Original Article

Snag Distributions in Relation to Human Access in Ponderosa Pine Forests

JEFF P. HOLLENBECK,[1,2] *United States Forest Service, Rocky Mountain Research Station, Montana State University Campus, Bozeman, MT 59717, USA*

LISA J. BATE, *Glacier National Park, 389 LaBrant Road, Kalispell, MT 59901, USA*

VICTORIA A. SAAB, *United States Forest Service, Rocky Mountain Research Station, Montana State University Campus, Bozeman, MT 59717, USA*

JOHN F. LEHMKUHL, *United States Forest Service, Pacific Northwest Research Station, 1133 N. Western Ave., Wenatchee, WA 98801, USA*

ABSTRACT Ponderosa pine (*Pinus ponderosa*) forests in western North America provide habitat for numerous cavity-using wildlife species that often select large-diameter snags for nesting and roosting. Yet large snags are often removed for their commercial and firewood values. Consequently we evaluated effects of human access on snag densities and diameter-class distributions at nine locations in ponderosa pine forests throughout the interior western United States. We found no relationship between small-diameter (23–50 cm diam breast ht [dbh]) snags and human access measures (i.e., road density, distance to nearest town, and topography). However, large-snag ($\geq$50 cm dbh) density was best predicted by road density, which suggested a decline, on average, of 0.7 large snags/ha for every km of road/km^2. Most locations had relatively high densities of small-diameter snags (<23 cm dbh) and diminishing density as diameter class increased. Idaho and Colorado study locations had higher snag densities in the largest diameter classes compared with remaining locations. These locations experienced minimal commercial timber harvest, were situated far from towns, and had few or no roads. Persistence of large-diameter snags and adequate snag densities for wildlife requires consideration of human access characteristics at coarse spatial scales. Snag management guidelines may need to incorporate these measures and focus more on retention of large-diameter snags than minimum density targets. © 2013 The Wildlife Society.

KEY WORDS cavity-user, human access, ponderosa pine, road density, snag densities, snag diameter distribution, wildlife habitat.

Ponderosa pine (*Pinus ponderosa*) forests in western North America provide essential wildlife habitat for numerous species, including many species of concern to state and federal agencies (Rabe et al. 1998, Wisdom et al. 2000, Raphael et al. 2001, Baker and Lacki 2006). Large-diameter ponderosa pine snags (standing dead trees) are strongly selected by many cavity-using wildlife species because they provide some of the most suitable nest and roost sites due to wood and decay characteristics (Bull et al. 1997, Rabe et al. 1998, Rose et al. 2001, Chambers and Mast 2005). Mature ponderosa pine trees constitute a source for continued snag recruitment (Ligon 1973, Bull et al. 1997, Harrod et al. 1999, Rose et al. 2001, Mellen et al. 2002). Large trees and snags also provide foraging resources, such as seeds and deeply furrowed bark, that support numerous arthropods and their larvae (Ligon 1973, Garrett et al. 1996, Bull et al. 1997), some of which play important roles in sustaining soil health and productivity (Niwa et al. 2001). Exfoliating bark on large snags provide critical roosting sites for several species of bats (Rabe et al. 1998, Baker and Lacki 2006, Arnett and Hayes 2009, Solvesky and Chambers 2009). Large fallen snags provide critical downed wood habitats for invertebrate and vertebrate species (Bull et al. 1997), and are key fuel components of the typical frequent low-intensity fire regimes that strongly influence ponderosa pine stands (Agee 1993).

Woodpeckers play an integral part in the functioning of forest ecosystems by excavating cavities in decayed portions of live trees or snags for nest and roost sites. These cavities are subsequently used by numerous secondary cavity-nesting or non-excavating vertebrates (Martin and Eadie 1999). Woodpeckers are often considered focal species because of their role in providing cavities needed by many other vertebrates (Thomas et al. 1979, Neitro et al. 1985, Lambeck 1997, Martin and Eadie 1999). Thus, if the needs of woodpeckers are met, the needs of a larger set of species are presumably provided. Consequently, the U.S. Department of Agriculture (USDA) Forest Service includes woodpeckers (e.g., white-headed woodpecker [*Picoides albolarvatus*] and black-backed woodpecker [*P. arcticus*]) as Management Indicator Species that are monitored to help inform evaluations of forest management activities (or lack thereof) for ecological integrity.

Received: 26 August 2011; Accepted: 24 July 2012
Published: 28 February 2013

[1]*E-mail: jhollenbeck@usgs.gov*
[2]*Present address: United States Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.*

Maintaining adequate densities of suitable snags is essential for the persistence of cavity-nesting and tree-decay-dependent wildlife species (e.g., woodpeckers and bats). As suggested by Conner (1979), the persistence of sensitive wildlife species may be jeopardized by management directives based on minimum thresholds rather than conditions that are resilient to ecosystem perturbations. Snag management guidelines first proposed by Thomas et al. (1979) and Neitro et al. (1985) were based on the minimum diameter of snags used by nesting woodpeckers. This may have resulted in the removal of many larger snags from federal lands because retention of smaller snags met specified guidelines. Large trees and snags are often removed for their commercial and firewood values (Morrison et al. 1986, Bate et al. 2007, Wisdom and Bate 2008) and to reduce risks associated with safety, fire, insects, and disease (Dickson et al. 1983). Snags and dying trees are also routinely removed during salvage logging (Saab et al. 2007), and snag retention programs on National Forests and other federal lands are hampered by conflicts with safety requirements, funding, and inconsistent standards and guidelines (Hope and McComb 1994). Consequently, the density, size, and condition of snags on federal lands often do not meet management standards (Morrison et al. 1986, Ganey 1999) or the needs of dependent wildlife species.

Across western United States forests, most cavity-nesting bird species select significantly larger snags than average for nesting, roosting, and foraging (Bull and Holthausen 1993, Conway and Martin 1993, Bagne et al. 2008, Lyons et al. 2008, Saab et al. 2009). Small-diameter trees and snags rarely have the decay characteristics that make them suitable for nest cavity excavation (Conner 1979, Bull et al. 1997). Large-diameter snags provide better protection against weather and predation than small snags (Moore 1945, Kilham 1971, Wiebe 2001), and may be critically important for resident species that overwinter in cold regions (Kendeigh 1961, Coombs et al. 2010). Higher snag densities than previously suggested for retention may be necessary to provide adequate nesting, roosting, and foraging habitat for snag-dependent species (Bull et al. 1997, Rose et al. 2001, Mellen et al. 2002, Saab et al. 2009, Marcot et al. 2010). Preference for nest sites with high snag densities and large-diameter trees has been documented for cavity-nesting birds in both unburned and burned forests (Raphael and White 1984, Bull et al. 1997, Lyons et al. 2008, Vierling et al. 2008, Saab et al. 2009).

Although natural resource managers recognize that human access negatively affects large-snag densities, few studies have quantified these relations. Human access was shown to negatively affect snag densities on some federal lands in Oregon and Montana (Bate et al. 2007, Wisdom and Bate 2008). However, it is unknown if this relationship can be generalized to other landscapes in the western United States. Furthermore, the effect of human access on size (diam) classes of snags retained on forested lands has not been investigated. Timber harvest and fire suppression over the past century has skewed diameter distributions of trees in coniferous forests toward smaller diameter trees (Parker et al. 2006). A similar pattern may occur with snags (Korol et al. 2002). Understanding the effects of patterns of human access on snag densities and diameter distributions over large geographic areas will assist the development of snag management standards and guidelines.

In 2002, we began a regional study (Birds and Burns Network; Saab et al. 2006, Russell et al. 2009) to investigate the effects of prescribed fire in reducing fuels and to assess the effects of fuels reduction on bird habitats and populations in ponderosa pine forests throughout much of its range in the interior western United States (i.e., AZ, CO, ID, MT, NM, OR, and WA). We focused on ponderosa pine forests because current and historic human activities, including timber harvest, fire exclusion, road building, and residential development, have led to considerable alterations to these forests (Theobald 2003, Noss et al. 2006). In support of our investigation, we evaluated densities and size-class distributions of snags in ponderosa pine forests on a broad spatial scale across primarily federally managed forest lands in the western United States. Our objectives were to 1) determine the relationship between human access and snag densities, and 2) evaluate the influence of human access on snag size classes in ponderosa pine forests of the interior western United States.

STUDY AREA

We selected 35 study units dominated by mature ponderosa pine at nine locations in the interior western United States on National Forest and The Nature Conservancy lands where fuel reduction treatments were planned (Table 1; Fig. 1). Within each location, we selected 2–6 sampling units, approximately 200–400 ha each, based on similarities in land cover, topography, aspect, and management history. We established six units on the Payette National Forest in Idaho (hereafter, Payette); seven on the Okanogan–Wenatchee National Forest in Washington (hereafter, Okanogan); four on the Helena National Forest in Montana (hereafter, Helena); four on the San Juan National Forest in Colorado (hereafter, San Juan); four in Oregon (two on Fremont National Forest and two on nearby The Nature Conservancy Sycan Marsh; hereafter Fremont/Sycan), three each on the Apache–Sitgreaves (hereafter, Apache–Sitgreaves), and Kaibab (hereafter, Kaibab) National Forests, and two each on the Coconino (hereafter, Coconino) and Gila National Forests (hereafter, Gila) in Arizona and New Mexico, respectively. Total area sampled at all locations was 10,750 ha.

All study locations were managed as multiple-use landscapes, with uses that include timber harvest, recreation, wildlife, and watershed management. In the absence of reports documenting timber harvest history or firewood collection, we used the density of cut stumps as an indicator of these activities within each study unit. Based on the cut-stump indicator, four locations (Apache–Sitgreaves, Gila, Helena, Okanogan) were moderately impacted by timber or firewood harvest, three locations (Coconino, Kaibab, Fremont/Sycan) were heavily impacted, and two locations

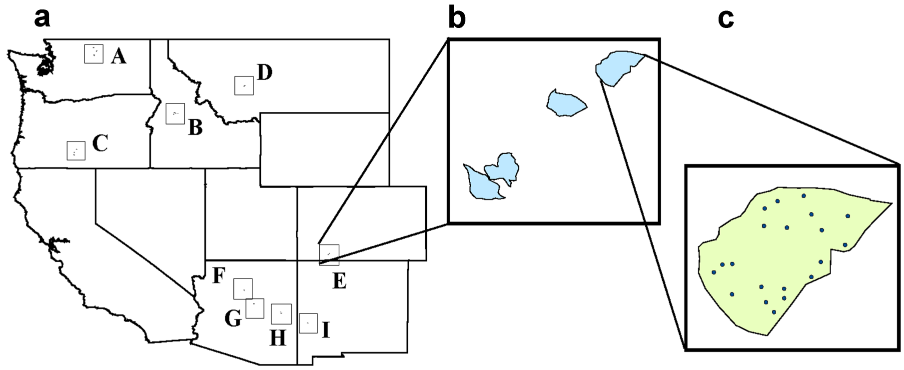

Figure 1. Locations, units, and plots in predominantly ponderosa pine forest in the western United States sampled for snag density, 2004–2008: (a) locations (A, Okanogan National Forest [WA]; B, Payette National Forest [ID]; C, Fremont/Sycan [OR]; D, Helena National Forest [MT]; E, San Juan National Forest [CO]; F, Kaibab National Forest [AZ]; G, Coconino National Forest [AZ]; H, Apache–Sitgreaves National Forest [AZ]; I, Gila National Forest [NM]); (b) example of units within a location; (c) example of sample plot locations within a unit.

(Payette, San Juan) had little human impact as indicated by the near absence of cut stumps (Table 2).

Mature ponderosa pine dominated the overstory (trees ≥23 cm dbh) at all locations and was the primary characteristic driving study-unit selection (Table 1). Ponderosa pine was the dominant large (≥50 cm dbh) tree species at all study locations except Gila, where alligator juniper (*Juniperus deppeana*) was more abundant (but ponderosa pine was the dominant overstory species). In Southwest locations (i.e., AZ, NM, and CO), Arizona fescue (*Festuca arizonica*) and blue gramma (*Bouteloua gracilis*) were the most common understory species. Green rabbitbrush (*Chrysothamnus viscidiflorus*) and Fendler rose (*Rosa woodsii*) also occurred at Arizona locations, and Gambel oak (*Quercus gambelii*) dominated the understory in New Mexico. Elevation at Southwest locations ranged from 2,072 m to 2,500 m. In Northwest locations (i.e., WA, OR, ID, and MT), understory vegetation included snowberry (*Symphoricarpos albus*), Oregon grape (*Berberis repens*), kinnickinnick (*Arctostaphylos uva-ursi*), spirea (*Spirea* spp.), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus* spp.). Bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) were the common grass species. Elevations at Northwest locations ranged from 670 m to 2,680 m. Annual precipitation (USDA NRCS 2009) among all locations averaged 66 cm and ranged from 55 cm (Gila) to 86 cm (San Juan; Table 1).

METHODS

Data Collection

We established 20–40 permanently marked 0.4-ha random plots in each unit. Plot centers were ≥250 m apart from each other and from unit boundaries (Fig. 1c). At each plot, we counted all snags ≥23 cm dbh and ≥1.4 m in height within 2 20-m × 100-m rectangles that crossed at the center (a rectangular cross plot). Snag measurements followed methods outlined by Bate et al. (2007). We also tallied human-cut stumps and derived plot-level cut-stump density (stumps/ha). This field-collected covariate provided an indicator of past timber management (Table 2).

We derived four covariates from remotely sensed or previously mapped data sources that were related to human access (Table 2). Slope and aspect were derived from digital elevation models (USGS EROS, http://eros.usgs.gov). Slope was expressed as percentage slope and aspect was cosine-transformed to range from 1 (North) to −1 (South). Road density was derived from data supplied by National Forests and expressed as km of mapped roads (paved and unpaved)/ km^2 within unit boundaries. We also calculated the driving

Table 1. Forest characteristics at nine ponderosa pine-dominated locations across the interior western United States, 2004–2008. Percent pine composition is the average of ponderosa pine trees among all tree species.

	Trees/ha[a]		% pine		Precipitation (cm/yr)[b]	
Location (National Forest)	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Apache–Sitgreaves, AZ	148	24	81	2.0	66	3.2
Coconino, AZ	153	8	85	3.9	65	8.0
Gila, NM	120	27	61	2.7	55	2.4
Helena, MT	222	19	59	11.4	69	2.4
Kaibab, AZ	109	12	99	1.1	67	4.0
Okanogan, WA	114	4	55	7.6	57	3.1
Payette, ID	83	12	67	6.5	62	4.5
San Juan, CO	158	15	65	6.2	86	3.8
Fremont/Sycan, OR	118	13	82	3.8	68	3.4

[a] Trees ≥23 cm dbh.
[b] Precipitation data derived from nearest U.S. Department of Agriculture Natural Resources Conservation Service Snopack Telemetry (SNOTEL) station.

Table 2. Mean (SE) for covariates included in candidate models relating snag density to human access at nine locations in ponderosa pine forests across the interior western United States, 2004–2008.

Location[a]	Median_slope[b]		Road_dens[c]		Median_cosasp[d]		Nearest_town[e]		Cut_ha[f]	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
ASAZ	5.8	2.0	2.93	0.60	−0.31	0.40	11	1.5	1,375	857.0
COAZ	7.5	1.5	1.80	0.10	−0.28	0.30	60	1.0	2,419	481.0
GINM	17.3	4.7	2.33	0.20	0.81	0.01	90	0.0	1,357	582.0
HEMT	19.7	2.9	1.95	0.60	−0.34	0.30	17	1.7	1,376	524.0
KAAZ	2.3	0.2	1.39	0.30	−0.17	0.20	40	0.3	2,083	949.0
OKWA	37.2	1.5	1.55	0.40	−0.02	0.30	52	10.0	1,348	461.0
PAID	57.8	1.7	0.57	0.20	−0.49	0.20	64	3.1	0	0.0
SJCO	26.7	4.9	0.02	0.02	−0.88	0.03	80	10.0	6.3	6.3
SYOR	14.0	4.8	3.53	0.70	0.30	0.20	90	0.0	2,067	683.0

[a] ASAZ, Apache–Sitgreaves National Forest (AZ); COAZ, Coconino National Forest (AZ); GINM, Gila National Forest (NM); HEMT, Helena National Forest (MT); KAAZ, Kaibab National Forest (AZ); OKWA, Okanogan National Forest (WA); PAID, Payette National Forest (ID); SJCO, San Juan National Forest (CO); SYOR, Fremont/Sycan (OR).
[b] Median slope of each unit expressed as % slope.
[c] Road_dens = road density of each unit expressed as km (road)/km^2.
[d] Median_cosasp = median cosine of aspect for each unit. Scales from 1 to −1: values closer to 1 face north, −1 face south, 0 faces either east or west.
[e] Nearest town = distance (km) to nearest town along roads.
[f] Cut_ha = cut stumps/ha; indicator of timber management.

distance on navigable roads from each unit to the nearest town with ≥1,000 inhabitants (Bate et al. 2007, Wisdom and Bate 2008). All remotely sensed covariates were extracted or derived in ArcGIS 9.3.

We summarized all response variables and covariates to the unit level for analysis and log-transformed large-snag density to meet assumptions of normality. We also checked for correlation among covariates. Because road density was correlated with cut-stump density (Pearson's $r = 0.68$), we adjusted our analyses to account for this where appropriate.

Statistical Methods

For each unit, we summarized snag densities (snags/ha) into nine size classes using 10-cm-dbh increments except for the smallest (23 cm to <30 cm; 23 cm was smallest diam measured) and largest (>100 cm; very large snags were rare) classes. We also binned snag densities into two coarse size classes (≥23 to <50, and ≥50 cm dbh) for use in *post hoc* comparisons of snag density and proportion because these size classes are related to both wildlife use and public-land management guidelines (cf. Mellen et al. 2002, Marcot et al. 2010). The lower cutoff diameter (23 cm dbh) is the smallest diameter that woodpeckers typically use for nesting (Bull et al. 1997, Bunnell et al. 2002, Saab et al. 2004) and is frequently the smallest sized trees and snags harvested for timber values (USDA Forest Service 2002). Snags in the larger size class (≥50 cm dbh) are most valuable (for nesting, roosting, and foraging) to a wide range of animals (Marcot et al. 2010). Additionally, snag retention guidelines implemented by the USDA Forest Service in the western United States frequently define large snags as ≥50 cm dbh (e.g., Ohmann and Waddell 2002, Stephens and Moghaddas 2005, Marcot et al. 2010, Wightman et al. 2010).

Snag density distributions were non-normal, so we used Multi-Response Permutation Procedure to examine similarity of snag densities among size classes across locations (Mielke and Berry 2007). Multi-Response Permutation Procedure is robust for violations of the assumptions of normality, homogeneity of variances, and independence among samples (Pellicane and Mielke 1999, Mielke and Berry 2007). Our Multi-Response Permutation Procedure analysis tested for greater differences among units within a location compared with between locations and generated an *A*-statistic, which indicates "effect size," or distinctiveness, of groups. *A*-statistic values may range from 0 to 1, with values >0.3 indicating substantial distinctiveness of groups. We subsequently compared groups (study locations) using Peritz's closed procedure for multiple comparisons (Begun and Gabriel 1981, Petrondas and Gabriel 1983) to control family-wise error associated with multiple hypothesis tests. We specified $\alpha = 0.10$ as the threshold of significance for our multiple comparisons to optimize statistical power and Type 1 error rates (Zar 1999).

We used information-theoretic model selection to evaluate candidate models relating snag density to human and abiotic covariates. We separately modeled human, abiotic (topographic), and combined human and abiotic effects on both small (23 cm to <50 cm) and large (≥50 cm dbh) snag diameter classes. We constructed 21 *a priori* candidate models from five potential covariates that were hypothesized to affect human access to snags and subsequent snag density (Table 3). In general, slope and aspect are topographic conditions that may influence ease of access to snags, either through steepness or because north-facing slopes are typically wetter and more densely vegetated and snags are less visible or less accessible. Distances to nearest town and road density are direct access measures and snag density was hypothesized to decrease as either distance to nearest town decreases or road density increases. Human-cut stump density indicates recent timber management or firewood gathering activities and is directly related to human access. Because cut-stump density was moderately correlated with road density, these covariates were mutually excluded among candidate models.

Table 3. Candidate models relating snag density to human access at nine ponderosa pine-dominated locations (Apache–Sitgreaves National Forest [AZ], Coconino National Forest [AZ], Gila National Forest [NM], Helena National Forest [MT], Kaibab National Forest [AZ], Okanogan National Forest [WA], Payette National Forest [ID], San Juan National Forest [CO], and Fremont/Sycan [OR]), dominated by ponderosa pine forest, across the interior western United States, 2004–2008.

Model category	Model[a]	Alternative hypotheses
Null	Intercept only	Null model; snag density random
Human	Nearest_town	Snag densities increase with increasing distance away from nearest town because of less impact from human access
	Road_dens	Snag densities decrease as road densities increase because of greater impacts from human access
	Cut_ha	As stump densities increase (indicator of past management activity and human access) snag densities decrease
	Nearest_town + Road_dens	Snag densities decrease with distance to nearest town and increasing road density
	Nearest_town + Cut_ha	Snag densities decrease with distance to nearest town and increasing cut-stump density
Abiotic	Median_slope	Lower slopes will have lowered snag densities because of greater human access
	Median_cosasp	Snag density increases with northern aspect due to denser vegetation
	Median_cosasp + Median_slope	Snag density increases with slope and northern aspect
Combination	Nearest_town + Median_slope	Snag densities determined by a combination of human and abiotic factors
	Nearest_town + Median_cosasp	"
	Median_cosasp + Road_dens	"
	Median_cosasp + Cut_ha	"
	Median_slope + Road_dens	"
	Median_slope + Cut_ha	"
	Nearest_town + Road_dens + Median_cosasp	"
	Nearest_town + Road_dens + Median_slope	"
	Nearest_town + Road_dens + Median_cosasp + Median_slope	"
	Nearest_town + Cut_ha + Median_cosasp	"
	Nearest_town + Cut_ha + Median_slope	"
	Nearest_town + Cut_ha + Median_cosasp + Median_slope	"

[a] Nearest town = distance to nearest town along roads; Road_dens = road density of each unit expressed as km (road)/km^2; Cut_ha = cut stumps/ha; Median slope of each unit expressed as percent slope; Median_cosasp = median cosine of aspect for each unit. Scales from 1 to −1: values closer to 1 face north, −1 face south, 0 faces either east or west.

For all locations collectively, we fit models using generalized least squares with a first-order autoregressive (AR1) correlation structure to model potential autocorrelation among units within locations. We evaluated the goodness-of-fit of the most highly parameterized candidate models as global models (Burnham and Anderson 2002) using Nagelkerke's R^2 (Nagelkerke 1991) and ranked models using small-sample-corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). We evaluated the relative support for each model using both AIC_c and Akaike weights (w). Models within 2 AIC_c units of the top-ranked model ($\Delta AIC_c \leq 2$) were considered plausible (Burnham and Anderson 2002). Where appropriate, we report the model coefficients and 95% confidence intervals for covariates occurring in supported models.

RESULTS

Snag Size-Class Distributions

Multi-Response Permutation Procedure results for all locations suggested distinctive diameter-class distributions among locations ($A = 0.24$, $P < 0.001$). We did not detect a difference in snag distribution at six locations (Apache–Sitgreaves, Coconino, Gila, Helena, Okanogan, and Fremont/Sycan; $P > 0.10$; Fig. 2). At each of these locations, the highest snag density occurred in the smallest size classes (23 cm and 30 cm dbh; Fig. 2). Three locations had significantly different distributions ($P \leq 0.10$; Table 4). The Kaibab location had low snag densities in all size classes (<1 snag/ha in all nine size classes; Fig. 2). Although most locations had relatively high snag densities in the two smallest size classes (23 cm and 30 cm dbh) that diminished to few or no snags in the largest size classes (Fig. 2), the Payette and San Juan locations differed in having high snag densities in the five largest size classes (≥50 cm dbh) compared with other locations (Fig. 2). The San Juan location had the highest snag densities of any location (Fig. 2), which resulted in a significant difference between San Juan and Payette.

In general, most locations had a large (≥80%) proportion of small (23 cm to <50 cm dbh) snags compared with large (≥50 cm dbh; Table 4). The Payette and San Juan locations had fewer (60%) small snags and more (40%) large snags (≥50 cm dbh). The Kaibab location had 32% of its snags in the ≥50-cm size class; however, the density was only 0.6 large snags/ha.

Model Selection

We found an adequate fit (variation explained by predictor covariates) for the global candidate model for large (≥50 cm dbh) snag density (Nagelkerke's $R^2 = 0.40$), but not for small (23 cm to <50 cm dbh) snag density (Nagelkerke's $R^2 = 0.03$). The top-ranked model for small (23 cm to <50 cm dbh) snag density (and the only model with $\Delta AIC_c \leq 2$) was the null model, which suggested no

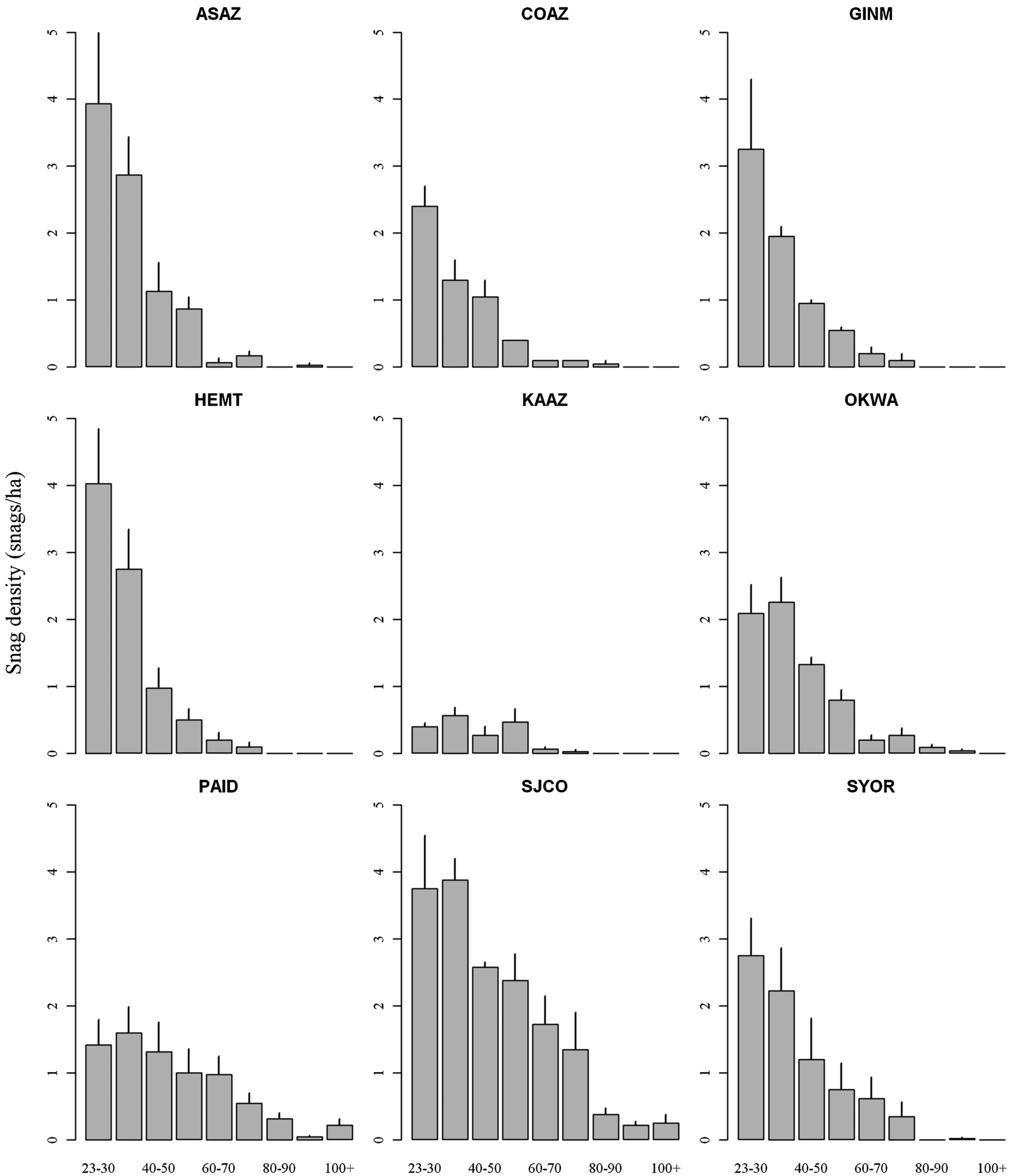

Figure 2. Snag diameter distributions (snags/ha) for nine size classes at nine locations (ASAZ, Apache–Sitgreaves National Forest [AZ]; COAZ, Coconino National Forest [AZ]; GINM, Gila National Forest [NM]; HEMT, Helena National Forest [MT]; KAAZ, Kaibab National Forest [AZ]; OKWA, Okanogan National Forest [WA]; PAID, Payette National Forest [ID]; SJCO, San Juan National Forest [CO]; SYOR, Fremont/Sycan [OR]), dominated by ponderosa pine forest, across the interior western United States during 2004–2008. Error bars indicate standard error. Classes are 10 cm wide except smallest (23 cm to <30 cm dbh) and largest (≥100 cm dbh).

relationship between measured covariates and small-snag density (Table 5).

Four models for large (≥50 cm dbh) snag density were well-supported by the data ($\Delta AIC_c \leq 2$; Table 5). Each of the four plausible models included the road density covariate, and distance to nearest town and slope occurred in two models each. Combined, these models had 74% of Akaike model weights supporting their plausibility, given our data and candidate model sets. Models containing the aspect covariate were not among the top-ranked models

Table 4. Snag density (SE) and proportion in small (23 cm to <50 cm dbh) and large (≥50 cm dbh) size classes at nine ponderosa pine dominated locations across the interior western United States, 2004–2008.

Location[a,b]	Density (snags/ha)		Proportion	
	(23–50 cm)	(≥50 cm)	(23–50 cm)	(≥50 cm)
ASAZ[A]	7.9 (1.9)	1.1 (0.2)	90	10
COAZ[A]	4.7 (0.8)	0.6 (0.6)	88	12
GINM[A]	6.2 (0.9)	0.9 (0.2)	88	12
HEMT[A]	7.7 (1.6)	0.8 (0.3)	91	9
KAAZ[B]	1.2 (0.1)	0.6 (0.2)	68	32
OKWA[A]	5.7 (0.7)	1.3 (0.2)	80	20
PAID[C]	4.3 (1.0)	3.1 (0.7)	58	42
SJCO[D]	10.2 (0.9)	6.3 (1.3)	63	37
SYOR[A]	6.2 (1.4)	1.8 (0.9)	78	22

[a] ASAZ, Apache–Sitgreaves National Forest (AZ); COAZ, Coconino National Forest (AZ); GINM, Gila National Forest (NM); HEMT, Helena National Forest (MT); KAAZ, Kaibab National Forest (AZ); OKWA, Okanogan National Forest (WA); PAID, Payette National Forest (ID); SJCO, San Juan National Forest (CO); SYOR, Fremont/Sycan (OR).
[b] [A–D]Indicate differences in size-class distributions. Locations followed by the same letter are not statistically different from each other.

Table 5. Top-ranked models ($\Delta AIC_c \leq 2$) for large (≥50 cm dbh) and small (23–50 cm dbh) snag density in ponderosa pine dominated sites (Apache–Sitgreaves National Forest [AZ], Coconino National Forest [AZ], Gila National Forest [NM], Helena National Forest [MT], Kaibab National Forest [AZ], Okanogan National Forest [WA], Payette National Forest [ID], San Juan National Forest [CO], and SYOR, Fremont/Sycan [OR]) in the interior western United States, 2004–2008.

Size class	Model[a]	−2log Lik[b]	K^c	ΔAIC_c	w^d
≥50 cm	Median_slope + Road_dens	71.8	4	0	0.259
	Nearest_town + Road_dens + Median_slope	69.9	5	0.9	0.165
	Road_dens	75.3	3	0.9	0.161
	Nearest_town + Road_dens	72.8	4	1.1	0.153
23–50 cm	Intercept-only	173.9	2	0	0.278

[a] Median_slope = median slope (%), Road_dens = road density (km/km^2), Nearest_town = nearest town (km).
[b] Model likelihood.
[c] No. of estimated model parameters.
[d] Akaike wt.

($\Delta AIC_c \leq 2$). Relatively little support existed for models containing cut-stump density; the highest-ranked model containing that covariate (Median_slope + Cut_ha) was not well-supported ($\Delta AIC_c = 4.5$, $w = 0.03$).

In general, large-snag density decreased as road density increased or as distance to nearest town or slope decreased (Table 6). Among the four plausible models for large-snag density, only the road-density covariate was significant (95% CI did not overlap zero, Table 6; Arnold 2010), which suggested that the single covariate model (Intercept + Road_dens) is the most useful and appropriate for predicting large-snag density. This model suggests a decline, on average, of 0.7 snags/ha (back-transformed from log scale) for every km of road/km^2 (Fig. 3).

Table 6. Parameter estimates, standard errors (SE), and 95% lower (LCL) and upper (UCL) confidence limits for top-ranked ($\Delta AIC_c \leq 2$) models relating large-snag densities (≥50 cm dbh) to human and abiotic covariates at nine locations (Apache–Sitgreaves National Forest [AZ], Coconino National Forest [AZ], Gila National Forest [NM], Helena National Forest [MT], Kaibab National Forest [AZ], Okanogan National Forest [WA], Payette National Forest [ID], San Juan National Forest [CO], and Fremont/Sycan [OR]) across the interior western United States, 2004–2008.

Model[a]	Covariate	Estimate	SE	95% LCL	95% UCL
Road_dens + Median_slope ($\Delta AIC_c = 0$)	Intercept	0.23	0.403	−0.56	1.02
	Road_dens[b]	−0.277	0.111	−0.496	−0.059
	Median_slope	0.018	0.01	−0.001	0.038
Nearest_town + Road_dens + Median_slope ($\Delta AIC_c = 0.9$)	Intercept	−0.038	0.446	−0.913	0.836
	Nearest_town	0.007	0.005	−0.003	0.017
	Road_dens[b]	−0.311	0.113	−0.532	−0.089
	Median_slope	0.016	0.01	−0.003	0.034
Road_dens ($\Delta AIC_c = 0.9$)	Intercept[b]	0.81	0.258	0.303	1.316
	Road_dens[b]	−0.363	0.104	−0.567	−0.159
Nearest_town + Road_dens ($\Delta AIC_c = 1.1$)	Intercept	0.407	0.36	−0.298	1.112
	Nearest_town	0.009	0.005	−0.002	0.019
	Road_dens[b]	−0.396	0.103	−0.598	−0.194

[a] Median_slope = median slope (%), Road_dens = road density (km/km^2), Nearest_town = nearest town (km).
[b] CI does not contain zero.

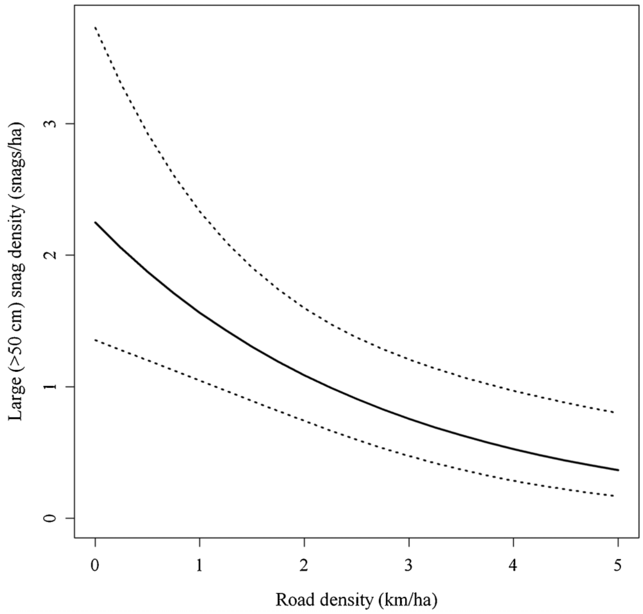

Figure 3. Relationship between large (≥50 cm dbh) snag density (back-transformed from log scale) and road density (solid line) estimated by the top-ranked single-covariate model (Table 3) for ponderosa pine-dominated sites in the interior western United States, 2004–2008. Dotted lines are 95% confidence limits.

DISCUSSION

Among eight federally managed forest locations, and one private multiple-use location, we found a strong negative association between human access and densities of large (≥50 cm dbh) snags and snag size-class distributions. Although we could not determine causation, our results suggest that human access reduced large-snag density across our study locations, even when accounting for past harvest activity. The results of our broad-scale study corroborate findings of other fine-scale studies (Bate et al. 2007, Wisdom and Bate 2008) showing negative effects of human access on large-snag densities. We also found that human access affects the size-class distributions of snags. This has been suspected, but not yet demonstrated for ponderosa pine forests over the western United States. At sites with easy human access, few if any large (≥50 cm dbh) snags occurred and snag diameter distributions were skewed toward small-diameter classes; similar to the patterns reported by Parker et al. (2006) for live trees in ponderosa pine forests of interior western North America, and Korol et al. (2002) for snags within the interior Columbia River Basin.

Two locations (Payette and San Juan) with the least human access had significantly higher densities of snags ≥50 cm dbh than the remaining locations. This is likely because limited (human) accessibility at these locations reduced timber harvest and firewood cutting activities. Cut-stump density suggested these locations were never harvested or received little commercial timber harvest. Commercial timber harvests generally favor sites with high accessibility. Topography, in particular slope, is a major consideration for harvest operations because of cost, logistics, and environmental concerns. Slopes at the Payette and San Juan locations were two of the three steepest locations.

Additionally, road densities among all locations were lowest in Payette and San Juan. Roads facilitate access to timber resources for commercial harvest. Roads also allow increased human access for recreational and consumptive purposes, which results in potentially widespread habitat modifications (e.g., cutting of snags for firewood) and disturbances to wildlife (e.g., through vehicle traffic and hunting) that alter biotic communities (e.g., DellaSala et al. 1995, Allen et al. 1998).

Wisdom and Bate (2008) observed significantly higher snag densities in areas without roads at locations in Oregon. In this study, the relatively roadless Payette and San Juan locations tended to be farther from human settlement, and had higher snag densities, than most of the remaining locations. This suggests that low road density and farther distances from human settlement, along with steep topography (i.e., reduced human access), explain the observed snag size-class distributions at the Payette and San Juan locations. The snag size-class distributions at Payette and San Juan locations differed from other locations with high densities in the larger size classes, yet their distributions were not similar. This is likely because the Payette has a drier climate than San Juan, with fewer live trees and lower subsequent snag recruitment, which results in lower overall snag densities.

Snag size-class distributions at the Payette and San Juan locations were similar to those of unharvested forest in the mixed-conifer forests of eastern Oregon and Washington, where 60% of snags occurred in small size classes (23 cm to <50 cm dbh) and 40% in large size classes (≥50 cm dbh; cf. Marcot et al. 2010). These two locations in relatively unharvested, unroaded forest may approximate historical conditions prior to European settlement, although this is difficult to assess because these forests have likely been influenced by fire suppression and other anthropogenic factors. Decades of fire exclusion in ponderosa pine forests with historically frequent fire regimes may have caused several fire cycles to be missed, resulting in smaller more shade-tolerant tree species. Tree mortality as a result of suppression, increased insect activity, or increased diseases in these denser stands may have increased density of smaller snags but not necessarily larger snags (Korol et al. 2002). However, historical snag distributions reported from other locations in the dry coniferous forests of the interior western United States (Agee 1993, Korol et al. 2002, Brown et al. 2003) are similar to those on the relatively unharvested, unroaded Payette and San Juan locations.

The Kaibab location differed from all other locations because it had few snags in all size classes (cf. Ganey 1999). This location was highly accessible to humans because of low slope, close proximity to a town, and moderate road density. Furthermore, the influence of road density may be of less consequence at the Kaibab location because the gentle topography at this location allows relatively easy vehicle access, even in roadless areas.

Model uncertainty was high among candidate models relating small (23 cm to <50 cm dbh) snag densities and human access, which suggested no relationships. This contrasts with Bate et al. (2007) and Wisdom and Bate (2008), who found a negative relationship between human access and small-snag densities in Oregon and Montana. This may be due to different sampling approaches. Bate et al. (2007) and Wisdom and Bate (2008) used individual forest stands as sample units, which, by definition, are homogeneous units of forest type and structure. In contrast, we used landscape units, potentially composed of multiple stands, as our sampling unit. The resulting heterogeneity may have diminished our ability to detect patterns in small snag abundance relative to human access, resulting in poor performance of all candidate models for the small size class. For the large size class ($\geq$50 cm dbh), however, we found a substantial negative relationship between road density and snag density, in concurrence with previous work (Bate et al. 2007, Wisdom and Bate 2008). Therefore, the apparent lack of relationship between small-snag density and human access may reflect the efficiency of firewood collection; large snags are selected and removed before small snags because they increase return for effort of cutting and collection.

We also found a negative relationship between human access and snag size-class distributions that included large-diameter snags. It is unclear whether this pattern is due largely to timber harvest or firewood cutting. However, Bate et al. (2007) and Wisdom and Bate (2008) implicate firewood cutting as an important process at locations in Oregon and Montana. Their results suggested that forests closer to towns are disproportionately used for firewood gathering, even when road access is limited.

Impacts on wildlife may not be straightforward and involves more than minimum diameter requirements (Ganey and Vojta 2004, Chambers and Mast 2005). Some wildlife species, such as snag-roosting bats, prefer large snags adjacent to open areas, such as roads (Solvesky and Chambers 2009). Clearly, the consideration of a buffer zone around roads, where human access is substantial (cf. Matlack 1993, Trombulak and Frissell 2000), may be an important component of effective snag management. Removal and revegetation of roads that are no longer needed for management purposes (cf. Switalski et al. 2004, Roedenbeck et al. 2007) would presumably reverse many road impacts and potentially create habitat for a variety of wildlife, although further testing of this approach is needed (Switalski et al. 2004, Roedenbeck et al. 2007). Regardless of road proximity, management for large diameter trees that become large diameter snags after death is beneficial (Lehmkuhl et al. 2003).

MANAGEMENT IMPLICATIONS

Snag management guidelines that incorporate strategies to retain or create large-diameter snags and place less emphasis on minimum-density targets (especially when these consist of the smallest diameter allowed) are important for ensuring the persistence of cavity-using wildlife species. In areas where large snag numbers are low as a result of human activity, silvicultural treatments that maintain or grow large green trees, and maintain or enhance the natural processes (e.g., pathogens, insects) that ultimately kill large trees and create snags, may be necessary to restore large-snag and associated down-wood habitats. Subsequent or concurrent management of human access, particularly open road density in accessible terrain (i.e., not steep), is critical for maintaining snags and protecting investments to maintain or restore snags as wildlife habitat over broad spatial scales. If access management is difficult, then the anticipated loss of large snags next to roads might be mitigated by retaining or creating more large snags beyond the firewood retrieval distance from roads, which may vary with the steepness of the terrain and whether up-slope or down-slope from the road. We acknowledge the challenges these issues present because of the complexities associated with managing both wildlife and human access; however, understanding how human access impacts snags provides a useful coarse-scale perspective for assigning priorities.

ACKNOWLEDGMENTS

This study was funded by the Joint Fire Science Program (no. 01-1-3-25), National Fire Plan (02.RMS.C.2 and 01.PNW.C.2), and the USDA Forest Service Rocky Mountain Research Station, Pacific Northwest Research Station, and Intermountain and Pacific Northwest Regions. The Nature Conservancy of Oregon and the Payette, Fremont–Winema, Okanogan–Wenatchee, Helena, San Juan, Kaibab, Coconino, Apache–Sitgreaves, and Gila National Forests also contributed to the project. We thank W. Block and site managers at each location for overseeing the data collection, including K. Woodruff, A. Markus, S. Story, G. Vos, B. Dickson, S. Jentsch, and A. Garcia. A. Jacobs and M. Wisdom provided thoughtful comments on the manuscript. R. King provided guidance on statistical analyses. We are grateful to S. Vojta and many other field assistants who worked long, hot days to collect the field data.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Allen, C. D., J. L. Bettencourt, and T. W. Swetnam. 1998. Landscape changes in the southwestern United States: techniques, long-term data sets, and trends. Pages 71–84 *in* T. D., Sisk, editor. Perspectives on the land use history of North America: a context for understanding our changing environment. U.S. Geological Survey Biological Resources Division USGS/BRD/BSR-1998-0003, Washington, D.C., USA.

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

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178.

Bagne, K. E., K. L. Purcell, and J. T. Rotenberry. 2008. Prescribed fire, snag population dynamics, and avian nest site selection. Forest Ecology and Management 255:99–105.

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

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

Begun, J. M., and K. R. Gabriel. 1981. Closure of the Newman–Keuls multiple comparisons procedure. Journal of the American Statistical Association 76:241–245.

Brown, J. K., E. D. Reinhardt, and K. A. Kramer. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. U.S. Department of Agriculture Forest Service RMRS-GTR-105, Ogden, Utah, USA.

Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. Journal of Wildlife Management 57:335–345.

Bull, E. L., C. G. Parks, and T. R. Torgersen. 1997. Trees and logs important to wildlife in the interior Columbia River basin. U.S. Department of Agriculture Forest Service, PNW-GTR-391, Portland, Oregon, USA.

Bunnell, F. L., E. Wind, M. Boyland, and I. Houde. 2002. Diameters and heights of trees with cavities: their implications to management. Pages 717–738 *in* W. F. Laudenslayer, P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Department of Agriculture Forest Service PSW-GTR-181, Albany, California, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Chambers, C. L., and J. N. Mast. 2005. Ponderosa pine snag dynamics and cavity excavation following wildfire in northern Arizona. Forest Ecology and Management 216:227–240.

Conner, R. N. 1979. Minimum standards and forest wildlife management. Wildlife Society Bulletin 7:293–296.

Conway, C. J., and T. E. Martin. 1993. Habitat suitability for Williamson's sapsuckers in mixed-conifer forests. Journal of Wildlife Management 57:322–328.

Coombs, A. B., J. Bowman, and C. J. Garroway. 2010. Thermal properties of tree cavities during winter in a northern hardwood forest. Journal of Wildlife Management 74:1875–1881.

DellaSala, D. A., D. M. Olson, S. E. Barth, S. L. Crane, and S. A. Primm. 1995. Forest health: moving beyond rhetoric to restore healthy landscapes in the Inland Northwest. Wildlife Society Bulletin 23:346–356.

Dickson, J. G., R. N. Connor, and J. H. Williamson. 1983. Snag retention increases bird use of a clear-cut. Journal of Wildlife Management 47: 799–804.

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.

Ganey, J. L., and S. C. Vojta. 2004. Characteristics of snags containing excavated cavities in northern Arizona mixed-conifer and ponderosa pine forests. Forest Ecology and Management 199:323–332.

Garrett, K. L., M. G. Raphael, and R. D. Dixon. 1996. White-headed woodpecker (*Picoides albolarvatus*). Account 252 *in* A. Poole, editor. Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. http://bna.birds.cornell.edu/bna/species/252/articles/introduction Accessed 10 Dec 2010.

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

Hope, S., and W. C. McComb. 1994. Perceptions of implementing and monitoring wildlife tree prescriptions on National Forests in western Washington and Oregon. Wildlife Society Bulletin 22:383–392.

Kendeigh, C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bulletin 73:140–147.

Kilham, L. 1971. Reproductive behavior of yellow-bellied sapsuckers. I. Preference for nesting in Fomes-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals. Wilson Bulletin 83:159–171.

Korol, J. J., M. A. Hemstrom, W. J. Hann, and R. A. Gravenmier. 2002. Snags and down wood in the Interior Columbia Basin Ecosystem Management Project. Pages 649–664 *in* W. F. Laudenslayer, P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Department of Agriculture Forest Service PSW-GTR-181, Albany, California, USA.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11:849–856.

Lehmkuhl, J. F., R. L. Everett, R. Schellhaas, P. Ohlson, D. Keenum, H. Riesterer, and D. Spurbeck. 2003. Cavities in snags along a wildfire chronosequence in eastern Washington. The Journal of Wildlife Management 67:219–228.

Ligon, J. D. 1973. Foraging behavior of the white-headed woodpecker in Idaho. Auk 90:862–869.

Lyons, A. L., W. L. Gaines, J. F. Lehmkuhl, and R. J. Harrod. 2008. Short-term effects of fire and fire surrogate treatments on foraging tree selection by cavity-nesting birds in dry forests of central Washington. Forest Ecology and Management 255:3203–3211.

Marcot, B. G., J. L. Ohmann, K. L. Mellen-McLean, and K. L. Waddell. 2010. Synthesis of regional wildlife and vegetation field studies to guide management of standing and down dead trees. Forest Science 56:391–404.

Martin, K., and J. M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115:243–257.

Matlack, G. R. 1993. Sociological edge effects: spatial distribution of human impact in suburban forest fragments. Environmental Management 17: 829–835.

Mellen, K., B. G. Marcot, J. L. Ohmann, K. L. Waddell, E. A. Willhite, B. B. Hostetler, S. A. Livingston, and C. Ogden. 2002. DecAID: a decaying wood advisory model for Oregon and Washington. Pages 527–534 *in* W. F. Laudenslayer, P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Department of Agriculture Forest Service PSW-GTR-181, Albany, California, USA.

Mielke, P. W., and K. J. Berry. 2007. Permutation methods: a distance function approach. Springer, New York, New York, USA.

Moore, A. D. 1945. Winter night habits of birds. Wilson Bulletin 57: 253–260.

Morrison, M. L., F. F. Dedon, M. G. Raphael, and M. P. Yoder-Williams. 1986. Snag requirements of cavity-nesting birds: are USDA Forest Service guidelines being met? Western Journal of Applied Forestry 1:38–40.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

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, editor. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Department of Agriculture Forest Service Publication no. R6-F&WL-192-1985, Portland, Oregon, USA.

Niwa, C. G., R. W. Peck, and T. R. Torgersen. 2001. Soil, litter, and coarse woody debris habitats for arthropods in eastern Oregon and Washington. Northwest Science 75:141–148.

Noss, R. F., P. Beier, W. W. Covington, R. E. Grumbine, D. B. Lindenmayer, J. W. Prather, F. Schmiegelow, T. D. Sisk, and D. J. Vosick. 2006. Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. Restoration Ecology 14:4–10.

Ohmann, J. L., and K. L. Waddell. 2002. Regional patterns of dead wood in forested habitats of Oregon and Washington. Pages 535–560 *in* W. F. Laudenslayer, P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, editors. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Department of Agriculture Forest Service PSW-GTR-181, Albany, California, USA.

Parker, T. J., K. M. Clancy, and R. L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agricultural and Forest Entomology 8: 167–189.

Pellicane, P. J., and P. W. Mielke. 1999. Permutation procedures for multi-dimensional applications in wood related research. Wood Science and Technology 33:1–13.

Petrondas, D. A., and K. R. Gabriel. 1983. Multiple comparisons by rerandomization tests. Journal of the American Statistical Association 78:949–957.

Rabe, M. J., T. E. Morrell, H. Green, J. C. deVos, and C. R. Miller. 1998. Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. Journal of Wildlife Management 62:612–621.

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

Raphael, M. G., M. J. Wisdom, M. M. Rowland, R. S. Holthausen, B. C. Wales, B. G. Marcot, and T. D. Rich. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia River basin. Forest Ecology and Management 153:63–88.

Roedenbeck, I. A., L. Fahrig, C. S. Findlay, J. E. Houlahan, J. A. G. Jaeger, N. Klar, S. Kramer-Schadt, and E. A. V. derGrift. 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society 12:11.

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, USA.

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

Saab, V., L. Bate, J. Lehmkuhl, B. Dickson, S. Story, S. Jentsch, and W. Block. 2006. Changes in downed wood and forest structure after prescribed fire in ponderosa pine forests. Pages 477–487 *in* P. L. Andrews, and B. W. Butler, editors. Proceedings of Fuels Management—how to measure success. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, RMRS-P-41.

Saab, V. A., J. Dudley, and W. L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106:20–36.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor 109:97–108.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2009. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. Forest Ecology and Management 257:151–159.

Solvesky B. G., and C. L. Chambers. 2009. Roosts of Allen's lappet-browed bat in northern Arizona. Journal of Wildlife Management 73:677–682.

Stephens, S. L., and J. J. Moghaddas. 2005. Fuel treatment effects on snags and coarse woody debris in a Sierra Nevada mixed conifer forest. Forest Ecology and Management 214:53–64.

Switalski, T. A., J. A. Bissonette, T. H. DeLuca, C. H. Luce, and M. A. Madej. 2004. Benefits and impacts of road removal. Frontiers in Ecology and the Environment 2:21–28.

Theobald, D. M. 2003. Targeting conservation action through assessment of protection and exurban threats. Conservation Biology 17:1624–1637.

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 in the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture Forest Service, Handbook no. 553, Washington, D.C., USA.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

U.S. Department of Agriculture [USDA] Forest Service. 2002. Timber management control handbook. U.S. Department of Agriculture Forest Service Handbook FSH 2409.21e. Misoula, Montana, USA.

U.S. Department of Agriculture, Natural Resources Conservation Service [USDA NRCS]. 2009. National Water and Climate Center, SNOTEL data collection network. Portland, Oregon, USA. http://www.wcc.nrcs.usda.gov/snow/ Accessed 20 Jul 2009.

Vierling, K. T., L. B. Lentile, and N. Nielsen-Pincus. 2008. Preburn characteristics and woodpecker use of burned coniferous forests. Journal of Wildlife Management 72:422–427.

Wiebe, K. L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in northern flickers? Auk 118:412–421.

Wightman, C. S., V. A. Saab, C. Forristal, K. Mellen-McLean, and A. Markus. 2010. White-headed woodpecker nesting ecology after wildfire. Journal of Wildlife Management 74:1098–1106.

Wisdom, M. J., and L. J. Bate. 2008. Snag density varies with intensity of timber harvest and human access. Forest Ecology and Management 255:2085–2093.

Wisdom, M. J., R. S. Holthausen, B. C. Wales, C. D. Hargis, V. A. Saab, D. C. Lee, W. J. Hann, T. D. Rich, M. M. Rowland, W. J. Murphy, and M. R. Eames. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad-scale trends and management implications. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA, PNW-GTR-485.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River New Jersey, USA.

Associate Editor: Grado.