Wildl. Soc. Bull. 22:607–620, 1994

SNAG ABUNDANCE FOR PRIMARY CAVITY-NESTING BIRDS ON NONFEDERAL FOREST LANDS IN OREGON AND WASHINGTON

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Key words: ecosystem management, managed forests, snags, wildlife habitat, wildlife trees

More than 100 species of vertebrates in the Pacific Northwest use standing dead trees (snags) at one time or another in their lifecycle (Thomas et al. 1979*a*, Neitro et al. 1985). With few exceptions, investigators have found significant correlations between snag density and the abundance of primary cavity-nesters in North American coniferous forests (Raphael and White 1984:47–53, Madsen 1985, Zarnowitz and Manuwal 1985, McComb et al. 1986, Land et al. 1989, Carey et al. 1991, Schreiber and deCalesta 1992). Similar relationships have been detected for secondary cavity-nesters (Schreiber and deCalesta 1992). Thomas et al. (1979*a*) and Neitro et al. (1985) suggested that timber management practices and changing land-use patterns in the Northwest are reducing snag abundance and thus dependent populations of wildlife species (also see Morrison et al. 1986 and Schreiber and deCalesta 1992). Snag abundance in unmanaged Douglas-fir (*Pseudotsuga menziesii*) forests >40 years old have been quantified by Spies et al. (1988), Carey et al. (1991), and Spies and Franklin (1991). However, patterns of snag abundance across a broader region, especially in young managed stands, are poorly understood. Regional assessments can help guide planning and policy for managing Northwest forests for wood production and wildlife in public and private forests. In this study we assessed patterns of snag abundance among plant communities and stand conditions in managed and natural forests on nonfederal lands in Oregon and Washington. Our objectives were to: (1) quantify densities and characteristics of snags across a range of forest conditions; (2) assess snag origin, whether from death of trees in the present stand or carried over from a previous stand; (3) use models of snag-bird relationships to predict the role that nonfederal lands might play in providing habitat for primary cavity-nesters; and (4) discuss implications for forest management in the Northwest.

METHODS

Sample Design and Data

We analyzed data collected from 2,715 permanent plots in Oregon and western Washington (Fig. 1). Plots were established and measured as part of the ongoing inventory of nonfederal forest lands conducted by the Inventory and Economics Research Development and Application Program (IE), Pacific Northwest Research Station, U.S. Department of Agriculture (USDA) Forest Service. Comparable data were unavailable for federal lands. In Oregon, plots were established at intersections of a 5.5-km square grid. In western Washington, plots were established at intersections of 2 independent 5.5-km grids superimposed over the same area. Plots were established at all grid points outside National Forests, Bureau of Land Management lands in western Oregon, and parks.

We analyzed data from western Oregon (1984–1986), eastern Oregon (1986–1987), and western Washington (1988–1990) (Fig. 1). Each plot on forest land consisted

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of a cluster of 5 subplots evenly spaced over 3 ha of homogeneous size and density of live trees. At each subplot crews tallied live trees and snags on nested plots as follows: (1) in Oregon: a 2.4- or 3.0-m fixed-radius plot for trees <13 cm diameter at breast height (dbh); a variable-radius plot (7.0 or 4.6 metric basal area factor [m^2/ha]) for trees 13–89 cm dbh; a 17.0- or 20.7-m fixed-radius plot for trees >89 cm dbh; (2) in Washington: a 3.3-m fixed-radius plot for trees <18 cm dbh; a variable-radius plot (7.0 metric basal area factor [m^2/ha]) for trees 18–89 cm dbh; a 17.0-m fixed-radius plot for trees >89 cm dbh. Crews recorded the species, dbh, height, and decay class (from Cline et al. 1980) of each snag.

The plots sampled a wide range of stand ages (Table 1). Stand age was computed as the average age of trees in the main canopy, determined by increment boring. Timber management was the dominant disturbance around the plots. Most plots in our analysis (78% in western Oregon and western Washington, 20% in eastern Oregon) had been clearcut at least once, and additional plots (13% in western Oregon and western Washington and 68% in eastern Oregon) had undergone partial harvests or other removals such as firewood cutting (IE, Pacific Northwest Res. Stn., Portland, Oreg., unpubl. data).

Stand and Snag Classification

We classified the plant community and stand condition of each plot (Ohmann 1992) with classification systems of Hall et al. (1985) (Tables 2–3) for western Oregon and western Washington and Thomas et al. (1979*b*) (Tables 4–5) for eastern Oregon. Stand conditions are defined by characteristics of vegetation structure that typify stages of development, or successional stages, along an ecological sere. We therefore treated our sample as a chronological sequence in analyses.

In our analysis we used only snags ≥28.0 cm dbh and ≥2 m tall. Large-diameter snags are used more frequently as nest sites and also show more evidence of woodpecker foraging than smaller snags (Neitro et al. 1985). Of those species using plant communities considered in this study, 15% of the primary cavity-nesters and none of the secondary cavity-nesters have a recommended snag dbh for optimum nesting opportunity of <28.0 cm (Brown 1985: Appendices 18 and 19). We grouped snags into dbh size-classes used in the Snag Recruitment Simulator (SRS; B. G. Marcot, Snag Recruitment Simulator Computer model, USDA For. Serv., Region 6, Portland, Oreg., 1992) and Cline et al. (1980). We grouped snags of decay classes 1–3 as "hard" and classes 4–5 as "soft" following groupings used in SRS.

Snags were classified as remnant (formed in a previous stand, usually from large old-growth trees) or recruited (originated from the current stand). Recruited snags most frequently result from suppression mortality during the stem exclusion stage of stand development (Oliver and Larson 1990:140–154). The classification followed these rules: (1) if the density of live trees on the plot was <10% of full stocking (MacLean 1979), all snags were classified as remnant; (2) if live tree stocking was ≥10%, then snags with dbh of ≥1.1 times the mean stand dbh (the dbh [cm] of the tree of mean basal area) were classified as remnant and all other snags were classified as recruited; or (3) if live-tree stocking was ≥10% and the stand met the definition of old-growth (Old-Growth Definition Task Group 1986), all snags were classified as recruited. We used the factor of 1.1 because snags recruited through suppression mortality are nearly always smaller in diameter than the mean stand dbh (Oliver and Larson 1990:146–151). Classifications based on this method appeared reasonable, although errors are certainly possible, especially in uneven-aged stands common in eastern and southwestern Oregon. Detailed descriptions of plot design and calculation of tree expansion factors, mean stand dbh, and stand age are available in unpublished IE field and office manuals on file in Portland, Oregon.

Snag Density and Habitat Capability

We compared snag densities among stand conditions within each of 4 plant communities sampled by ≥25 plots: temperate coniferous forest and conifer–hardwood forest in western Oregon and Washington, and ponderosa pine (*Pinus ponderosa*) forest and mixed-conifer forest in eastern Oregon. For $n < 25$ within any stand condition, plots in consecutive stand conditions were combined to achieve $n \geq 25$. Such combinations were not possible in the large sawtimber and old-growth stand conditions in conifer–hardwood forest, however. Because plot-level snag densities were not normally distributed within stand conditions, we compared densities among stand conditions with a Wilcoxon rank-sum test. Significance was assigned to differences at alpha = 0.01.

We used the SRS model, based on Thomas et al. (1979*a*), Cline et al. (1980), and Neitro et al. (1985), to estimate snag habitat capability for each species of primary cavity-nesting bird that breeds in any of the 4 plant communities and for the complete assemblage of these species that breeds in each plant community. The SRS model aids managers in estimating the snag diameters, decay stages, and densities (based on the biological characteristics of each wildlife species) that could support a given percent of the maximum documented abundance, or maximum potential population (MPP), for each primary cavity-nesting species. However, because many factors affecting population levels are not explicitly considered in the SRS model, model output expressed as MPP is best interpreted as habitat capability. In western Oregon and western Washington, Neitro et al. (1985) assumed snag requirements for supporting multiple species simultaneously to be additive of individual species requirements; in eastern Oregon, Thomas et al. (1979*a*) assumed the snag density required was the maximum density necessary for an individual species. When comparing our observed snag densities against snag habitat requirements, we substituted larger snags for smaller ones as needed (assuming species can use snags larger than minimum size but not smaller); we did not substitute soft snags for hard snags, nor vice versa. For eastern Oregon we used data on species' use of plant communities and stand conditions summarized in Thomas (1979: Appendix 22). For western Washington and western Oregon, we took data on species' use of plant communities from Brown (1985: Appendix 8); species use of stand conditions was defined in the SRS model.

The SRS model for eastern Oregon estimates the number of snags by decay class and dbh class *inside* bark that are needed to support a given percent of MPP of designated species, whereas the western Washington and western Oregon model predicts the number of snags needed by decay class and diameter *outside* bark. Because snag dbh was measured outside bark, we used the western Washington and Oregon model to identify appropriate dbh classes for species that we considered in the eastern Oregon analyses. The SRS model does not explicitly consider snag height.

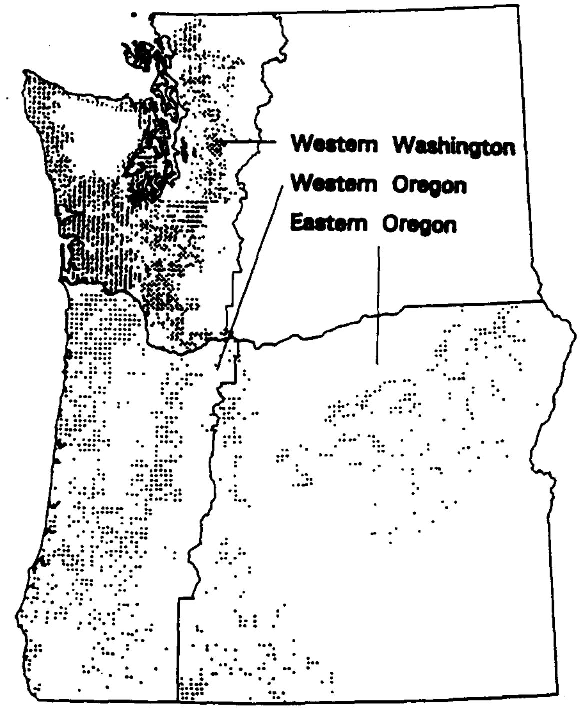

Fig. 1. Locations of 2,715 plots in temperate coniferous forest and conifer–hardwood forest on nonfederal lands in western Washington (1988–1990) and western Oregon (1984–1986), and ponderosa pine forest and mixed-conifer forest in eastern Oregon (1986–1987).

RESULTS

Snag Abundance

Temperate Coniferous Forest.—Densities of snags of all dbh and decay classes differed among stand conditions in temperate coniferous forest ($P < 0.01$; Table 2). Snag abundance generally increased with stand development (successional stage) except for snags

Table 1. Mean (SE) of stand ages in years of plots by stand condition and plant community in Oregon and Washington forests, 1984–1990.

Stand conditions[a]	Temperate coniferous forest	Conifer–hardwood forest	Ponderosa pine forest	Mixed-conifer forest
Western Oregon and western Washington				
Grass–forb	3 (0.2)			
Shrub[b]	3 (0.3)	6 (0.6)		
Open sapling–pole	18 (0.4)	20 (1.0)		
Closed sapling–pole–sawtimber	51 (1.0)	52 (1.4)		
Open sawtimber	49 (1.9)	59 (3.4)		
Large sawtimber	112 (8.8)			
Old-growth[c]	243 (22.4)	99 (16.3)		
Eastern Oregon				
Grass–forb–shrub–seedling			<1 (0.3)	0
Sapling–pole			51 (5.5)	45 (3.4)
Young			65 (1.9)	67 (1.2)
Mature-old-growth			129 (9.2)	134 (8.7)

[a] See Tables 2–5 for definitions of stand conditions.
[b] Includes grass–forb plots in conifer–hardwood forest.
[c] Includes large sawtimber plots in conifer–hardwood forest.

Table 2. Mean density of snags/40 ha (SE) on plots in temperate coniferous forest in relation to stand condition[a] in western Oregon (1984–1986) and western Washington (1988–1990).

Snag Dbh class (cm)	Decay class	Grass–forb (n = 207)	Shrub (n = 163)	Open sapling-pole (n = 407)	Closed sapling-pole-sawtimber (n = 590)	Open sawtimber (n = 272)	Large sawtimber (n = 78)	Old-growth (n = 25)	P[b]
28.0–38.1	Soft	4 (3)	5 (4)	24 (7)	47 (7)	40 (10)	41 (18)	165 (81)	<0.01
	Hard	14 (8)	31 (11)	32 (9)	145 (15)	107 (20)	263 (53)	85 (47)	<0.01
38.2–43.1	Soft	2 (2)	0	11 (3)	22 (4)	16 (5)	28 (15)	93 (57)	<0.01
	Hard	0	11 (6)	4 (2)	30 (5)	11 (5)	20 (15)	135 (62)	<0.01
43.2–48.2	Soft	7 (3)	4 (3)	11 (3)	20 (4)	12 (4)	12 (7)	104 (49)	<0.01
	Hard	2 (2)	8 (4)	2 (1)	14 (3)	17 (5)	23 (10)	94 (58)	<0.01
48.3–63.5	Soft	10 (4)	4 (2)	15 (3)	47 (5)	29 (8)	62 (15)	219 (59)	<0.01
	Hard	11 (3)	12 (7)	4 (2)	22 (4)	13 (4)	82 (20)	197 (51)	<0.01
>63.5	Soft	46 (7)	32 (7)	30 (4)	134 (11)	84 (10)	204 (37)	363 (74)	<0.01
	Hard	14 (3)	8 (3)	8 (2)	30 (4)	18 (4)	64 (15)	416 (99)	<0.01
All classes	Soft	69 (10)	45 (9)	91 (13)	270 (19)	182 (22)	348 (55)	944 (273)	<0.01
	Hard	40 (11)	70 (16)	50 (11)	241 (19)	166 (23)	452 (74)	927 (245)	<0.01
	Total	109 (15)	115 (19)	141 (20)	511 (28)	348 (32)	800 (104)	1,871 (315)	<0.01

[a] Grass–forb: shrub cover <40%; stand dbh <2.5 cm. Shrub: shrub cover ≥40%; stand dbh <2.5 cm. Open sapling-pole: stand dbh 2.5–22.9 cm; tree cover <60%. Closed sapling-pole–sawtimber: stand dbh 2.5–53.3 cm; tree cover ≥60%. Open sawtimber: stand dbh 23.0–53.3 cm; tree cover <60%. Large sawtimber: stand dbh ≥53.4 cm. Old-growth: density of old live trees, understory trees, and snags as defined by the Old-Growth Definition Task Group (1986).
[b] Based on Wilcoxon rank-sum test to detect differences among stand conditions.

>63.5 cm dbh, which were least abundant in open sapling-pole stands. Early stages of stand development (grass–forb, shrub, and open sapling–pole stands) contained the fewest snags, and all were remnant (Fig. 2). In these early successional stands 72–92% of snags were <12 m tall. Recruited snags were most abundant in stand conditions with closed canopies (closed sapling-pole–sawtimber, large sawtimber, and old-growth). Snags were most abundant and tallest in the old-growth stand condition, where 43% were >12 m tall.

Open sawtimber stands did not fit the model of stand development used by Hall et al. (1985)

Table 3. Mean density of snags/40 ha (SE) on plots in conifer–hardwood forest in relation to stand condition[a] in western Oregon (1984–1986) and western Washington (1988–1990).

Snag Dbh class (cm)	Decay class	Grass–forb and shrub (n = 36)	Open sapling-pole (n = 139)	Closed sapling-pole–sawtimber (n = 284)	Open sawtimber (n = 105)	Large sawtimber and old-growth (n = 18)	P[b]
28.0–38.1	Soft	0	34 (13)	57 (13)	67 (21)	68 (47)	0.28
	Hard	0	15 (9)	126 (19)	129 (35)	31 (31)	<0.01
38.2–43.1	Soft	0	19 (9)	14 (5)	12 (7)	27 (27)	0.79
	Hard	39 (28)	0	16 (5)	13 (7)	25 (25)	0.18
43.2–48.2	Soft	0	4 (3)	10 (4)	2 (2)	18 (18)	0.47
	Hard	0	5 (4)	9 (5)	21 (8)	20 (20)	0.15
48.3–63.5	Soft	0	15 (8)	25 (5)	22 (7)	23 (16)	0.11
	Hard	26 (26)	9 (4)	16 (4)	23 (9)	68 (27)	<0.01
>63.5	Soft	19 (9)	28 (9)	86 (9)	81 (14)	119 (33)	<0.01
	Hard	2 (2)	6 (3)	16 (3)	18 (5)	80 (32)	<0.01
All classes	Soft	19 (9)	102 (21)	193 (19)	184 (27)	255 (65)	<0.01
	Hard	67 (53)	36 (11)	184 (21)	204 (39)	224 (66)	<0.01
	Total	86 (56)	138 (25)	377 (24)	388 (42)	479 (71)	<0.01

[a] Grass–forb: shrub cover <40%; stand dbh <2.5 cm. Shrub: shrub cover ≥40%; stand dbh <2.5 cm. Open sapling-pole: stand dbh 2.5–22.9 cm; tree cover <60%. Closed sapling-pole–sawtimber: stand dbh 2.5–53.3 cm; tree cover ≥60%. Open sawtimber: stand dbh 23.0–53.3 cm; tree cover <60%. Large sawtimber: stand dbh ≥53.4 cm. Old-growth: density of old live trees, understory trees, and snags as defined by the Old-Growth Definition Task Group (1986).
[b] Based on Wilcoxon rank-sum test to detect differences among stand conditions.

Table 4. Mean density of snags/40 ha (SE) on plots in ponderosa pine forest in relation to stand condition[a] in eastern Oregon, 1986–1987.

Snag Dbh class (cm)	Decay class	Grass-forb and shrub (n = 33)	Sapling-pole (n = 34)	Young (n = 46)	Mature and old-growth (n = 55)	P[b]
28.0–38.1	Soft	24 (24)	26 (26)	0	14 (14)	0.71
	Hard	44 (31)	26 (26)	94 (45)	39 (23)	0.54
38.2–43.1	Soft	0	0	0	0	1.00
	Hard	18 (18)	14 (14)	7 (7)	0	0.66
43.2–48.2	Soft	0	0	0	0	1.00
	Hard	0	0	0	10 (7)	0.25
48.3–63.5	Soft	0	0	0	28 (13)	0.01
	Hard	15 (10)	8 (8)	14 (8)	5 (5)	0.63
>63.5	Soft	3 (3)	0	5 (3)	0	0.30
	Hard	4 (4)	6 (4)	2 (2)	4 (3)	0.85
All classes	Soft	27 (24)	26 (26)	5 (3)	42 (19)	0.42
	Hard	81 (36)	53 (30)	116 (45)	58 (25)	0.76
	Total	108 (42)	79 (38)	121 (45)	100 (30)	0.90

[a] Grass–forb: stand dbh <2.5 cm; tree seedling and shrub cover <10%. Shrub–seedling: stand dbh <2.5 cm; tree seedling and shrub cover ≥10%. Sapling–pole: stand dbh 2.5–22.9 cm. Young: stand dbh ≥23.0 cm and stand age <80 years. Mature: stand dbh ≥23.0 cm and stand age ≥80 years. Old-growth: density of old live trees and snags as defined by Thomas (1979).
[b] Based on Wilcoxon rank-sum test to detect differences among stand conditions.

and were omitted from their classification system. The abundance and height of snags in these stands were greater than in open sapling–pole stands and less than in closed sapling–pole–sawtimber and large sawtimber stands.

Conifer-Hardwood Forest.—The abundance of hard snags 28.0–38.1-cm dbh, hard snags 48.3–63.5-cm dbh, hard and soft snags >63.5 cm dbh, and hard and soft snags of all dbh classes combined differed among stand conditions in conifer–hardwood forest ($P < 0.01$; Table 3). As in temperate coniferous forest, snag abundance generally increased with stand development. Snags were most abundant

Table 5. Mean density of snags/40 ha (SE) on plots in mixed-conifer forest in relation to stand condition[a] in eastern Oregon, 1986–1987.

Snag Dbh class (cm)	Decay class	Grass-forb and shrub (n = 39)	Sapling-pole (n = 45)	Young (n = 74)	Mature and old-growth (n = 65)	P[b]
28.0–38.1	Soft	24 (18)	30 (21)	48 (22)	8 (8)	0.52
	Hard	131 (46)	61 (37)	106 (31)	153 (40)	0.26
38.2–43.1	Soft	0	0	29 (13)	25 (12)	0.13
	Hard	23 (16)	0	4 (4)	28 (17)	0.31
43.2–48.2	Soft	8 (8)	0	14 (8)	11 (8)	0.61
	Hard	27 (15)	22 (12)	0	16 (9)	0.15
48.3–63.5	Soft	11 (8)	7 (7)	10 (6)	24 (11)	0.59
	Hard	20 (11)	32 (18)	31 (11)	67 (24)	0.57
>63.5	Soft	18 (8)	7 (4)	16 (5)	23 (7)	0.42
	Hard	16 (8)	22 (10)	22 (8)	48 (19)	0.51
All classes	Soft	61 (26)	44 (24)	116 (31)	90 (26)	0.21
	Hard	216 (60)	137 (55)	163 (33)	311 (66)	0.23
	Total	277 (63)	181 (62)	279 (46)	401 (78)	0.09

[a] Grass–forb: stand dbh <2.5 cm; tree seedling and shrub cover <10%. Shrub–seedling: stand dbh <2.5 cm; tree seedling and shrub cover ≥10%. Sapling–pole: stand dbh 2.5–22.9 cm. Young: stand dbh ≥23.0 cm and stand age <80 years. Mature: stand dbh ≥23.0 cm and stand age ≥80 years. Old-growth: density of old live trees and snags as defined by Thomas (1979).
[b] Based on Wilcoxon rank-sum test to detect differences among stand conditions.

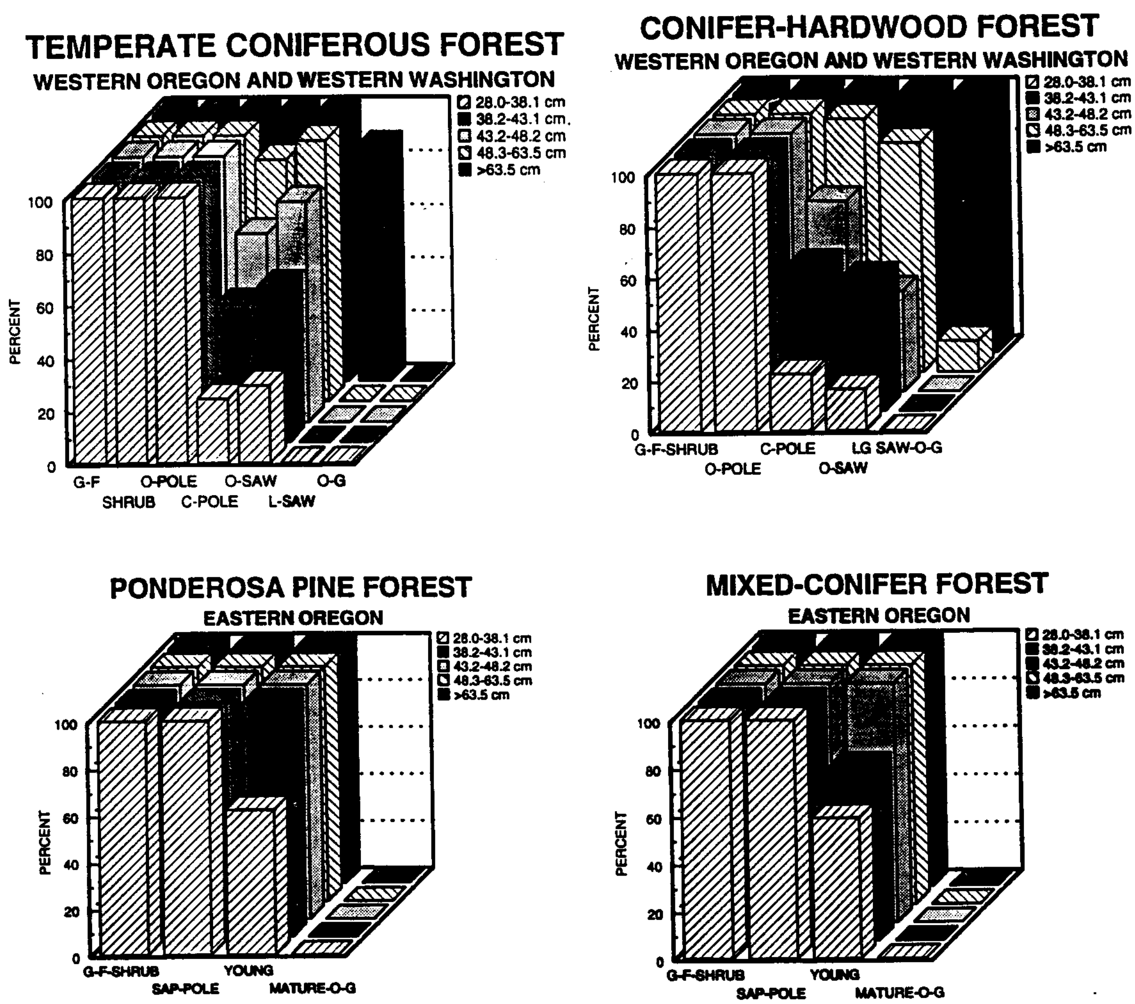

Fig. 2. Percent of total snags that are remnants by snag dbh class. G–F = grass–forb, O–POLE = open sapling–pole, SAP–POLE = sapling–pole, C–POLE = closed sapling–pole–sawtimber, O–SAW = open sawtimber, LG–SAW = large sawtimber, O–G = old-growth, L–SAW = large sawtimber.

in large sawtimber–old-growth stands and least abundant in grass–forb–shrub stands. All snags in grass–forb–shrub and open sapling–pole stands were remnants (Fig. 2). About one-third of the snags in grass–forb–shrub stands were 2.4–3.0 m tall, whereas only 10% of the snags in large sawtimber–old-growth stands were that size.

Ponderosa Pine and Mixed-Conifer Forest.—We detected differences in snag densities among stand conditions in only 1 snag class (soft snags 48.3–63.5 cm dbh) in ponderosa pine forest ($P < 0.01$; Table 4) and in none of the dbh classes in mixed-conifer forest ($P > 0.09$; Table 5). In both plant communities, snags were most abundant in mature-old-growth stands. All snags were remnants in grass–forb–shrub and sapling–pole stands in these plant communities (Fig. 2). Snags in ponderosa pine forest were taller on average than in the other 3 plant communities: 36–58% of snags in a given stand condition were >12 m tall.

Habitat Capability for Primary Cavity-Nesters

Temperate Coniferous Forest.—On average, temperate coniferous forest met the pre-

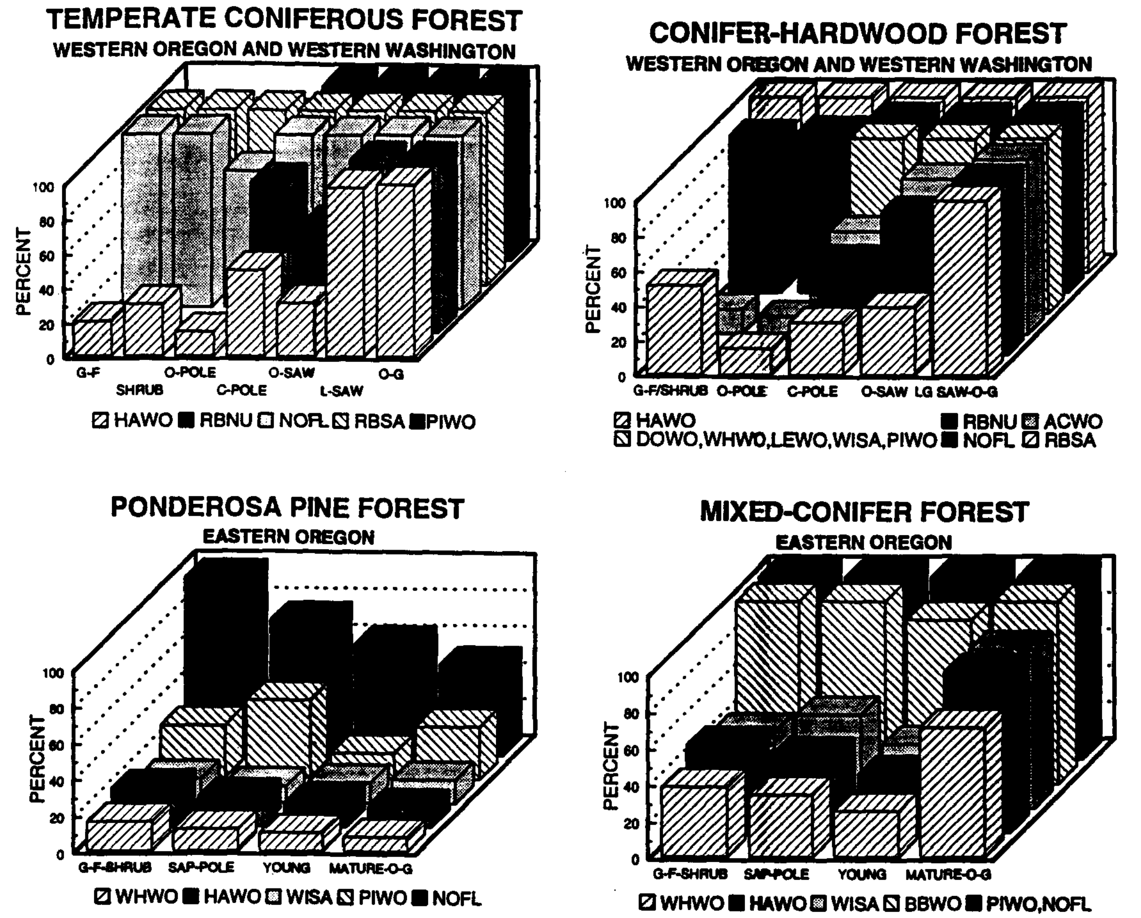

Fig. 3. Habitat capability (percent of maximum potential populations that could be supported) for each species individually. ACWO = acorn woodpecker (*Melanerpes formicivorus*), BBWO = black-backed woodpecker (*Picoides arcticus*), DOWO = downy woodpecker (*Picoides pubescens*), HAWO = hairy woodpecker (*Picoides villosus*), LEWO = Lewis' woodpecker (*Melanerpes lewis*), NOFL = northern flicker (*Colaptes auratus*), PIWO = pileated woodpecker (*Dryocopus pileatus*), RBNU = red-breasted nuthatch (*Sitta canadensis*), RBSA = red-breasted sapsucker (*Sphyrapicus ruber*), WHWO = white-headed woodpecker (*Picoides albolarvatus*), WISA = Williamson's sapsucker (*Sphyrapicus thyroideus*). G–F = grass–forb, O–POLE = open sapling–pole, C–POLE = closed sapling–pole–sawtimber, O–SAW = open sawtimber, LG–SAW = large sawtimber, O-G = old-growth.

dicted snag needs for 100% of MPP of 1 (red-breasted sapsucker [*Sphyrapicus ruber*]) of the 3 primary cavity-nesters that breed in early successional stand conditions (grass–forb, shrub, and open sapling–pole; W. McComb and C. Chambers, Oregon State Univ., Corvallis, unpubl. data; Fig. 3). Mid- to late-successional stand conditions (closed sapling–pole–sawtimber, open sawtimber, large sawtimber, and old-growth) met the snag needs of 100% of MPP for 3 of 5 primary cavity-nesters that breed in these stand conditions: red-breasted sapsucker, northern flicker (*Colaptes auratus*), and pileated woodpecker (*Dryocopus pileatus*). The hairy woodpecker (*Picoides villosus*) uses all stand conditions of temperate coniferous forest, but observed snag densities could support 100% MPP only in old-growth. Snag abundance was predicted to support 100% of MPP of all species simultaneously only in old-growth, 79% in large sawtimber, 52% in closed sapling–pole–sawtimber, and <50% in all other stand conditions (Fig. 4). When MPP's for each stand condition were weighted by their proportional

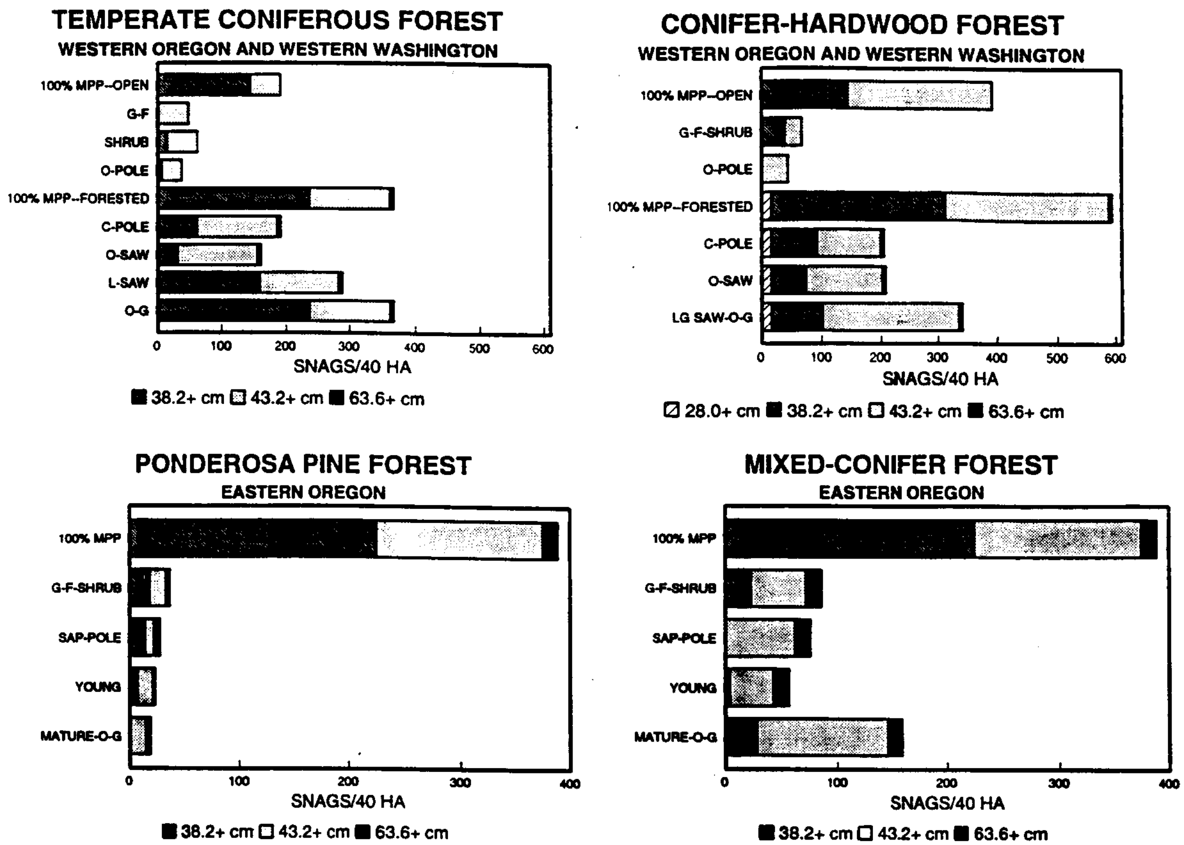

Fig. 4. Snag densities suggested by the Snag Recruitment Simulator model and Neitro et al. (1985) to meet 100% of maximum potential populations of indigenous primary cavity-nesters simultaneously (100% MPP bars) compared with the snag density present on nonfederal lands, by snag dbh. See Fig. 2 for abbreviations.

occurrence on nonfederal lands (IE, Pacific Northwest Res. Stn., Portland, Oreg., unpubl. data), the overall MPP for 3.3 million ha of temperate coniferous forest was 40%.

Conifer–Hardwood Forest.—On average, snags in conifer–hardwood forest met the predicted snag needs for 100% of MPP of 1 (red-breasted sapsucker) of the 4 primary cavity-nesters that breed in early successional stands (Fig. 3). Snags met the needs of 100% of MPP for 7 of the 10 species that breed in mid- to late-successional stands (Fig. 3). Snag densities required to support 100% of MPP for the hairy woodpecker, northern flicker, and red-breasted nuthatch (*Sitta canadensis*) were found only in the large sawtimber–old-growth stand condition. None of the stand conditions of conifer–hardwood forest could simultaneously support 100% MPP of all species that breed there (Fig. 4). Habitat capability, as represented by MPP, ranged from 11% in open sapling–pole to 57% in large sawtimber–old-growth. The area-weighted average of MPP across all stand conditions of the 1.2 million ha of conifer–hardwood forest in nonfederal ownership was 28%.

Ponderosa Pine Forest.—Average snag densities in ponderosa pine forest were inadequate to meet requirements for 100% of MPP for each of the 5 species of primary cavity-nesters that breed in this plant community (Fig. 3). Habitat capability, as represented by MPP, was greatest for the northern flicker. Habitat capability was ≤21% of MPP in all stand conditions for the white-headed woodpecker (*Pi-*

coides albolarvatus), hairy woodpecker, and Williamson's sapsucker (*Sphyrapicus thyroideus*). Each stand condition of ponderosa pine forest could support ≤10% of MPP of all 5 species simultaneously (Fig. 4). The area-weighted average MPP across all stand conditions of the 500,000 ha of ponderosa pine forest on nonfederal lands was 6%.

Mixed-Conifer Forest.—Whereas 6 species of primary cavity-nesters breed in mixed-conifer forest, average snag densities could support 100% of MPP only of the pileated woodpecker and northern flicker in all stand conditions, and for the black-backed woodpecker (*Picoides arcticus*) in all but young stands (Fig. 3). All stand conditions of mixed-conifer forest could support ≤41% of MPP of all cavity-nesters simultaneously (Fig. 4). The area-weighted average of MPP across all stand conditions of the 600,000 ha of mixed-conifer forest in nonfederal ownership was 24%.

DISCUSSION

Variability in Snag Populations

The snag densities we describe should be considered regional averages for 5.6 million ha of these plant communities on nonfederal forest lands in Oregon and western Washington. Snag abundance among stands was highly variable and non-normally distributed, complicating efforts to quantify these populations. This variability reflects the high spatial and temporal variation in natural and human disturbances, and was strongly influenced by remnant snags from previous harvests. Stand-level variability in tree size and density is particularly high in uneven-aged forests characteristic of eastern Oregon, where our sample did not allow us to distinguish significant differences in snag densities among stand conditions.

Our primary objective was to quantify snag populations across the range of current stand conditions, not to explain sources of variation in snag populations. Our stratification of the field plots by plant communities and stand conditions, which are significant from a wildlife habitat standpoint (Thomas et al. 1979*b*, Hall et al. 1985), did not control for factors that influence amounts and characteristics of snags and logs, such as stand age, disturbance history, live tree density, climate, and site productivity (Spies et al. 1988). Nevertheless, mean stand ages indicate that the stand conditions approximated a chronological sequence (Table 1).

Successional Trends in Snag Abundance

In temperate coniferous and conifer–hardwood forest in western Washington and western Oregon, we found that snag abundance generally increased with succession, from grass–forb to old-growth, for snags of all sizes combined as well as for snags ≥48.3 cm dbh. Similarly, Cline et al. (1980) found that density of snags ≥9 cm dbh increased with stand age in managed stands in the Oregon Coast Range, whereas they decreased in density in natural stands. In a study of natural, >40-year-old stands of Douglas-fir in western Oregon and Washington, Spies et al. (1988) also found a negative association between total snag density and stand age. Decreasing snag density with stand age in natural stands can be attributed to the inverse relationship between tree size and density (i.e., small trees are more abundant than large trees; Cline et al. 1980). Indeed, when only larger snags (≥48.3 cm dbh) were considered, Spies et al. (1988) found them most numerous in young (40–80 years) and old-growth (≥200 years) stands and least abundant in mature (80–200 years) stands. We suspect that stand management activities largely explain the lower abundances of large snags in the young, managed forests that dominated our sample. We found no differences in snag densities among stand conditions in ponderosa pine and mixed-conifer forest, so we cannot generalize successional trends. No other empirical, regional characterizations of snag populations in eastern Oregon forests are available for comparison.

Comparisons of successional trends in snag densities among existing studies are of limited value. Rigorous comparisons of snag densities in natural and managed stands of similar age are particularly difficult. Comparisons are confounded by study differences in snag definitions (dbh, height, and decay classes), sampling designs, and stand classifications. Most study locations have been restricted to either federal or nonfederal ownerships and tend to represent different ecological conditions (e.g., disturbance history, climate, site productivity, stand age, and species composition). A previous analysis of data from IE plots in western Oregon found densities of snags and large live trees 3–5 times more dense in unharvested plots than in clearcut plots for 40–79 and 80–200 year age classes (Hansen et al. 1991). Stands <40 years old had to be excluded because of the rarity and limited spatial distribution of natural, early successional stands. Furthermore, snag densities in older stands on previously harvested sites reflect logging practices quite different from those used today.

Habitat Capability for Cavity-Nesters

Model Assumptions.—Our assessments of habitat capability, as represented by MPP, must be interpreted with caution: many underlying assumptions of Thomas et al. (1979*a*), Cline et al. (1980), and Neitro et al. (1985), and consequently the SRS model, are untested. These assumptions are discussed by Neitro et al. (1985) and summarized below.

The SRS model assumes that meeting snag requirements of woodpeckers and nuthatches during the breeding season also will provide needed habitat for other snag-dependent species. Furthermore, in the western Washington and western Oregon version of the model, snag densities needed to support multiple species simultaneously are assumed to be additive of individual species requirements. In the eastern Oregon version, meeting the needs of the individual species with the maximum snag requirement is assumed to support all species simultaneously. When we compared our observed snag densities to the sum of snag requirements of all species, MPP percent for supporting all species simultaneously in ponderosa pine forest dropped from ≤10% to ≤6% and the area-weighted average from 6% to 4%. In mixed-conifer forest, MPP percent dropped from ≤41% to ≤24% and the area-weighted average from 24% to 14%. Management strategies based on the above assumptions may not meet the needs of secondary cavity-nesters such as the brown creeper (*Certhia americana*), nor of species that use large natural cavities (e.g., Vaux's swift [*Chaetura vauxi*], raccoon [*Procyon lotor*], black bear [*Ursus americanus*]; Neitro et al. 1985).

In determining percent of MPP supported, Neitro et al. (1985) assumed a linear relationship between densities of species and suitable snags. The model also assumes a 4:1 ratio of potentially suitable snags to snags actually used for nesting. Observed variability in this ratio among species and study locations is quite high (Neitro et al. 1985). It is unknown to what degree the additional snags may be needed to meet foraging habitat requirements.

The model assumes that primary cavity-nesters will use snags that are larger but not smaller than the minimum dbh specified (i.e., larger snags can substitute for smaller snags but not vice versa). We also assumed that soft snags could not substitute for hard ones and vice versa. These assumptions remain untested by existing studies. The model also assumes that a given snag during a given year will be occupied by not more than 1 primary cavity-nesting pair and a given snag over a number of years may be reused by the same or different species of woodpecker. Again, empirical evidence to support this assumption is lacking. Finally, the model does not explicitly consider the spatial arrangement, species, or height of snags, any of which we believe may influence habitat capability.

Uncertainty in Habitat Capability Estimates.—Several factors contribute to uncertainty about our assessments of habitat capability, as represented by MPP. Application of habitat models without considering use of space by each species can lead to exaggerated estimates of habitat capability, especially where habitat is highly variable (Schulz and Joyce 1992). In addition, recent research data on use of snags by cavity-nesting birds (e.g., Lundquist 1988, Nelson 1989, Carey et al. 1991) has not been incorporated into the distributed version of the SRS model used by forest managers. Data collected in recent studies in the Cascade Mountains of western Oregon (W. McComb and N. Hunter, unpubl. data) and in the Blue Mountains of eastern Oregon (Bull and Holthausen 1993) indicate that the SRS model overestimates habitat capability to support primary cavity-nesters.

Because the SRS model does not explicitly consider snag height, our methods overestimate habitat capability where snags are shorter than required by wildlife species. For example, the 5 species breeding in temperate coniferous forest use snags at least 3–12 m tall (Brown 1985, Appendix 19). Our data show that 5–30% of snags in the various stand conditions were <3 m tall, so MPP may have been even lower than we estimated. The importance of snag height relative to other factors such as snag dbh and decay class, plant community, and stand condition in predicting wildlife use has not been tested.

Lastly, we doubt that our estimated snag abundances will be maintained over time unless management practices are altered, especially if remnant snags are not retained (or created) after harvest in all plant communities. Snags recruited in younger forests are generally smaller, and greater numbers of cavity-nesting wildlife are present when large snags are available than where few or no large snags exist (Neitro et al. 1985).

MANAGEMENT RECOMMENDATIONS

Stand-Level

At the stand level, managers can use the SRS model to predict the characteristics and dynamics of snag habitat over time. Our results illustrate the importance of retaining large snags and live trees during thinning and harvesting operations in forests managed for both wood production and snag-using wildlife. Large remnant snags provided most of the existing nesting habitat for cavity-excavators in early- and mid-successional stands. These large snags will gradually be lost and not replaced in stands managed using traditional silvicultural practices and rotation lengths that optimize timber production. Also, precommercial and commercial thinning operations keep stand density below the zone of imminent mortality (Oliver and Larson 1990:205–227) and will probably result in future densities of recruited snags lower than we observed in closed sapling–pole–sawtimber and large sawtimber stands. However, aggressive density management can produce large trees faster than they would be produced without density management, and some of those trees can be killed to create snags or treated to induce rot. Snags also can be created in established stands with open canopies, where snag recruitment from suppression mortality is expected to be low. The value of killed or treated trees for cavity-nesters has not been adequately documented.

Landscape- to Regional-Level

If management for cavity-nesters is to be effective at landscape and regional levels, snag resources must be assessed at spatial scales related to the territory sizes of each species, regardless of land ownership (Schulz and Joyce 1992). Federal and nonfederal forests are managed under very different objectives and constraints. National Forest land managers are mandated by law (36 CFR 219.19) to manage for viable populations of all native and desired nonnative species. As a minimum, federal land managers need to more fully consider habitat conditions on adjacent land ownerships as they influence ability to meet management objectives for federal lands. At a regional level, the challenge will be to coordinate management activities on land of various ownerships in ways that best provide the mix of forest values desired by society in ways that are most compatible with management objectives of individual landowners.

In a regional context, nonfederal lands can contribute to maintaining populations of cavity-nesters. These forests provide most of the snags on sites of low elevation, moderate climate, and high net primary productivity. Nonfederal lands also provide habitat for animal movement among some forest habitats on federal lands. Management of snag habitat on nonfederal lands could be influenced by education, financial incentives, and regulation. The Oregon Forest Practices Act (ORS 527.710) requires 5 live trees or snags/ha ≥28.0 cm dbh be retained after harvest and provides rules for snag and live tree retention in riparian zones and wetlands. Such legislation may help ensure snags for cavity-nesters on nonfederal lands. However, the Oregon requirements are not stratified by plant community or snag species, size, or decay class. In particular, these regulations may not provide for species that use large, hard snags. If nonfederal lands are to continue contributing to cavity-nester habitat in the region, the most critical needs are to ensure that large snags are retained following harvest, that sufficient live trees are retained for future snags, and that snag and stand dynamics are considered over longer time frames (at least 1 entire stand rotation).

SUMMARY

We estimated densities of remnant snags and snags recruited through natural mortality on 2,715 plots in 4 plant communities: temperate coniferous and conifer–hardwood forest in western Oregon and western Washington, and ponderosa pine and mixed-conifer forest in eastern Oregon. We compared estimated snag densities among stand conditions that generally reflect stages of stand development in each plant community. In western Washington and western Oregon, abundance of snags ≥28.0 cm dbh increased with stand development. In temperate coniferous forest, densities differed among all stand conditions ($P < 0.01$), ranging from 109 snags/40 ha in grass–forb to 1,871 snags/40 ha in old-growth. Density in conifer–hardwood forest ranged from 86 snags/40 ha in grass–forb and shrub stand conditions to 479 snags/40 ha in large sawtimber and old-growth. We detected differences in densities among stand conditions in eastern Oregon forests only for soft snags 48.3–63.5 cm dbh in ponderosa pine forest ($P = 0.01$; all others $P \geq 0.09$). Among-plot variability was extremely high in all plant communities and heavily influenced by snags remnant from harvested old-growth stands. All snags in grass–forb, shrub, and open sapling–pole stands were remnants. Snags ≥48.3 cm dbh generally were not recruited until stands reached large sawtimber or mature condition.

Snag abundance on nonfederal lands was inadequate to support 100% of maximum potential population (MPP) of indigenous species of primary cavity-nesting birds simultaneously in all stand conditions of ponderosa pine, mixed–conifer, and conifer–hardwood forest and in all but old-growth stands in temperate coniferous forest. However, old-growth stands represented only 1% of temperate coniferous forest in nonfederal ownership. When MPP's for each stand condition were weighted by their proportional occurrence in nonfederal ownership, MPP's were 40% for temperate co-

niferous forest, 28% for conifer–hardwood forest, 6% for ponderosa pine forest, and 24% for mixed-conifer forest.

Large remnant snags provided much of the snag habitat for cavity-nesters in early- to mid-successional stands. This habitat will be lost gradually and may not be replaced using current timber management practices. If nonfederal lands are going to contribute habitat for snag-using wildlife, greater attention is needed to retaining large snags and live trees when thinning and regenerating stands. On federal lands, management for viable populations of cavity-nesting wildlife needs to more fully consider snag habitat conditions on adjacent land in determining needed habitat quantities, characteristics, and placement that best meet management objectives.

Acknowledgments.—Funding for this project was provided by the Inventory and Economics Program, Pacific Northwest Research Station, U.S. Department of Agriculture Forest Service. We thank B. Marcot, M. Raphael, D. Conner, L. Bednar, and two anonymous reviewers for their helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

BROWN, E. R., TECHNICAL EDITOR. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Dep. Agric. For. Serv. Publ. R6-F&WL-192-1985. 332pp. + Appendices.

BULL, E. L., AND R. S. HOLTHAUSEN. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. J. Wildl. Manage. 57:335–345.

CAREY, A. B., M. M. HARDT, S. P. HORTON, AND B. L. BISWELL. 1991. Pages 122–142 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Dep. Agric. Gen. Tech. Rep. PNW-GTR-285.

CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:773–786.

HALL, F. C., L. W. BREWER, J. F. FRANKLIN, AND R. L. WERNER. 1985. Plant communities and stand conditions. Pages 17–31 *in* E. R. Brown, tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Dep. Agric. For. Serv. Publ. R6-F&WL-192-1985.

HANSEN, A. J., T. A. SPIES, F. J. SWANSON, AND J. L. OHMANN. 1991. Conserving biodiversity in managed forests. BioScience 41:382–392.

LAND, D., W. R. MARION, AND T. E. O'MEARA. 1989. Snag availability and cavity nesting birds in slash pine plantations. J. Wildl. Manage. 53:1,165–1,171.

LUNDQUIST, R. W. 1988. Habitat use by cavity-nesting birds in the southern Washington Cascades. M.S. Thesis, Univ. of Washington, Seattle. 168pp.

MACLEAN, C. D. 1979. Relative density: the key to stocking assessment in regional analysis—a Forest Survey viewpoint. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-78. 5pp.

MADSEN, S. J. 1985. Habitat use by cavity-nesting birds in the Okanogan National Forest, Washington. M.S. Thesis, Univ. of Washington, Seattle. 113pp.

MCCOMB, W. C., S. A. BONNEY, R. M. SHEFFIELD, AND N. D. COST. 1986. Snag resources in Florida—are they sufficient for average populations of primary cavity-nesters? Wildl. Soc. Bull. 14:40–48.

MORRISON, M. L., M. F. DEDON, M. G. RAPHAEL, AND M. P. YODER-WILLIAMS. 1986. Snag requirements of cavity-nesting birds: are USDA Forest Service guidelines being met? West. J. Appl. For. 1:38–40.

NEITRO, W. A., V. W. BINKLEY, S. P. CLINE, R. W. MANNAN, B. G. MARCOT, D. TAYLOR, AND F. F. WAGNER. 1985. Snags. Pages 129–169 *in* E. R. Brown, tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Dep. Agric. For. Serv. Publ. R6-F&WL-192-1985.

NELSON, S. K. 1989. Habitat use and densities of cavity-nesting birds in the Oregon Coast Ranges. M.S. Thesis, Oregon State Univ., Corvallis. 157pp.

OHMANN, J. L. 1992. Wildlife habitats of the North Coast of California: new techniques for extensive forest inventory. U.S. Dep. Agric. For. Serv. Res. Pap. PNW-RP-440. 48pp.

OLD-GROWTH DEFINITION TASK GROUP. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. U.S. Dep. Agric. For. Serv. Res. Note PNW-447. 7pp.

OLIVER, C. D., AND B. C. LARSON. 1990. Forest stand dynamics. McGraw-Hill, Inc., New York, N.Y. 467pp.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86. 66pp.

SCHREIBER, B., AND D. S. DECALESTA. 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. For. Ecol. and Manage. 50:299–316.

SCHULZ, T. T., AND L. A. JOYCE. 1992. A spatial application of a marten habitat model. Wildl. Soc. Bull. 20:74–83.

SPIES, T. A., AND J. F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 90–109 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Dep. Agric. Gen. Tech. Rep. PNW-GTR-285.

———, ———, AND T. B. THOMAS. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1,689–1,702.

THOMAS, J. W., TECHNICAL EDITOR. 1979. Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Dep. Agric. Agric. Handb. No. 553. 512pp.

———, R. G. ANDERSON, C. MASER, AND E. L. BULL. 1979*a*. Snags. Pages 60–77 *in* J. W. Thomas, tech. ed. Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Dep. Agric. Agric. Handb. No. 553.

———, R. J. MILLER, C. MASER, R. G. ANDERSON, AND B. E. CARTER. 1979*b*. Plant communities and successional stages. Pages 22–39 *in* J. W. Thomas, tech. ed. Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington. U.S. Dep. Agric. Agric. Handb. No. 553.

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

Received 21 October 1993.
Accepted 8 April 1994.
Associate Editor: Steenhof.