	Large	5	12.7	3.1	0.0	22.9
Western White Pine	Control	1992	Small	5	12.5	8.5	2.1	45.8
		1998	Small	3	4.2	2.5	0.0	10.4
	State	1994	Small	5	31.3	26.7	2.1	137.5
		1998	Small	3	15.2	7.9	2.1	29.2
	Modified	1994	Small	1	4.2	0.0	4.2	4.2
		1998	Small	1	10.4	0.0	10.4	10.4
	Control	1992	Large	5	5.4	2.5	0.0	12.5
		1998	Large	3	3.5	1.9	0.0	6.3
	State	1994	Large	5	1.3	0.8	0.0	4.2
		1998	Large	0	0.0	0.0	0.0	0.0
	Modified	1994	Large	0	0.0	0.0	0.0	0.0
		1998	Large	0	0.0	0.0	0.0	0.0

TABLE 12. Continued.

Species	Treatment	Year	Size Class	n	$\bar{x}$	SE	Min	Max
Recent Snag	Control	1992	Small	7	172.9	50.4	72.9	431.3
		1998	Small	7	72.1	8.8	29.2	106.3
	State	1994	Small	6	81.9	33.1	10.4	231.3
		1998	Small	6	41.3	4.4	25.0	54.2
	Modified	1994	Small	5	82.1	32.1	29.2	195.8
		1998	Small	5	27.5	3.8	14.6	35.4
	Control	1992	Large	7	34.4	14.2	0.0	79.2
		1998	Large	7	29.0	10.8	2.1	75.0
	State	1994	Large	6	5.8	2.1	0.0	14.6
		1998	Large	6	4.6	1.9	0.0	10.4
	Modified	1994	Large	5	4.6	1.3	6.3	12.5
		1998	Large	5	4.6	1.5	0.0	8.3
Old Snag	Control	1992	Small	7	54.2	15.4	16.7	118.8
		1998	Small	7	48.5	16.0	16.7	120.8
	State	1994	Small	6	24.6	10.8	2.1	75.0
		1998	Small	5	8.3	0.6	6.3	10.4
	Modified	1994	Small	5	30.8	6.0	16.7	50.0
		1998	Small	5	38.3	11.0	12.5	75.0
	Control	1992	Large	7	17.1	6.5	6.3	47.9
		1998	Large	7	15.2	3.8	2.1	39.6
	State	1994	Large	6	10.4	1.3	2.1	16.7
		1998	Large	5	7.9	1.3	6.3	12.5
	Modified	1994	Large	5	10.0	1.3	6.3	12.5
		1998	Large	5	8.8	1.7	4.2	12.5

TABLE 13. Means (± SE) for canopy cover, snag height, and trees per hectare by type and size class measured on 15 upland plots on the 7 Control, 5 Modified, and 6 State TFW RMZ Study sites in northeastern Washington. Comparisons between treatments and times are based on ANOVA; < or > indicates $P < 0.05$; = indicates $P > 0.05$.

	Control				Modified				State				Treatment		Time		
	1992		1998		1995		1998		1995		1998						
Habitat Variable	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	1995	1998	Control	Modified	**State**
Overstory canopy cover (%)	82.4	1.0	88.6	.08	58.2	3.2	56.4	3.7	52.4	2.2	47.5	2.8	C>M>S	C>M>S	1992<1998	1995=1998	1995=1998
Snag height	15.4	0.9	10.7	0.9	8.9	0.8	8.1	0.9	7.6	0.7	6.5	0.7	C>M=S	C=M>S	1992>1998	1995=1998	1995=1998
Deciduous trees																	
5-10 cm DBH	37.5	9.4	6.3	2.5	31.3	6.3	3.1	1.6	15.6	3.1	0.3	0.3	C=M=S	C=M>S	1992>1998	1995>1998	1995=1998
11-25 cm DBH	6.3	2.5	3.1	1.3	6.3	3.1	0.3	0.3	3.1	3.1	0.3	0.3	C=M=S	C=M=S	1992>1998	1995=1998	1995>1998
26-50 cm DBH	0.3	0.3	0	0	1.9	0.9	1.3	0.6	0.6	0.6	0.3	0.3	C=M=S	C=M=S	1992=1998	1995>1998	1995>1998
>50 cm DBH	0	0	0	0	0	0	0	0	0.3	0.3	0	0	C=M=S	C=M=S	1992=1998	1995=1998	1995=1998
Coniferous trees																	
5-10 cm DBH	696.9	56.3	271.9	25.0	315.6	37.5	190.6	28.1	350.0	50.0	278.1	43.8	C>M=S	C=M=S	1992>1998	1995>1998	1995>1998
11-25 cm DBH	559.4	37.5	325.0	21.9	203.1	25.0	156.3	18.8	256.3	28.1	175.0	15.6	C>M=S	C>M=S	1992>1998	1995>1998	1995>1998
26-50 cm DBH	168.8	9.4	143.8	9.4	106.3	9.4	50.0	6.3	96.9	9.4	59.4	6.3	C>M=S	C>M=S	1992=1998	1995>1998	1995>1998
>50 cm DBH	31.3	3.1	34.4	3.1	9.4	3.1	3.1	1.6	9.4	2.2	3.1	1.3	C>M=S	C>M=S	1992=1998	1995>1998	1995>1998
Snags, condition 1																	
5-10 cm DBH	118.8	15.6	31.3	3.1	50.0	0.9	9.4	2.2	31.3	0.6	0.9	3.1	C>M=S	C>M=S	1992>1998	1995>1998	1995>1998
11-25 cm DBH	68.8	6.3	34.4	3.1	37.5	6.3	15.6	3.1	31.3	0.6	12.5	3.1	C>M=S	C>M=S	1992>1998	1995>1998	1995>1998
26-50 cm DBH	31.3	3.1	25.0	3.1	3.1	12.5	3.1	1.6	6.3	1.9	3.1	0.9	C>M=S	C>M=S	1992=1998	1995=1998	1995=1998
>50 cm DBH	31.3	0.9	3.1	1.3	0.9	0.6	0.9	0.6	0.3	0.3	0	0	C>M=S	C>M=S	1992=1998	1995=1998	1995=1998
Snags, condition 2																	
5-10 cm DBH	28.1	3.1	25.0	6.3	18.8	3.1	12.5	3.1	6.3	2.2	12.5	0.6	C=M>S	C>M=S	1992=1998	1995=1998	1995=1998
11-25 cm DBH	21.9	3.1	21.9	3.1	12.5	2.5	15.6	3.1	9.4	2.5	2.2	0.9	C=M>S	C>M=S	1992=1998	1995=1998	1995=1998
26-50 cm DBH	12.5	2.2	12.5	2.5	9.4	1.6	6.3	1.6	6.3	1.9	3.1	1.3	C=M=S	C>M=S	1992=1998	1995=1998	1995=1998
>50 cm DBH	2.8	0.9	1.3	0.6	2.8	0.9	1.3	0.6	3.1	1.6	0.6	0.6	C=M=S	C=M=S	1992=1998	1995=1998	1995=1998

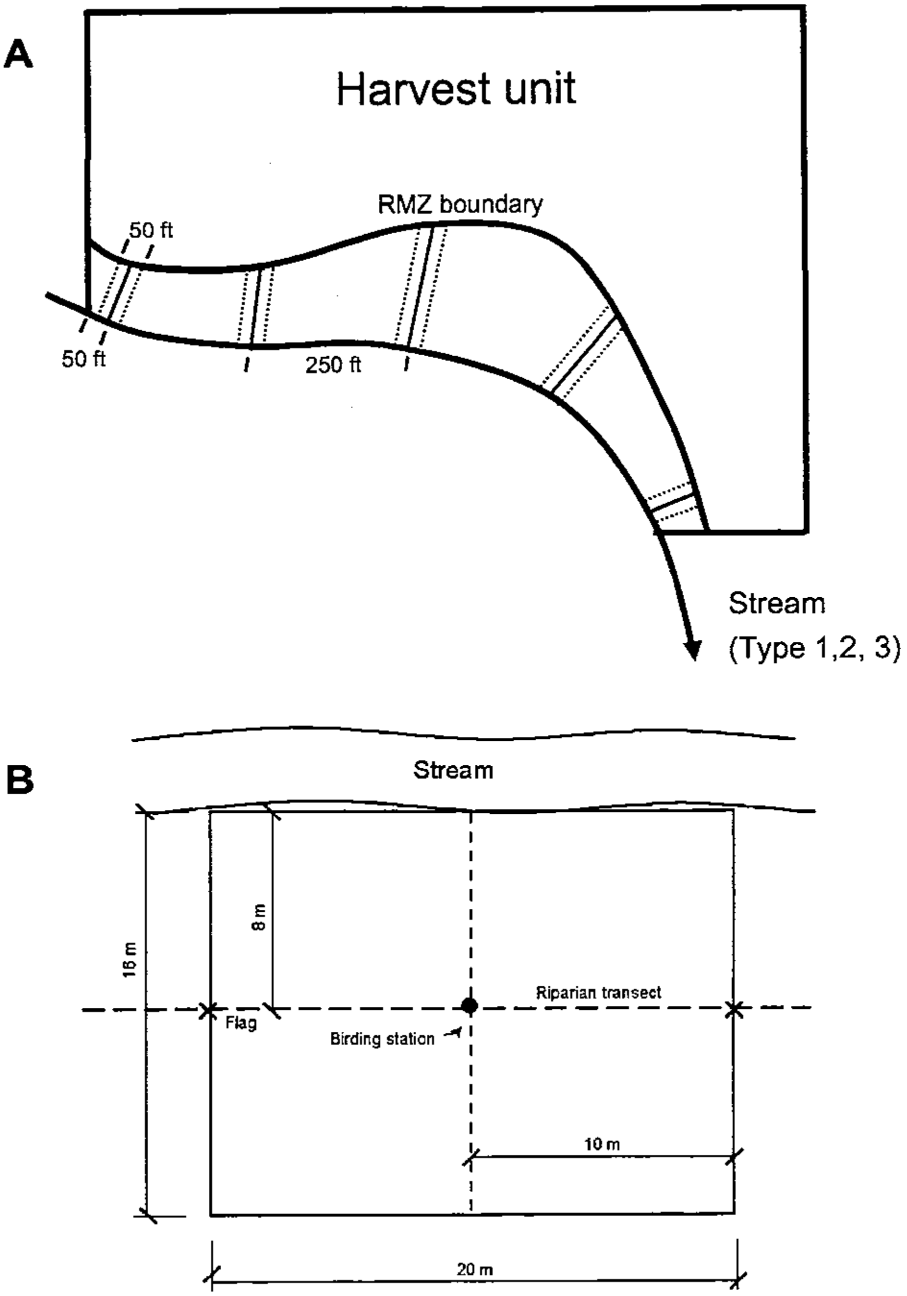


Figure 1. Sampling schemes used for (A) the WDFW RMZ project (Washington Department of Wildlife 1990) and (B) the TFW RMZ project in eastern Washington (O'Connell et al. 2000).

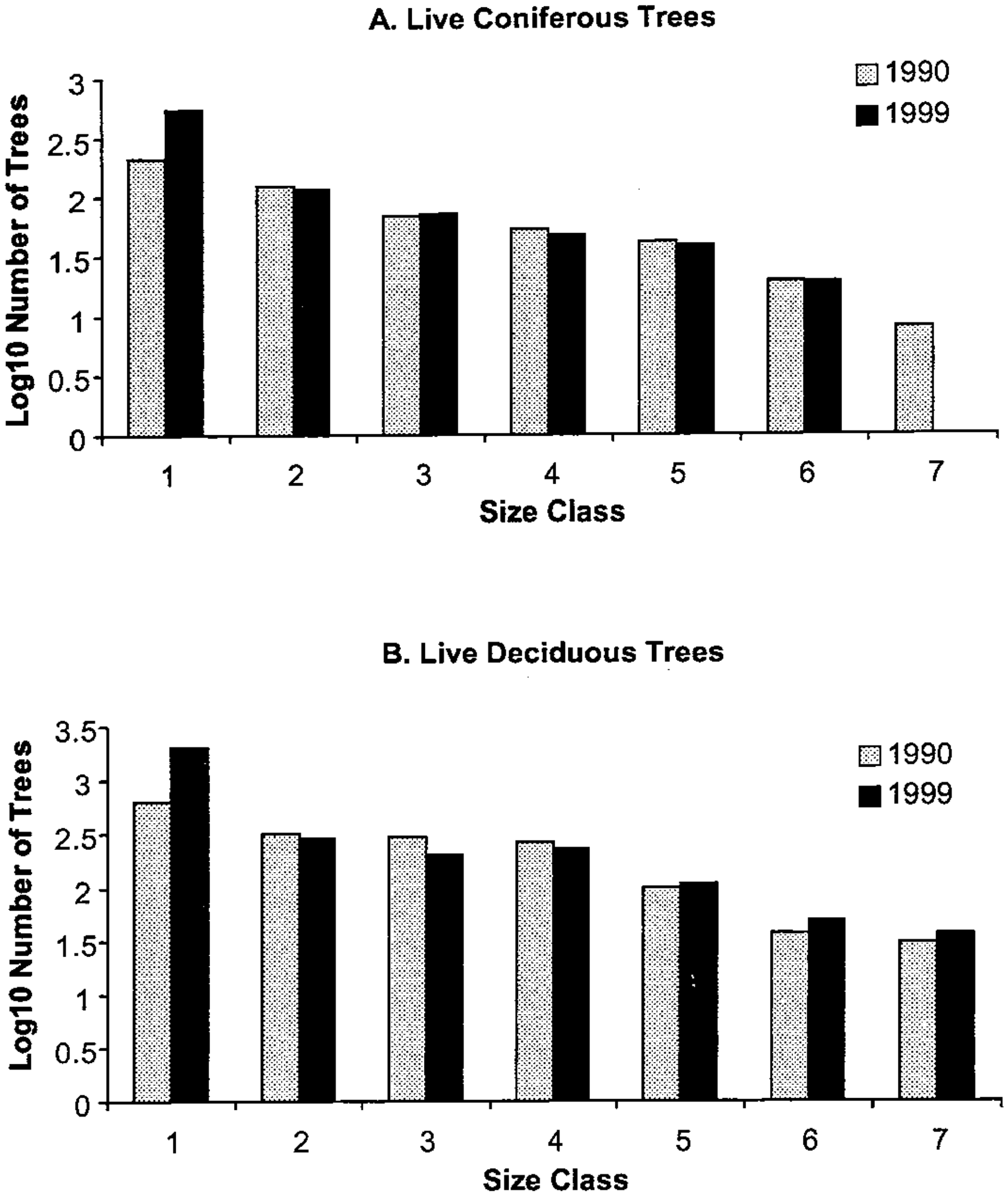
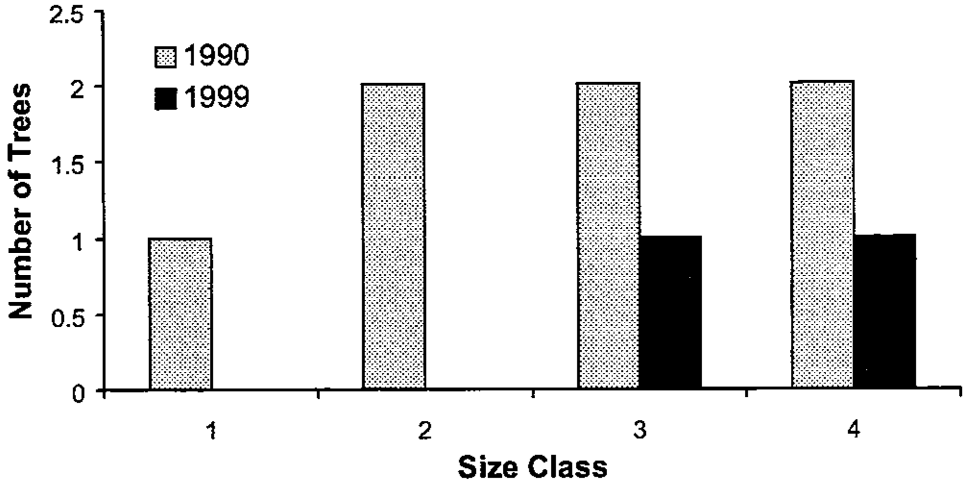


Figure 2. Number of live (A) coniferous and (B) deciduous trees on 19 western Washington WDFW RMZ Project sites measured in 1990 and 1999.

A. Broken-Top Coniferous Trees



B. Recent Coniferous Snags

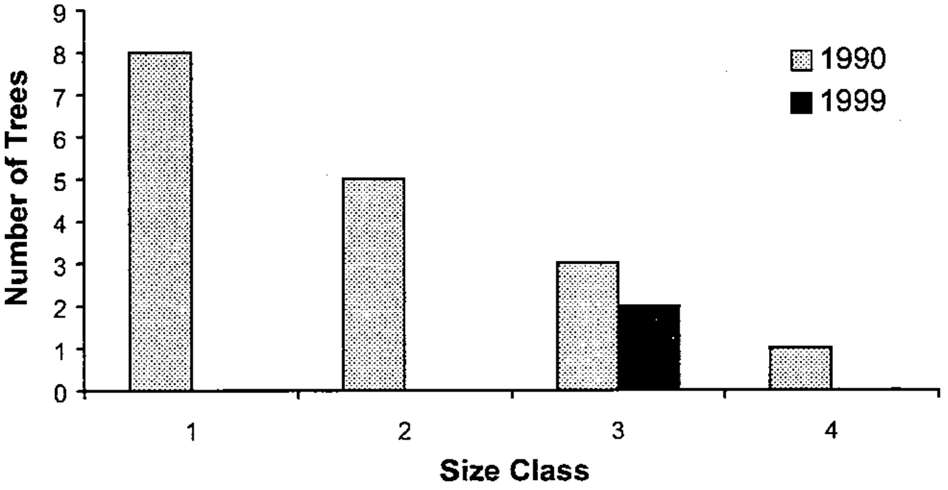


Figure 3. Number of live, broken-top coniferous trees and (B) recent coniferous snags on 18 western Washington WDFW RMZ Project sites measured in 1990 and 1999.

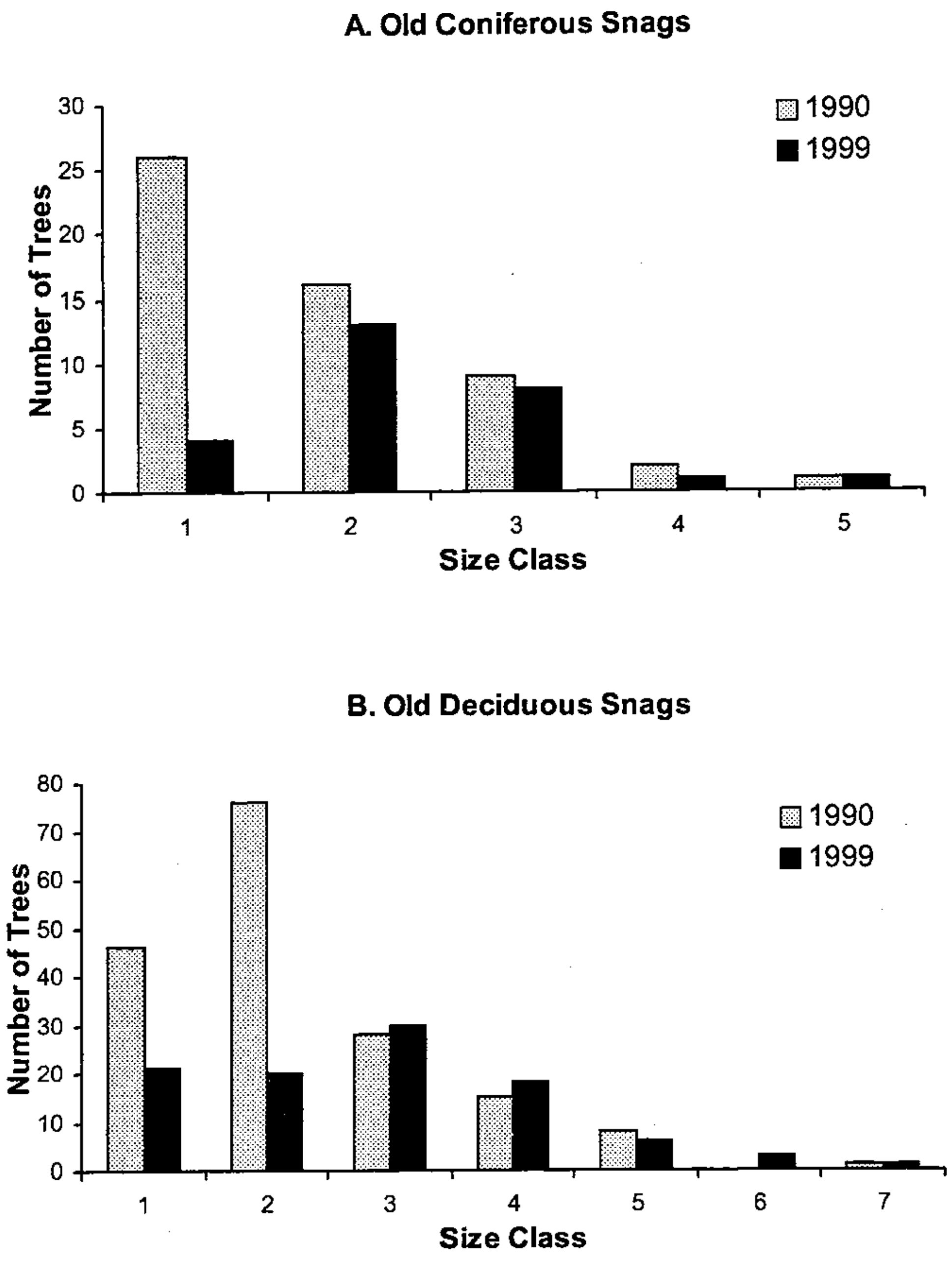


Figure 4.[illegible] Number of old (A) coniferous and (B) deciduous trees on 19 western Washington WDFW RMZ Project sites measured in 1990 and 1999.

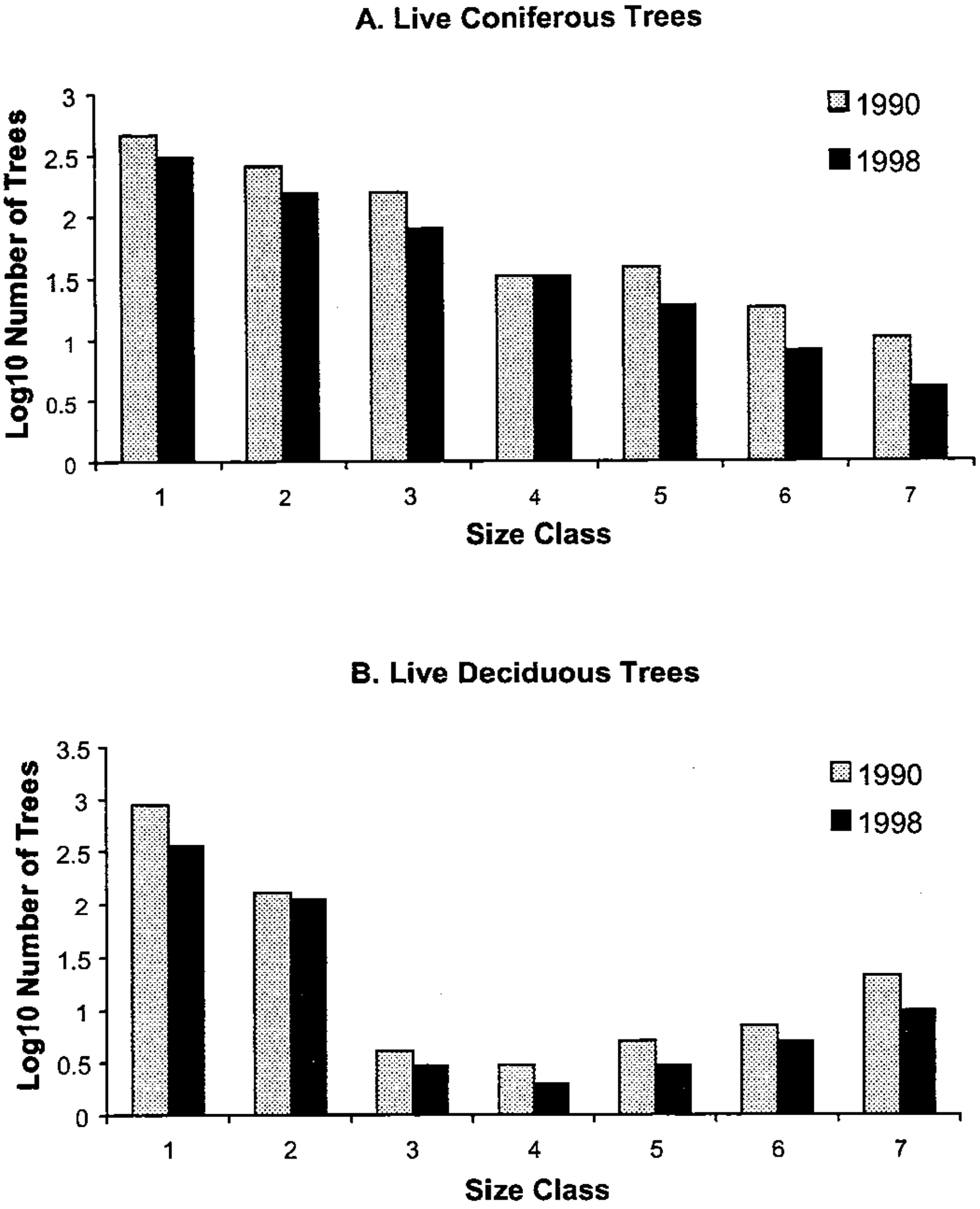
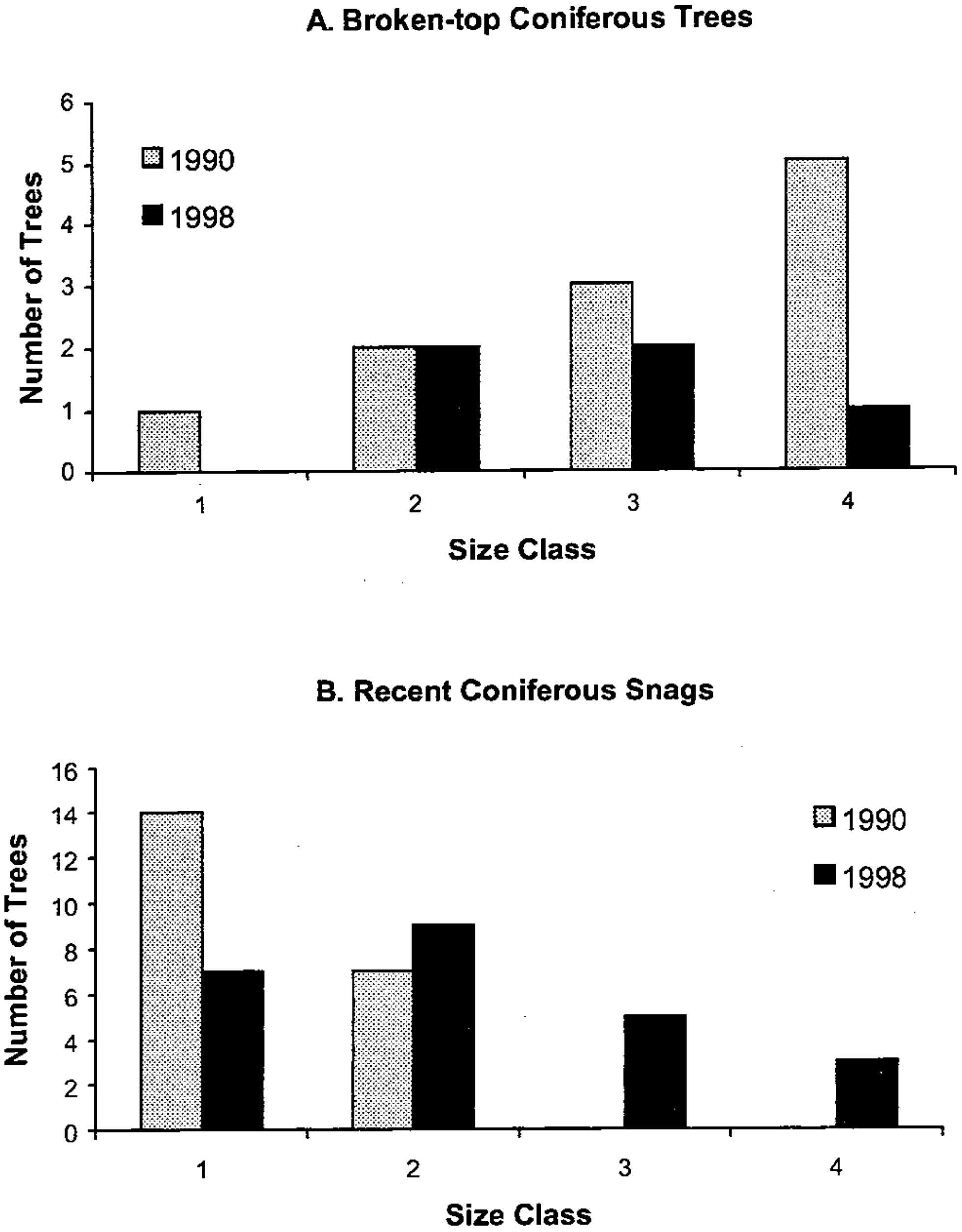


Figure 5. Number of live (A) coniferous and (B) deciduous trees on 8 eastern Washington WDFW RMZ Project sites measured in 1990 and 1998.



A. Broken-top Coniferous Trees

B. Recent Coniferous Snags

Figure 6. Number of (A) live, broken-top coniferous and (B) recent coniferous snags on 8 eastern Washington WDFW RMZ Project sites measured in 1990 and 1998.

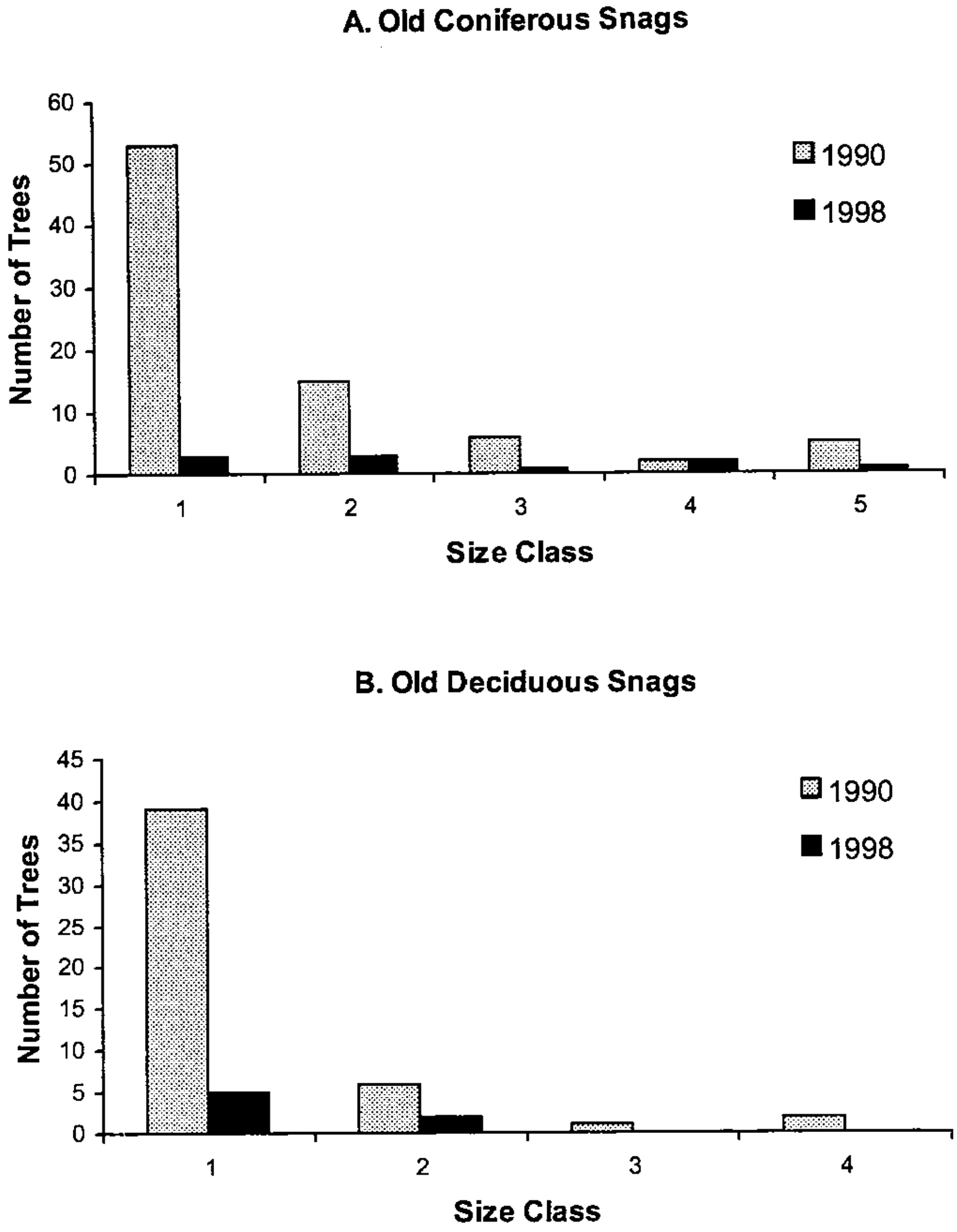


Figure 7. Number of old (A) coniferous and (B) deciduous snags on 8 eastern Washington WDFW RMZ Project sites measured in 1990 and 1998.

Chapter 5

Decay Dynamics and Avian Use of Artificially Created Snags

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Introduction

Standing dead trees (snags) are important resources for many species of wildlife because they provide foraging, roosting, perching, denning, and nesting habitat (McClelland and Frissell 1975, Ohmann et al. 1994, Campbell et al. 1996, Bull et al. 1997, Harrod et al. 1998, Lee 1998, McComb and Lindenmayer 1999). Primary cavity-nesting species (e.g., woodpeckers, nuthatches, and chickadees) excavate cavities in snags each year, and secondary cavity users (e.g., wrens, American kestrels, flying squirrels, and marten) may occupy these cavities in following years. Cavity-nesting birds play important roles in forest ecosystems, including reducing the magnitude of pest outbreaks by foraging on insects (McClelland et al. 1979, Mannan et al. 1980, Bull et al. 1997, Ganey 1999). The availability of suitable snags is considered to be the most important factor in sustaining populations of cavity-nesting species (McClelland et al. 1979, Scott 1979, Cline et al. 1980, Mannan et al. 1980, Zarnowitz and Manuwal 1985, Li and Martin 1991).

Snags are naturally produced by lightning strikes, forest fires, insect infestations, tree diseases, and suppression (McClelland and Frissell 1975, Mannan et al. 1980, Moorman et al. 1999). Snag density varies widely depending on stand age, forest type, location, disturbance regime, and degree of management (Cline et al. 1980, Zarnowitz and Manuwal 1985, McComb and Lindenmayer 1999). For example, old-growth ponderosa pine forests in Arizona had an average of 11.5 snags/ha (Scott 1978), whereas historical snag densities in ponderosa pine forests east of the Cascade Mountains in Washington were estimated to be between 14.5 to 34.6 snags/ha (Harrod et al. 1998). Intensive silvicultural management may greatly reduce the density of snags (Cline et al. 1980, Zarnowitz and Manuwal 1985). Snags have often been removed as fire and safety hazards during harvesting operations (Scott 1978, Mannan et al. 1980, Runde and Capen 1987). Although removal of snags may be offset somewhat by the death of mechanically injured trees, the natural recruitment of snags is disrupted and generally results in lower snag densities over time (Cline et al. 1980).

Various prescriptions have been suggested for providing adequate snag densities for different forest types (McClelland and Frissell 1975, Mannan 1977, Scott 1978, McClelland et al. 1979, Scott 1979, Cline et al. 1980, Steeger and Hitchcock 1998). State and federal regulatory agencies have responded by developing rules for the number of snags or green trees to be retained after harvest. To augment snag densities for wildlife, managers began experimenting with methods to create snags artificially ~30 yr ago (Lewis 1998). A recent survey of forest managers in the Pacific Northwest found that common methods used to create snags included fully or partially removing the crown of trees with chainsaws or explosives (i.e., topping), girdling in or near the base of the crown, and fungal inoculation (Lewis 1998). Although the use of these methods has become more widespread in the western U.S., their effectiveness has not been well documented (Parks et al. 1999).

Bull and Partridge (1986) evaluated six methods of snag creation in ponderosa pine (*Pinus ponderosa*) forests in northeastern Oregon. Over a 5-yr period, they compared rates at which trees died and subsequently fell over and avian use of snags created by girdling, topping with chainsaw, topping with dynamite and inoculating with fungi, girdling and inoculating with fungi, injecting with herbicide, and baiting with an insect pheromone. Although topping trees by chainsaw was the second most costly method, trees treated by this method died the fastest, remained standing the longest, and were most used by cavity nesters (Bull and Partridge 1986). From a safety standpoint, however, topping trees with chainsaws is considered the most dangerous method (Lewis 1998).

Further evaluation of methods to create snags must consider differences between tree species. For example, because ponderosa pine has a higher sapwood to heartwood ratio than many other conifers, woodpeckers typically excavate their cavities entirely within the sapwood (Bull et al. 1997). Therefore the effectiveness of methods that promote sapwood rot (e.g., girdling) versus those that promote heartwood rot (e.g., fungal inoculation) might vary between species (Lewis 1998). Recent studies comparing snag creation methods in western forests have been conducted in ponderosa pine (Bull and Partridge 1986, Parks et al. 1999). There is a clear need for similar studies in other forest types (Parks et al. 1999).

Our objective was to evaluate the effectiveness of artificially created snags by examining the effects of method of snag creation, tree species, and rate of decay on use by cavity-nesting birds in mixed coniferous forests. Specifically, we addressed the following questions: How quickly do trees decay following treatment, and how does this vary between snag creation methods and among tree species? How is foraging and nesting use by cavity nesters affected by the method of snag creation and degree of decay?

Methods

Study Area

The study was conducted on 23 different timber sales in the Sullivan Lake Ranger District on the 77,000-ha Colville National Forest, located in the northeastern corner of Washington State. The second-growth coniferous forests of this region vary in species composition (Table 1) and may have a small deciduous component. Most harvest units were in the western redcedar-western hemlock (*Thuja plicata-Tsuga heterophylla*) (81% of 120 units) or Douglas-fir- grand fir (*Pseudotsuga menziesii-Abies grandis*) (17%) associations with a few in the subalpine fir/Oregon boxwood (*Abies lasiocarpa/Pachistima myrsinites*) (2%) association. The terrain is rolling hills and the sales were at elevations of 750 to 1,500 m.

Creation of Snags

To meet the USDA Forest Service requirements of ≥10 snags per harvested hectare (Lowe 1995), snag creation was initiated in 1990. We selected trees that were representative of each stand and that were >28-cm diameter at breast height (dbh). We chose larger diameter trees because some species of cavity-nesting birds require them (Thomas et al. 1979), and because they are likely to remain standing over a longer time period than small diameter trees (Morrison and Raphael 1993). We treated fewer ponderosa pine later in the study because of the relative rarity of large diameter trees of this species in this region.

Snags were created by cutting the tops of trees or by girdling above the first whorl of live branches at a height >10 m. Girdles were created by using a hand saw to make two parallel cuts (about 15 cm apart) around the tree and then removing the intervening bark and cambium with an axe. We do not consider treatment of trees by fungal inoculation, which began in 1998, because insufficient time had elapsed for decay to occur. Treated trees were tagged with a wildlife sign and unique number, painted with an orange stripe and "T" at breast height on the tree, and located on area maps of each individual stand to aid in returning to them. Height of each tree was estimated with a clinometer before treatment, and species and dbh were recorded.

Treated trees were usually located near the boundary of a harvest unit, although in some cases they were spread across the entire unit. To the extent possible, treated trees were in areas that would reduce the likelihood of their loss to firewood cutters (e.g., steep slopes or away from access roads).

Monitoring

Trees were revisited at roughly 2-yr intervals between 1992 and 1999. At the time of monitoring, we measured height with a clinometer and noted any breakage of the trunk. We examined the bark of each tree for obvious evidence of foraging (i.e., presence of drill holes) by cavity-nesting birds. We used binoculars to scan each tree for signs of cavity excavation and for conks (fruiting bodies of fungi). We recorded foraging, nesting, and fungi as present or absent. Tree decay was evaluated on a scale consisting of nine sequential, non-overlapping stages as described by Thomas et al. (1979). The stages proceed from live tree (class 1) to decline (2–browning of needles), death (3–loss of needles, but fine branching still evident), loose bark (4–loss of fine branching, cracks in bark), bark lost (5–few branches remain), broken (6–top of tree lost), decomposed (7–advanced decay, additional breakage of the trunk), down material (8–most of trunk is on the ground), and stump (9).

Data Analysis

To examine the effects of tree species, method of snag creation, and species × method interaction on time to reach each decay class, we conducted separate two-way analyses of variance (ANOVA) for each decay class. We also considered models with dbh included as an additional covariate to assess the effects of tree size on time to decay. Following a significant analysis, we used Hochberg's GT2 multiple comparisons test to determine differences between tree species means. This method is appropriate for unequal sample sizes (Sokal and Rohlf 1995).

We examined changes in the frequencies of trees with conks between decay classes and between snag creation methods using χ^2 - tests (Sokal and Rohlf 1995). Similarly, we used χ^2 - tests to examine changes in frequency of foraging and nesting use by cavity-nesting birds between decay classes, snag creation methods, and tree species.

Tests were considered significant at $P \leq 0.05$. All analyses were conducted with the Statistical Analysis System (SAS Institute Inc. 1988).

Results

We girdled 797 trees and topped 392 to create 1,189 snags between 1990 and 1997 (mean = 51.7 trees/sale; range, 10-138 trees/sale). Topping was used initially in 1990 and 1991 (n = 387), but in 1992 only five trees were treated this way. Girdling became the principal method for creating snags from 1992 to 1997 (n = 797). Only four deciduous trees were treated and are not considered further. Douglas-fir and western larch (*Larix occidentalis*) accounted for 77% of all trees treated, and grand fir, western redcedar, and lodgepole pine (*Pinus contorta*) accounted for an additional 14% (Table 1).

Of the 1,189 treated trees, 67 were not monitored and 14 could not be located subsequently. We revisited 1,108 treated trees an average of 2.3 times (range, 1-6 times) and at an average interval of 2.4 yr. Trees were monitored for an average period of 5.5 yr (range, 1-8 yr). Only a few of the monitored trees were lost during the study period: 17 fell over (five at one site) and nine were cut for firewood. Twelve trees revisited at least once after treatment could not be located in subsequent visits, and these trees probably had fallen over or were cut.

Some trees (n = 131) showed no sign of decline by the end of the study. Of these, a greater proportion of trees treated by girdling (6.8% of 797) were still alive 4 yr after treatment (range 4 to 7 yr) than those treated by topping (0.3% of 392 trees; $\chi^2 = 36.6$, $P < 0.001$). In several cases, the girdle appeared to be healing over. The remaining 76 live trees were treated by girdling in 1996 and 1997, and sufficient time may not have elapsed for the trees to decline.

Decay Trajectories

Only 13 trees reached decay classes >4 and consequently we focus on decay classes 2 to 4. For each decay class, the overall ANOVA examining the effects of tree species, method of snag creation, and species × method interaction on time to reach the decay class was significant ($P < 0.001$ for all classes). Diameter at breast height was significant only for decay class 2 ($F = 8.1$, df = 1, 434, $P < 0.005$). Larger diameter trees declined faster initially, but subsequent decay was unaffected by tree size. There were interspecific differences in the time required to reach each decay class ($P < 0.001$ for all classes). Method of snag creation and species × method interaction were significant for decay classes 2 and 4 (method of snag creation: decay class 2, $F = 97.8$, df = 1, 434, $P < 0.0001$; decay class 3, $F = 1.84$, df = 1, 590, $P < 0.17$; decay class 4, $F = 102.5$, df = 1, 225, $P < 0.0001$; interaction: decay class 2, $F = 2.53$, df = 6, 434, $P < 0.02$; decay class 3, $F = 1.72$, df = 6, 590, $P < 0.11$; decay class 4, $F = 2.43$, df = 5, 225, $P < 0.04$).

Hochberg's GT2 comparisons between pairs of means revealed relatively few significant differences between species in the time to reach a decay class. In part this was due to differences in variances and sample sizes across species (Table 2). Douglas-fir took significantly longer to reach decay class 2 than western larch or ponderosa pine. These differences disappeared by decay class 3. Western hemlock, however, took significantly longer to reach decay class 3 than western larch or white pine. The time required to reach decay class 4 was similar for most species, but significantly less time was required for western larch than for Douglas-fir, grand fir, or Englemann spruce. We further examined the effects of snag-creation method on time to decay by conducting separate analyses for the three species with the largest sample sizes for each decay class (Table 3). For each species, initial decline (decay class 2) proceeded more quickly for trees treated by topping. Time to decay to class 3 was generally similar for both treatments. For class 4, however, time to decay was longer for trees created by topping for all three species (Table 3).

Conks were absent from live trees and rare on declining trees for both treatments (Table 4). The proportion of trees with conks increased significantly from decay class 2 to decay class 3 for both treatments (topping, $\chi^2 = 58.9$, $P < 0.0001$; girdling, $\chi^2 = 46.5$, $P < 0.0001$), although the proportion was greater for trees treated by topping by decay class 3. Topped trees showed no significant difference in the proportion with conks from decay class 3 to decay class 4 ($\chi^2 = 0.02$, $P = 0.9$), whereas girdled trees increased significantly ($\chi^2 = 6.9$, $P = 0.009$). The proportion of trees with conks did not differ significantly between the two treatments at decay class 4 (Table 4).

Only six (0.8%) of the girdled trees had broken tops by the end of our monitoring period. All of these trees were decay class 3 or 4, and the loss of the top was observed 4-6 yr after treatment.

Foraging Use

With the exception of the few Englemann spruce (*Picea engelmannii*) and white pine (*Pinus monticola*) monitored at decay class 2, some evidence of foraging was observed on all species at all decay classes (Table 5). A few trees were used for foraging as early as 1 yr after treatment. The percentage of trees used for foraging increased significantly between decay class 2 (17.2% of 454 trees) and decay class 3 (63.1% of 593 trees; $\chi^2 = 220.7$, $P < 0.0001$) and between decay class 3 and decay class 4 (86.5% of 237 trees; $\chi^2 = 44.1$, $P < 0.0001$). Compared across all species, there were no differences in the frequencies of foraging use between the different methods of snag creation at any stage of decay (Table 4).

Comparisons of foraging activity and snag creation method for the three most common tree species, western larch, Douglas-fir, and grand fir revealed more frequent foraging activity on topped than girdled trees at some decay classes for the latter two species. For Douglas-fir, 60.5% of 114 of the topped trees and 39.0% of 154 girdled trees had signs of foraging activity at decay class 3 ($\chi^2 = 7.59$, $P = 0.006$). At decay class 4, 88.0% of 25 topped Douglas-fir trees had signs of foraging, compared to 63.6% of 33 girdled trees ($\chi^2 = 4.40$, $P = 0.04$). Although few grand fir trees were observed at decay class 4, topped trees had more frequent foraging activity (85.7% of 14 trees) than girdled trees (33.3% of 6 trees; $\chi^2 = 5.49$, $P = 0.02$). When compared against all other species combined, western larch was used for foraging to a greater extent than other species at all decay classes (decay class 2, $\chi^2 = 25.9$, $P < 0.0001$; decay class 3, $\chi^2 = 82.5$, $P < 0.0001$; decay class 4, $\chi^2 = 23.0$, $P < 0.0001$).

Nesting Use

After 7 yr, none of the girdled trees in any decay class showed any evidence of nesting use as determined by the presence of cavities (Table 6). Some topped trees, however, had cavities as early as decay class 2 (1.4% of 146 trees of all species) with the first cavities observed 3 yr after treatment. The proportion of topped trees with cavities increased both at decay class 3 (8.9%, $n = 281$, $\chi^2 = 9.2$, $P < 0.002$) and at decay class 4 (34.8%, $n = 89$, $\chi^2 = 35.4$, $P < 0.0001$).

Of the five most common species observed with cavities at decay class 2 ($\chi^2 = 6.3$, df $= 4$, $P = 0.177$) and the seven most common species observed with cavities at decay class 3 ($\chi^2 = 10.6$, df $= 6$, $P = 0.10$), there were no significant differences between species in the frequency of trees with cavities (Table 6). In contrast, at decay class 4, there were significant differences among the six most common tree species in the frequency of trees with cavities ($\chi^2 = 20.1$, df $= 5$, $P = 0.001$; Table 6). Western larch had lower nesting use than Douglas-fir ($\chi^2 = 9.5$, $P = 0.002$), grand fir ($\chi^2 = 15.9$, $P < 0.0001$), and white pine ($\chi^2 = 5.6$, $P = 0.02$). The frequency of grand fir trees with cavities was greater than western larch, ponderosa pine ($\chi^2 = 7.99$, $P = 0.005$), and Engelmann spruce ($\chi^2 = 4.8$, $P = 0.03$).

Discussion

The creation of snags by killing healthy trees is one of several management strategies for maintaining wildlife species that require these habitat elements in managed forests. Cavity-nesting species use artificially created snags for foraging and nesting, but there are differences in this use due to treatment method, degree of decay, and tree species (Tables 5, 6). In the following, we consider these differences and suggest strategies for future snag creation given our current state of knowledge.

The two treatments differed somewhat in their success at killing trees. Nearly 7% of the trees treated by girdling remained vigorous after 4 yr, whereas only one tree (<1%) treated by topping remained alive after 4 yr. Bull and Partridge (1986) reported similar success with topped ponderosa pine trees in northeastern Oregon, but poorer success with girdling trees (<50% of girdled trees died). Parks et al. (1999), however, had close to 100% mortality of girdled ponderosa pine after 3 yr. The latter two studies both placed the girdle at 1 m above ground, but the procedure that Parks et al. (1999) used to girdle trees was similar to ours. Bull and Partridge (1986) girdled trees with two parallel saw cuts, but did not remove the bark and cambium.

Losses of trees to wind throw or woodcutters were minor (<3.5%). Even including the cut trees, the proportion of trees lost was less than the 13% of girdled trees in 5 yr observed by Bull and Partridge (1986) or the 27-43% girdled trees after 6-7 yr observed by Parks et al. (1999). These differences may be attributable to their inclusion of smaller diameter trees, which may be more susceptible to wind throw, or to the lower placement of the girdle where breakage usually occurs. Girdling trees above the first whorl of branches, as in our study, does not result in loss of the entire snag due to wind-shear breaks at the wound site (Lewis 1998).

Topped trees declined faster initially than girdled trees (Table 3), and evidence of decay (e.g., presence of conks) also occurred earlier in topped trees. Species-specific differences in the time to decline to decay class 2 were more pronounced for girdled trees (Table 3) with western larch and ponderosa pine declining more rapidly (Table 2). These differences largely disappeared by death of the tree (decay class 3). Interestingly, further decay after death of the tree was slower for topped trees than for girdled ones (Table 3). Although dbh also affects decay rates (Cline et al. 1980), trees in our study were large (>50 cm dbh on average) and dbh only affected initial decline.

As anticipated from other studies (Bull and Partridge 1986, Chambers et al. 1997), most trees that we treated by topping or girdling provided foraging habitat within 2-4 yr of treatment, and most trees showed evidence of foraging within 5-7 yr. Species-specific differences in decline were also associated with the proportion of trees used for foraging (Table 5). Western larch, in particular, declined quickly initially and was used most consistently for foraging.

Use of the artificial snags for excavation of cavities was not observed as early as foraging activity; only a small proportion of trees had cavities by decay class 4 (Table 6). Importantly, cavities were observed as early as 3 yr after topping, whereas none of the girdled trees had cavities after 7 yr. Bull and Partridge (1986) reported similar results, but they monitored trees over only 5 yr and had much poorer success killing trees by girdling. Parks et al. (1999) reported cavities in girdled ponderosa pine trees after 7 yr. We had only one girdled ponderosa pine in our study and can only speculate that species differences in the pattern of decay precluded use of girdled trees after 7 yr. Chambers et al. (1997) created Douglas-fir snags by topping and found a significant increase in cavities after 5 yr. However, their results are not directly comparable to ours because they reported the average number of cavities per tree, whereas we looked at presence or absence of cavities. Nest-site selection by primary cavity-nesting birds is influenced by dbh, sapwood and heartwood decay, and wood hardness (McClelland and Frissell 1975, Mannan et al. 1980, Swallow et al. 1986, Runde and Capen 1987, Harestad and Keisker 1989, Schepps et al. 1999). Topping exposes the upper heartwood to fungal attack and thus allows more rapid decay. This, in turn, makes it more readily accessible to primary cavity-nesting species. The greater proportion of grand fir trees with excavated cavities compared to several other species might reflect this species' relatively thin bark, soft wood, and susceptibility to fungal rot (Arno and Hammerly 1977). In contrast, the thick bark and dense wood of western larch (Arno and Hammerly 1977) might explain the fewer cavities observed in this species.

In conclusion, the results of our and other studies on artificial snag creation suggest that a strategy for creating snags that combines different treatment methods, a variety of species, and a staggered time schedule is appropriate until further monitoring and additional experiments are completed. The choice of snag creation method presents trade-offs in cost and safety versus effectiveness in providing habitat for cavity nesting species early on. The costs per tree for girdling are less than for topping (Lewis 1998), but girdling may be less cost-effective for two reasons: the kill rate is generally less than for topping, and girdled trees do not provide suitable conditions for cavity nesting as early as topped trees. Continued monitoring will be necessary to determine when girdled trees are used for cavity nesting, and if girdled trees remain standing longer than topped trees. Consequently, topping of some trees is advisable in the near term to ensure nesting habitat.

Bull and Partridge (1986) treated some girdled trees with fungal inoculation, but this was no more successful than girdling alone. Although our experiments-in-progress with fungal inoculation did not include a combined treatment with girdling, this may be an approach that could result in earlier use by cavity nesters. Other combined approaches (e.g., limbing and girdling) also need to be assessed.

The period of availability of artificial snags can be lengthened by selecting a mixture of tree species for snag creation and by staggering treatment. Western larch, for example, becomes useful for foraging earlier than other species, whereas species such as grand fir may provide nesting habitat earlier. Similar recommendations (Scott 1979; Mannen et al. 1980; Steeger and Hitchcock 1998; Zarnowitz and Manuwal 1985) have been made to forest managers to strive for high species richness, density, and diversity when selecting suitable habitat to preserve cavity nesters. It also would be advisable to stagger treatment of leave trees over a period greater than 10 yr. This strategy would ensure a more natural distribution of snags in all decay classes over a longer period of time.

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Literature Cited

Arno, S. F., and R. P. Hammerly. 1977. Northwest Trees. The Mountaineers, Seattle, Washington.

Bull, E. L., C. G. Parks, and T. R. Torgerson. 1997. Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391. Pacific Northwest Research Station, Portland, Oregon.

Bull, E. L., and A. D. Partridge. 1986. Methods of killing trees for use by cavity nesters. Wildlife Society Bulletin 14:142-146.

Campbell, L. A., J. G. Hallett, and M. A. O'Connell. 1996. Conservation of bats in managed forests: roost use by *Lasionycteris noctivagans*. Journal of Mammalogy 77:976-984.

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. Western Journal of Applied Forestry 12:93-97.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773-786.

Ganey, J. L. 1999. Snag density and composition of snag populations on two National Forests in northern Arizona. Forest Ecology and Management 117:169-178.

Harestad, A. S., and D. G. Keisker. 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. Canadian Journal of Zoology 67:1067-1073.

Harrod, R. J., W. L. Gaines, W. E. Hartl, and A. Camp. 1998. Estimating historical snag density in dry forests east of the Cascade Range. USDA Forest Service General Technical Report PNW-GTR-428. Pacific Northwest Research Station, Portland, Oregon.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105:263-272.

Lewis, J. C. 1998. Creating snags and wildlife trees in commercial forest landscapes. Western Journal of Applied Forestry 13:97-101.

Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. The Auk 108:405-418.

Lowe, J. E. 1995. Decision notice and environmental assessment for the continuation of interim management direction for establishing riparian, ecosystem, and wildlife standards for timber sales. USDA Forest Service, Pacific Northwest Region, Portland, Oregon.

Mannan, R. W. 1977. Use of snags by birds, Douglas-fir region, western Oregon. M.S. Thesis. Oregon State University, Corvallis, Oregon.

Mannan, R. W., E. C. Meslow, and H. M. Wight. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:787-797.

McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. Journal of Forestry 73:414-417.

McClelland, B. R., S. S. Frissell, W. C. Fischer, and C. H. Halvorson. 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. Journal of Forestry 77:480-483.

McComb, W. C., and D. Lindenmayer. 1999. Dying, dead, and down trees. Pages 335-372 In M. L. Hunter, Jr. (editor), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.

Moorman, C. E., K. R. Russell, G. R. Sabin, and D. C. Guynn. 1999. Snag dynamics and cavity occurrence in the South Carolina Piedmont. Forest Ecology and Management 118:37-48.

Morrison, M. L., and M. G. Raphael. 1993. Modeling the dynamics of snags. Ecological Applications 3:322-330.

Ohmann, J. L., W. C. McComb, and A. A. Zumrawi. 1994. Snag abundance for primary cavity-nesting birds on nonfederal forest lands in Oregon and Washington. Wildlife Society Bulletin 22:607-620.

Parks, C. G., D. A. Conklin, L. Bednar, and H. Maffei. 1999. Woodpecker use and fall rates of snags created by killing ponderosa pine infected with dwarf mistletoe. USDA Forest Service Research Paper PNW-RP-515. Pacific Northwest Research Station, Portland, Oregon.

Runde, D. E., and D. E. Capen. 1987. Characteristics of northern hardwood trees used by cavity nesting birds. Journal of Wildlife Management 51:217-223.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition, SAS Institute, Inc., Cary, North Carolina.

Schepps, J., S. Lohr, and T. E. Martin. 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? The Auk 116:658-665.

Scott, V. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. Journal of Forestry 76:26-28.

Scott, V. 1979. Bird response to snag removal in ponderosa pine. Journal of Forestry 77:26-28.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the Principles and Practice of Statistics in Biological Research (Third edition). W. H. Freeman and Company, New York.

Steeger, C., and C. L. Hitchcock. 1998. Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. Journal of Wildlife Management 62:1349-1358.

Swallow, S. K., R. J. Gutierrez, and R. A. Howard, Jr. 1986. Primary cavity-site selection by birds. Journal of Wildlife Management 50:576-583.

Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60-77 In J. W. Thomas (technical editor), Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook No. 553, USDA Forest Service, Washington, D.C.

Zarnowitz, J. E., and D. A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management 49:255-263.

TABLE 1. Tree species, number of trees treated by girdling and topping, mean diameter at breast height (cm), and mean height (m) at the time of treatment.

	Treatment type (*n*)				
Species	Girdled	Topped	Total	Mean dbh	Mean height
Douglas-fir	351	138	489	52.9	28.1
Western larch	331	94	425	49.0	33.2
Grand fir	38	29	67	50.5	27.9
Western redcedar	15	42	57	56.3	22.0
Lodgepole pine	34	5	39	37.5	27.0
Western hemlock	12	21	33	51.5	24.1
Ponderosa pine	1	31	32	62.1	22.3
Engelmann spruce	10	18	28	56.9	26.3
White pine	1	11	12	59.8	19.5
Subalpine fir	3	0	3	47.8	34.5
All species	796	389	1185	51.5	29.3

TABLE 2. Mean time (years) since treatment to reach decay classes 2 to 4 for each species. Means are not corrected for snag-creation method (i.e., topping or girdling). Sample sizes are the number of trees observed at each decay class.

	Decay class								
	2			3			4		
Species	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Western hemlock	2.0	0.4	14	5.4	0.7	15			
Douglas-fir	2.0	0.1	185	3.9	0.1	274	5.9	0.2	58
Lodgepole pine	1.9	0.2	12	3.5	0.5	17	4.8	0.9	6
Grand fir	1.9	0.3	21	4.1	0.5	22	6.1	0.4	20
Western redcedar	1.7	0.3	29	4.3	0.6	23	7.0	1.0	2
Western larch	1.5	0.1	170	3.6	0.1	208	4.9	0.2	123
Engelmann spruce	1.3	0.2	7	3.3	0.4	18	6.5	0.5	13
Ponderosa pine	1.0	0.0	15	3.4	0.6	23	5.1	0.6	9
White pine	1.0	0.0	1	2.3	0.3	6	5.8	0.9	8

TABLE 3. The effects of snag-creation method on decay time (years) for three tree species. F-values and associated *P*-values from ANOVA are provided for comparisons at each decay class.

		Girdled			Topped				
Species	Decay class	$\bar{x}$	SE	n	$\bar{x}$	SE	n	F	*P*
Douglas-fir	2	2.30	0.10	143	1.02	0.02	46	57.5	0.0001
	3	4.04	0.09	160	3.41	0.23	114	8.0	0.005
	4	5.30	0.14	33	6.64	0.28	25	20.9	0.001
Western larch	2	1.70	0.08	122	1.04	0.03	48	28.5	0.001
	3	3.53	0.23	70	3.41	0.11	138	0.26	0.61
	4	4.44	0.13	104	7.26	0.20	19	75.3	0.001
Grand fir	2	2.73	0.43	11	1.00	0.0	10	14.7	0.001
	3	4.21	0.68	14	3.87	0.23	8	0.13	0.72
	4	4.33	0.49	6	6.86	0.46	14	10.7	0.001

TABLE 4. Frequency of occurrence of conks and of evidence of foraging by cavity-nesting birds across all tree species by treatment and decay class. Differences between snag creation methods at each decay class were determined by χ^2.

		Girdled		Topped			
Tree condition	Decay class	%	n	%	n	χ^2	*P*
Conks	2	1.6	316	0.7	147		
	3	17.5	326	32.3	282	19.5	<0.0001
	4	28.0	150	33.7	89	0.86	0.35
Foraging	2	17.8	309	16.3	147	0.15	0.70
	3	60.9	312	65.2	282	1.20	0.27
	4	86.0	150	86.5	89	0.13	0.91

TABLE 5. Frequency of foraging activity on each tree species by decay class. Trees were considered to be used for foraging if signs of foraging activity were observed at any time while in a given decay class.

	Decay class					
	2		3		4	
Species	Trees used (%)	*n*	Trees used (%)	*n*	Trees used (%)	*n*
Western larch	28.8	170	88.1	202	96.8	123
Western hemlock	21.4	14	86.7	15		
Western redcedar	20.7	29	30.4	23		
Ponderosa pine	13.3	15	65.2	23	100.0	9
Douglas-fir	8.7	185	50.8	268	74.1	58
Lodgepole pine	8.3	12	35.3	17	100.0	6
Grand fir	4.8	21	38.1	21	70.0	20
Engelmann spruce	0.0	7	50.0	18	61.5	13
White pine	0.0	1	33.3	6	75.0	8

TABLE 6. The number of trees with nest cavities for each species by decay class and method of snag creation, and the proportion of trees with cavities and the number of trees examined for each treatment and decay class. Trees were considered to be used for nesting if signs of cavity building were observed at any time while in a given decay class.

	Decay class											
	2				3				4			
Species	Girdled (%)	*n*	Topped (%)	*n*	Girdled (%)	*n*	Topped (%)	*n*	Girdled (%)	*n*	Topped (%)	*n*
Douglas-fir	0	139	1 (2.2)	46	0	154	9 (7.9)	114	0	33	12 (48.0)	25
Western larch	0	122	0	48	0	132	4 (5.7)	70	0	104	1 (5.3)	19
Lodgepole pine	0	12			0	14	0	3	0	4	0	2
Western redcedar	0	12	0	17			1 (4.3)	23			1 (50.0)	2
Grand fir	0	11	1 (10.0)	10	0	7	4 (28.6)	14	0	6	10 (71.4)	14
Western hemlock	0	7	0	7			3 (20.0)	15				
Engelmann spruce	0	3	0	4	0	3	2 (13.3)	15	0	2	3 (27.3)	11
Ponderosa pine	0	1	0	14	0	1	2 (9.1)	22			1 (11.1)	9
White pine	0	1			0	1	0	5	0	1	3 (42.9)	7