



In My Opinion

Recommendations for Snag Retention in Southwestern Mixed-conifer and Ponderosa Pine Forests: History and Current Status

JOSEPH L. GANEY,¹ *United States Forest Service, Rocky Mountain Research Station, 2500 S Pine Knoll Drive, Flagstaff, AZ 86001, USA*

ABSTRACT Snags provide habitat for numerous species of wildlife. Several authors have provided recommendations for snag retention in southwestern mixed-conifer and ponderosa pine (*Pinus ponderosa*) forests. Most recommendations were presented in terms of minimum snag density and/or size. I summarized the history of recommendations for snag retention in these forest types, and used data from a current study of snag populations (conducted within Coconino and Kaibab National Forests, north-central AZ, USA, 1997 through 2012) to assess congruence between existing snag populations and various recommendations. Most recommendations were based on studies of cavity-nesting birds; therefore, this analysis emphasized characteristics of snags containing excavated nest cavities. Proportions of plots that met minimum management targets varied among recommendations, ranging from 34% to 100% in mixed-conifer forest and from 7% to 95% in ponderosa pine forest. Failure to meet density targets often was caused by a shortage of snags that met minimum size criteria rather than by a shortage of snags. Many snags containing excavated nest cavities did not meet the minimum size criteria in some recommendations. It may be possible to reduce those minimum size criteria while still providing substrates for cavity-nesting birds. Studies explicitly linking snag size and density to demography of cavity-nesting birds are badly needed, however, as are studies documenting ecologically sustainable snag densities. Until such data are available, managers should continue to emphasize snag recruitment and retention, with the focus on larger snags, and to ensure that snags are well-distributed, but not uniformly distributed, across the landscape. © 2016 The Wildlife Society.

KEY WORDS cavities, cavity-nesting birds, management guidelines, snag density, snag diameter, snag height, snags, snag size, snag species, wildlife habitat.

Snags (standing dead trees) provide important biological legacies, contribute to decay dynamics and other ecological processes in forested ecosystems, and provide important resources for native wildlife (Harmon et al. 1986, Bull et al. 1997, McComb and Lindenmayer 1999, Laudenslayer et al. 2002). As a result, land managers and researchers have focused special attention on snags in recent decades (Davis et al. 1983, Mellen et al. 2002, Hutto 2006, Marcot et al. 2010), and many public land agencies have established specific guidelines for retention of snags. Those guidelines have evolved over time as our knowledge of snag dynamics and use of snags by native wildlife has increased (Mellen et al. 2002, Marcot et al. 2010), but data on whether snag targets are met on public lands often are sparse (Morrison et al. 1986), and considerable debate continues about the adequacy of existing snag guidelines (e.g., Hutto 2006).

In the southwestern United States, the importance of snags as nest and roost sites for cavity-nesting birds and bats is well-

documented, especially in ponderosa pine (*Pinus ponderosa*) forest (Balda 1975; Scott 1978, 1979; Cunningham et al. 1980; Brawn and Balda 1988; Rabe et al. 1998; Solvesky and Chambers 2009). More limited information is available for mixed-conifer forests (Li and Martin 1991, Conway and Martin 1993).

Several authors have proposed recommendations for snag retention in these forests, primarily based on studies of cavity-nesting birds. Balda (1975) provided the first quantitative recommendations (Table 1), based on the estimated density of snags required to maintain natural species diversity of secondary cavity nesters. He estimated that mean densities of 4.2 and 6.7 snags/ha were required to maintain secondary cavity nesters at their average and maximum population densities, respectively. Importantly, he recommended against managing for the minimum density of snags because of natural fluctuations in density of cavity-nesting birds. Instead, he recommended managing for 6.7 snags/ha if possible, but suggested that an average value between his minimum and maximum density estimates (or 5.4 snags/ha) might be acceptable to maintain adequate snag numbers while minimizing constraints on forest management. He suggested that snags targeted for retention should

Received: 23 February 2015; Accepted: 11 September 2015

¹E-mail: jganey@fs.fed.us

Table 1. Quantitative management recommendations proposed for snag retention in southwestern mixed-conifer and ponderosa pine forests. Also shown are proportions of 1-ha plots meeting minimum targets for snag retention based on snag density or snag density and size in mixed-conifer ($n = 53$ plots) and ponderosa pine ($n = 60$ plots) forest in northern Arizona, USA, 2012. NR = No recommendation.

Forest type	Recommendation				% of plots meeting recommendation for...	
	Snags/ha	dbh (cm)	Ht (m)	Source	Density ^a	Density and size ^b
Mixed-conifer	4.2	≥25.4	NR	Balda (1975), low density ^c	100.0	100.0
Mixed-conifer	5.4	≥25.4	NR	Balda (1975), medium density ^c	100.0	100.0
Mixed-conifer	6.7	≥25.4	NR	Balda (1975), high density ^c	100.0	100.0
Mixed-conifer	7.4	≥45.7	≥9.2	Reynolds et al. (1992)	100.0	34.0
Ponderosa pine	4.2	≥25.4	NR	Balda (1975), low density ^c	78.3	70.0
Ponderosa pine	5.4	≥25.4	NR	Balda (1975), medium density ^c	76.7	53.3
Ponderosa pine	6.7	≥25.4	NR	Balda (1975), high density ^c	66.7	50.0
Ponderosa pine	6.4	NR	NR	Scott (1979)	71.7	71.7
Ponderosa pine	5.2	≥33.0	≥6.0	Cunningham et al. (1980) ^d	78.3	18.3
Ponderosa pine	4.9–7.4	≥48.3	NR	Scott and Oldemeyer (1983)	76.7	13.3
Ponderosa pine	4.9	≥45.7	≥9.2	Reynolds et al. (1992)	76.7	6.7

^a % of plots meeting recommendation for snags/ha, without considering min. snag size.

^b % of plots meeting recommendation for snags/ha of the recommended min. size.

^c Balda (1975) provided recommendations based on a 40-ha area. I converted those recommendations to numbers/ha to facilitate comparisons with other recommendations. Low- and high-density guidelines refer to snag densities required to maintain secondary cavity nesting birds at their average and max. population densities, respectively. The medium-density guideline represented a compromise considered acceptable to minimize management constraints (Balda 1975).

^d Cunningham et al. (1980) also recommended that retained snags should have ≥40% bark cover. I did not include that requirement in this analysis, which was based solely on snag density and/or size to facilitate comparison with other recommendations.

be ≥25.4 cm in diameter at breast height (dbh), but provided no explicit rationale for that specific minimum diameter. He also recommended that snags should be widely distributed across the landscape to allow for widespread distribution of secondary cavity nesters, and that snag densities be assessed at large spatial scales (e.g., ≥40 ha). These recommendations were derived using data on bird populations in ponderosa pine forest, but Balda (1975) tentatively concluded that snag requirements were similar in mixed-conifer forests.

Based on further work on secondary cavity nesters in ponderosa pine forest, Cunningham et al. (1980) concluded that a retention target of 5.2 snags/ha was more realistic than the upper value recommended by Balda (1975; see Table 1). They showed that secondary cavity nesters preferentially used snags that were large in diameter, tall, and retained considerable bark cover, and suggested that retained snags should be ≥33 cm dbh and ≥6 m tall, with ≥40% bark cover. Although these recommendations clearly were based on their observations of snag use, they did not explicitly state the logic underlying the specific recommendations for snag density, size, and bark cover.

Scott (1979) also proposed recommendations based on studies of cavity-nesting birds in ponderosa pine forest. He recommended retaining 6.4 snags/ha in ponderosa pine forest, but did not explicitly state the logic underlying that density recommendation. He did not specify a minimum snag size, but noted that the most commonly used snags were >38 cm dbh. Scott and Oldemeyer (1983) subsequently modified the recommendation in Scott (1979) based on further studies in ponderosa pine forest (Table 1). They did not recommend a specific minimum snag density, but suggested that if the target density was within the range of 4.9–7.4 snags/ha, then retained snags should be ≥48.3 cm dbh. They based that minimum dbh recommendation on the

finding that 54% of snags in their study area with dbh ≥48.3 cm contained nest cavities, versus only 28% of snags with dbh <48.3 cm.

Conway and Martin (1993) provided qualitative recommendations for snag management in mixed-conifer forest, based on nest-site selection by Williamson's sapsuckers (*Sphyrapicus thyroideus*). They recommended retaining large snags in clumps and at high densities in drainage or low-lying areas, but did not provide quantitative criteria for what constituted "large" snags or "high densities" of snags. They argued against uniform spacing of snags, and Chambers and Mast (2005) recommended retaining snags in clumps in ponderosa pine forest as well.

Reynolds et al. (1992) proposed separate recommendations for snag retention in mixed-conifer and ponderosa pine forests, based on a literature review of habitat requirements of prey species (including several species of cavity-nesting birds) used by northern goshawks (*Accipiter gentilis*). They recommended retaining ≥7.4 and 4.9 snags/ha in mixed-conifer and ponderosa pine, respectively, with retained snags ≥45.7 cm dbh and 9.2 m in height. The logic underlying their specific recommendations was not explicitly stated for either snag size or snag density.

Thus, recommendations for snag retention in southwestern ponderosa pine forests have evolved over time as additional studies of snag use by cavity-nesting birds were completed. Some authors provided specific quantitative recommendations for snag density and/or minimum snag size, some provided qualitative guidance on these topics, and others addressed spatial distribution of snags. In general, recommendations for minimum snag density changed little over time (especially in ponderosa pine forest; Table 1) from Balda's (1975) original recommendation, which was explicitly linked to populations of cavity-nesting birds that relied

heavily on those snags. In contrast, criteria for minimum snag size generally increased over time (e.g., from ≥ 25.4 cm dbh in Balda [1975] to ≥ 45.7 cm dbh and 9.2 m in height in Reynolds et al. [1992]) as additional information on snag use accumulated. No authors explicitly linked specific criteria for minimum snag size to either empirical data on snag use or populations of cavity-nesting birds using those snags, however.

Recent studies indicated that the latest guidelines proposed (Reynolds et al. 1992) were not met in large portions of a study area in northern Arizona, USA, particularly in ponderosa pine forest (Ganey 1999, Ganey and Vojta 2005, Ganey et al. 2015a). This could indicate that these forests were deficient in snags. Alternatively, it could indicate that the criteria on snag size defining which snags count toward snag-density targets (which typically were not strongly supported by empirical data) were more restrictive than necessary. To explore this issue, I evaluated the influence of various size criteria on the ability to meet snag retention guidelines, using data from a study of snag populations in mixed-conifer and ponderosa pine forest in northern Arizona. I compared characteristics of current snag populations with the various recommendations for minimum snag density and size discussed above, and asked the following questions: 1) How do mean and median densities of snags as defined under these recommendations compare with recommended densities? 2) What proportion of sampled plots satisfied different recommendations for minimum densities of snags? 3) Where plots failed to meet these recommendations, was this failure due to low numbers of snags overall or to low numbers of “large” snags as defined in those recommendations? 4) Which size criteria (snag dbh or snag ht) most limited the numbers of existing snags that met various requirements for minimum snag size? 5) Which characteristics of snags appeared to best predict whether or not those snags contained excavated nest cavities?, and 6) Do criteria for minimum snag size appear appropriate in light of empirical data on snags containing excavated nest cavities?

STUDY AREA

I sampled snags in 113 plots (1 ha each in area) randomly located in mixed-conifer and ponderosa pine forest within a 73,000-ha study area within the Coconino and Kaibab National Forests, north-central Arizona (Fig. 1). Details on plot selection and establishment were provided in Ganey (1999). Mixed-conifer forests were dominated numerically by ponderosa pine, white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*), which together accounted for approximately 90% of total trees in this forest type (Ganey and Vojta 2011). Other species included Gambel oak (*Quercus gambelii*), quaking aspen (*Populus tremuloides*), and limber pine (*P. flexilis*), in that order of frequency. Ponderosa pine accounted for >90% of trees in ponderosa pine forest (Ganey and Vojta 2011). Gambel oak also was relatively common (approx. 8% of total trees by frequency); and alligator juniper (*Juniperus deppeana*), Douglas-fir, quaking aspen, limber pine, pinyon pine (*P. edulis*), and

other species of juniper were present in small numbers in some stands.

The study plots were distributed across a wide range of topographic conditions and soil types, covered the entire elevational range of these forest types within this area (mixed-conifer median = 2,351 m, range = 1,886–3,050 m; ponderosa pine median = 2,144 m, range = 1,778–2,561 m), included both commercial forest lands and administratively reserved lands such as wilderness and other roadless areas, and consequently represented a wide range of forest structural conditions. Density of trees ≥ 20 cm in dbh (sampled in 2004) ranged from 78 to 489 (median = 266.7) trees/ha in mixed-conifer forest and from 11 to 689 (median = 227.8) trees/ha in ponderosa pine forest; and basal area ranged from 7 to 52 (median = 25.2) and from 1 to 44 (median = 19.7) m²/ha in mixed-conifer and ponderosa pine forest, respectively (Ganey and Vojta 2011).

METHODS

I established plots in 1997, using a stratified random sampling procedure (Ganey 1999; $n = 53$ and $n = 60$ plots in mixed-conifer and ponderosa pine forest, respectively). I sampled all snags > 2 m in height and ≥ 20 cm (dbh) in 1997, 2002, 2007, and 2012. I did not sample snags with dbh < 20 cm, based on the assumption that they were relatively unimportant as nesting substrates for cavity-nesting birds (Scott 1978, Cunningham et al. 1980). For all snags sampled, I recorded snag species, dbh (nearest cm), and height (nearest m, estimated using a clinometer). I also recorded presence-absence of excavated cavities in 2002 and 2007, based on a visual inspection of the trunk using binoculars (Ganey and Vojta 2004). I used data only from the 2007 and 2012 samples in analyses here. I used data from the 2007 sample in analyses involving snags containing excavated cavities because that was the last year in which I recorded presence or absence of excavated cavities, and I used the most recent data (2012) in all other analyses.

I summarized density of snags within each plot, both overall (i.e., all snags ≥ 20 cm dbh) and for snags that met the various sets of size criteria discussed above (Table 1), and compared snag-density estimates with various recommendations for snag density at 2 different scales. At the scale of individual plots, I estimated proportions of plots within each forest type that satisfied recommendations for minimum density. This provides information on proportions of the landscape on which snag recommendations were met. As Balda (1975) noted, however, not all areas need to be rich in snags, and snag populations may be better assessed at larger spatial scales. Therefore, I also compared mean and median density within each forest type with various recommendations for the relevant forest type. This provides information on central tendency in snag density at larger scales. I used both mean and median density here because previous studies (Ganey et al. 2015a) demonstrated that spatial variability in snag density was so pronounced that mean density estimates were strongly and positively influenced by high numbers of snags in a few plots. Consequently, these means did not provide a robust estimate of central tendency, and use of both

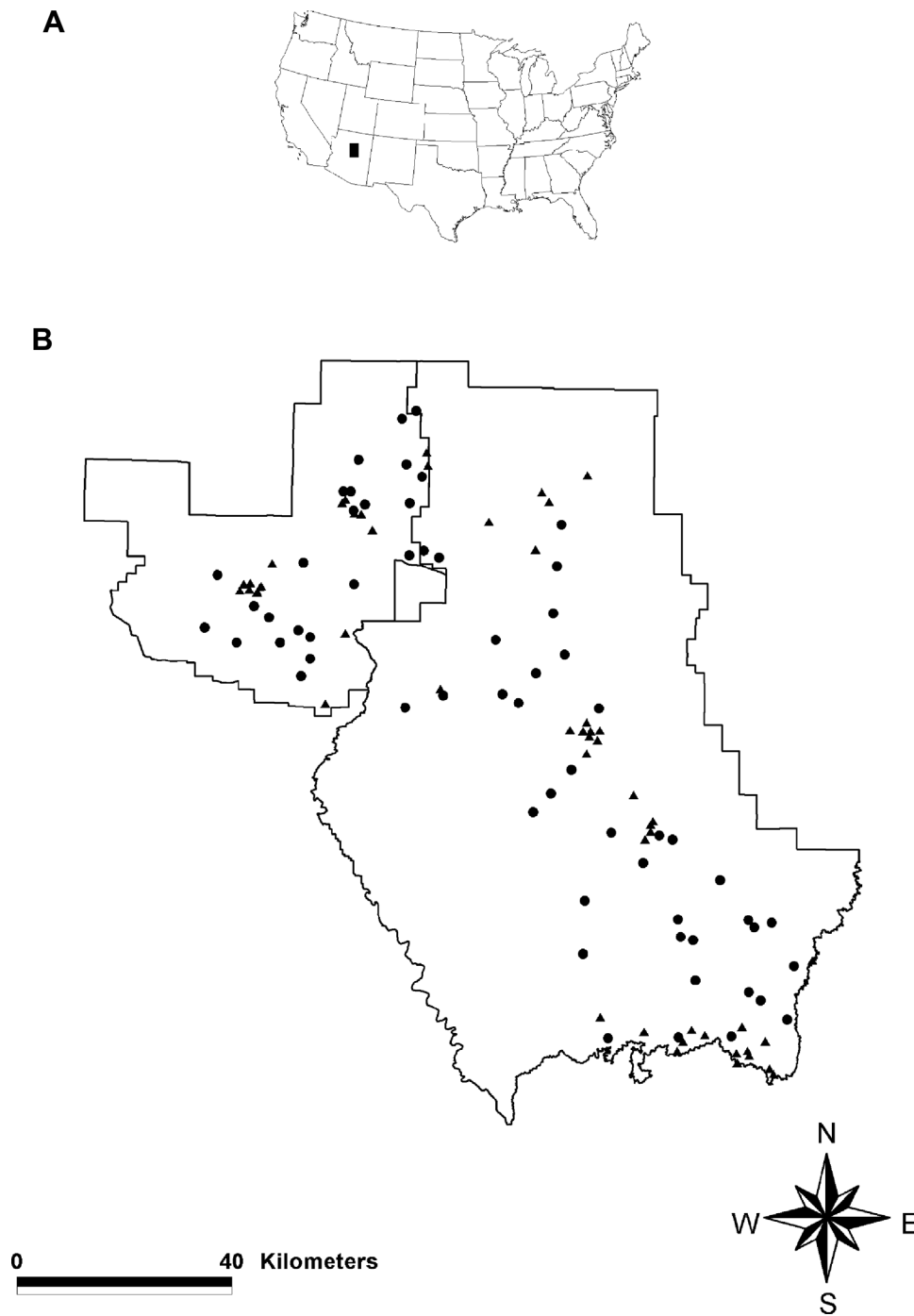


Figure 1. Location of the study area (black box, top) in northern Arizona, USA, and locations of snag-monitoring plots within the study area (bottom). Plots were located in the Kaibab (left) and Coconino (right) National Forests, north-central Arizona, and were sampled at 5-year intervals from 1997 to 2012. Plots in ponderosa pine forest ($n=60$) are indicated by circles, plots in mixed-conifer forest ($n=53$) by triangles.

mean and median values provided a more complete picture of snag density at these larger scales.

I also estimated proportions of snags that met various criteria for minimum diameter and height, both separately and in combination. Because minimum size requirements in most recommendations were proposed largely with requirements of cavity-nesting birds in mind (Balda 1975, Scott 1979, Cunningham et al. 1980, Scott and Oldemeyer 1983, but see Reynolds et al. 1992), I estimated this proportion

separately for snags containing excavated nest cavities (hereafter, cavity snags) as well as for all snags ≥ 20 cm dbh.

I used generalized linear models with a binary logistic response variable to evaluate the importance of selected snag characteristics as predictors of the probability that those snags contained an excavated nest cavity. I pooled snags across forest types for this analysis. I included snag diameter and height as predictor variables because one or both of those characteristics were used in many sets of historical snag

recommendations, and snag species because several studies suggested differential use of snag species for nest-cavity excavation (Li and Martin 1991, Conway and Martin 1993, Ganey and Vojta 2004). I rescaled diameter and height to zero mean with unit variance (Legendre and Legendre 1998) to facilitate interpretation of parameter estimates, and recognized 6 major species or species groups (white fir, Douglas-fir, quaking aspen, ponderosa pine, Gambel oak, and a composite group including all other snag species).

I evaluated 8 models representing all possible combinations of snag diameter, height, and species using the *glmulti* package in the R computing environment (Calcagno 2013, R Core Team 2013). I ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c), and considered any models with $\Delta AIC_c \leq 2$ to be competing models (Burnham and Anderson 2002). I computed model weights after Burnham and Anderson (2002) and estimated relative variable importance by summing model weights across all models containing that variable. Estimates of relative variable importance were informative in this context (Doherty et al. 2012) because all variables were included in the same number of models. I calculated model-averaged parameter estimates and 95% confidence intervals (CI) around those estimates using unconditional variance.

Because snag breakage can result in changes to snag height, some sampled snags may have been taller at the time of cavity excavation than when sampled for this study, potentially biasing model results with respect to snag height. Consequently, I ran all models using 2 data sets—one containing all sampled snags and one containing only unbroken snags with intact tops. I compared results between these model sets to estimate the potential extent of bias caused by snag breakage subsequent to cavity excavation.

RESULTS

All mixed-conifer plots and 95% of ponderosa pine plots contained ≥ 1 snag ≥ 20 cm dbh in 2012, indicating that snags were widely distributed within these forest types. However, the proportion of plots that met minimum snag-

density targets varied widely among sources of recommendations, forest types, and based on whether density estimates included all snags ≥ 20 cm dbh or only snags meeting the minimum size criteria in various recommendations (Table 1).

For those authors who offered recommendations for both forest types (Balda 1975, Reynolds et al. 1992), proportions of plots meeting snag-density targets were greater in mixed-conifer than in ponderosa pine forest. All mixed-conifer plots met snag-density targets when all snags ≥ 20 cm dbh were included, and all also met Balda's (1975) recommendations based on minimum snag diameter and density (Table 1). In contrast, only 34% of mixed-conifer plots met minimum targets for large snags in Reynolds et al. (1992). Thus, failure to meet guidelines from Reynolds et al. (1992) in mixed-conifer forest was due to failure of many snags to meet criteria for minimum snag size rather than to an overall shortage of snags.

None of the recommendations for minimum snag density were met in 100% of ponderosa pine plots (Table 1). Relatively high proportions of ponderosa pine plots met minimum targets in all recommendations when all snags ≥ 20 cm dbh were included, but proportions of plots meeting minimum targets declined rapidly as criteria for minimum snag size increased. Thus, failure to meet guidelines in ponderosa pine forest was due partly to an overall shortage of snags, but that shortage was exacerbated greatly by increasing criteria for minimum snag size.

Both mean and median densities of snags greatly exceeded Balda's (1975) recommendations for snag density in mixed-conifer forest (Table 2). Mean density approached the recommended level from Reynolds et al. (1992) in mixed-conifer forest, but median density fell below their recommended level. Mean snag densities in ponderosa pine forest exceeded the recommended minimum levels in Balda (1975) and Scott (1979), but fell below minimum levels recommended in Cunningham et al. (1980), Scott and Oldemeyer (1983), and Reynolds et al. (1992). Median snag densities in ponderosa pine forest exceeded the minimum level from Scott (1979), approximated the upper density level recommendation from Balda (1975), and fell well below the

Table 2. Mean and median density (snags/ha) of snags meeting size criteria^a in various recommendations for snag retention in mixed-conifer ($n = 53$ plots) and ponderosa pine ($n = 60$ plots) forest in northern Arizona, USA, 2012. Also shown are recommended snag densities for comparison. Only Balda (1975) and Reynolds et al. (1992) proposed guidelines for mixed-conifer forest. NA = not applicable.

Source	Mixed-conifer forest ^b			Ponderosa pine forest		
	Recommendation	Mean	Median	Recommendation	Mean	Median
Balda (1975)	4.2–6.7 ^c	51.5	36.0	4.2–6.7 ^c	9.4	6.5
Scott (1979)	NA	72.9 ^d	47.0 ^d	6.4	13.4 ^d	10.0 ^d
Cunningham et al. (1980)	NA	22.6	18.0	5.2	4.5	3.0
Scott and Oldemeyer (1983)	NA	12.0	9.0	4.9–7.4	2.5	2.0
Reynolds et al. (1992)	7.4	7.3	5.0	4.9	1.6	1.0

^a Size criteria for various recommendations are presented in Table 1.

^b Scott (1979), Cunningham et al. (1980), and Scott and Oldemeyer (1983) did not propose recommendations for mixed-conifer forest. I estimated mean and median snag densities in this forest type based on their size criteria proposed for ponderosa pine forest.

^c Balda (1975) provided 3 recommendations, with the upper and lower limits aimed at maintaining populations of cavity-nesting birds at their average and max. population densities, respectively, and an intermediate value representing a compromise considered acceptable to minimize management constraints.

^d Mean and median based on all snags ≥ 20 cm dbh because Scott (1979) did not recommend a min. snag size.

Table 3. Percentage of snags that met selected size criteria^a for snag retention in mixed-conifer and ponderosa pine forest, northern Arizona, USA. Data are shown separately for all snags ($n = 3,874$ and 905 snags in mixed-conifer and ponderosa pine forest, respectively), and snags containing excavated cavities ($n = 196$ and 106 snags in mixed-conifer and ponderosa pine forest, respectively). Only snags sampled in 2007 were included here because that was the last year in which I recorded presence/absence of excavated nest cavities. NR = no recommendation for min. ht., NA = not applicable.

Forest type	All snags			Cavity snags			Source for recommendation
	dbh	Ht	Both	dbh	Ht	Both	
Mixed-conifer	69.5	NR	NA	95.9	NR	NA	Balda (1975)
Mixed-conifer	19.7	55.2	10.5	63.3	87.8	42.3	Reynolds et al. (1992)
Ponderosa pine	67.6	NR	NA	91.6	NR	NA	Balda (1975)
Ponderosa pine	45.5	51.2	22.8	84.1	93.3	66.0	Cunningham et al. (1980)
Ponderosa pine	16.6	NR	NA	43.9	NR	NA	Scott and Oldemeyer (1983)
Ponderosa pine	20.4	35.3	8.3	51.4	76.7	32.1	Reynolds et al. (1992)

^a Criteria for min. snag size are listed in Table 1.

recommended level for all other sets of recommendations (Table 2).

Evaluation of criteria for snag size indicated that for those sets of recommendations that included both snag diameter and height, fewer snags met recommendations for minimum diameter than recommendations for minimum height, and fewer snags met diameter and height criteria jointly than met either criterion alone (Table 3). This pattern was consistent across recommendations, in both forest types, and both for all snags and for cavity snags. Proportions of cavity snags meeting minimum size criteria exceeded proportions of all snags meeting those criteria for all recommendations, indicating that snags containing excavated nest cavities generally were large (Table 3).

Model results were virtually identical for 2 sets of models (one including all sampled snags and the other including only unbroken snags) evaluating the influence of snag characteristics on the probability of containing an excavated nest cavity. Consequently, I report model results here based on the more inclusive and larger sample of snags.

Table 4. Model results for generalized linear models evaluating the influence of snag covariates on presence or absence of excavated cavities in northern Arizona, USA, mixed-conifer and ponderosa pine forest. Number of snags included = 4,779, including 302 snags with excavated nest cavities. Only snags sampled in 2007 were included here because that was the last year in which I recorded presence-absence of excavated nest cavities.

Model ^a	ΔAIC_c^b	w_i^c
dbh + species + height	0.000	0.889
dbh + species	4.153	0.111
dbh + height	75.282	<0.001
dbh	97.290	<0.001
Species + height	113.252	<0.001
Species	175.157	<0.001
Height	233.052	<0.001
Null (no covariates)	254.076	<0.001

^a dbh (diam. at breast height) and height refer to variables standardized to mean zero and unit variance (originally sampled in cm and m, respectively). Species recognized included Douglas-fir, Gambel oak, ponderosa pine, quaking aspen, white fir, and "other," which included all other species.

^b Change in Akaike's Information Criterion corrected for small sample size (AIC_c) relative to the model with lowest AIC_c .

^c w_i = Model wt calculated following Burnham and Anderson (2002).

There was only one competitive model describing the influence of snag characteristics on the probability of containing an excavated nest cavity (Table 4). This model included snag diameter, height, and species, and contributed >88% of total model weight. Importance values indicated that snag diameter and species were better predictors of the probability of containing an excavated nest cavity than was snag height (Table 5). The probability that a snag contained an excavated nest cavity was positively associated with snag diameter and negatively associated with snag height, and CIs around parameter estimates did not include zero for either variable. Probability of containing a nest cavity was greater for all other snag species than for white fir, and CIs around parameter estimates for snag species did not include zero for any species except Douglas-fir.

Empirical data on snags with and without excavated cavities supported the model results. Cumulative diameter distributions diverged considerably between snags with and without excavated cavities (Fig. 2), height distributions were similar between snags with and without cavities (Fig. 3), and proportions of snags containing excavated cavities varied widely among species (Table 6). These results suggest that

Table 5. Model-averaged parameter estimates from a suite of models evaluating the influence of snag covariates on presence or absence of excavated cavities in those snags in northern Arizona, USA, mixed-conifer and ponderosa pine forest. Only snags sampled in 2007 were included here because that was the last year in which I recorded presence-absence of excavated nest cavities. Parameter estimates for dbh and height refer to standardized variables used to place continuous variables on similar scales.

Parameter	Estimate	95% CI	Importance ^a
Intercept	0.016	0.010–0.022	1.000
dbh	0.051	0.046–0.056	1.000
Species = QUGA ^b	0.075	0.061–0.088	1.000
Species = POTR ^b	0.059	0.049–0.069	1.000
Species = OTHER ^b	0.058	0.036–0.080	1.000
Species = PIPO ^b	0.045	0.037–0.052	1.000
Species = PSME ^b	0.005	–0.006 to 0.015	1.000
Height	–0.013	–0.020 to –0.006	0.889

^a Relative variable importance was computed by summing model weights across all models containing that variable.

^b Estimates are relative to the reference category (white fir). PIPO = ponderosa pine; QUGA = Gambel oak; POTR = quaking aspen; PSME = Douglas-fir; and OTHER = all other species except white fir.

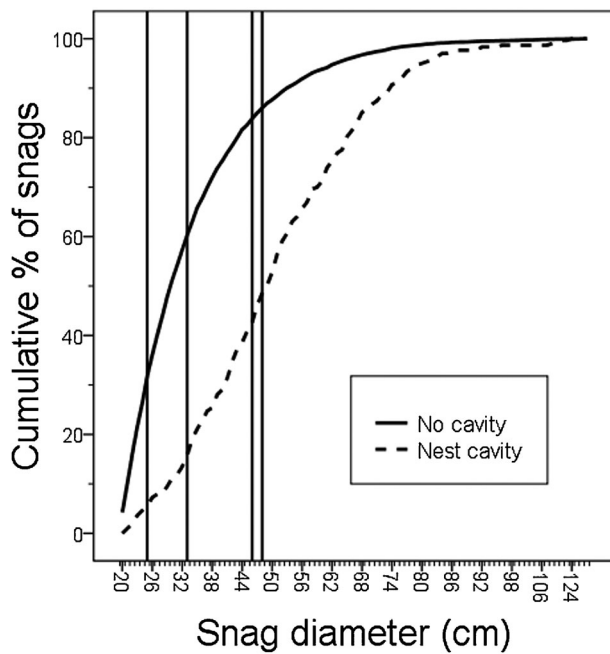


Figure 2. Cumulative percentage of snags sampled in 2007 with and without excavated nest cavities in mixed-conifer and ponderosa pine forest, northern Arizona, USA, by snag diameter. From left to right, the vertical reference lines indicate minimum snag-diameter recommendations proposed by Balda (1975), Cunningham et al. (1980), Reynolds et al. (1992), and Scott and Oldemeyer (1983). Approximately 95% of ponderosa pine snags containing excavated cavities exceeded the minimum diameter proposed by Balda (1975). In contrast, approximately 55% of ponderosa pine snags with excavated cavities were smaller than the minimum diameter proposed by Scott and Oldemeyer (1983). Based on 4,779 snags, including 302 snags with excavated nest cavities.

cavity excavators targeted larger diameter snags relative to availability, did not select taller snags, and showed differential use among snag species. Thus, empirical data also indicate greater importance for snag diameter and species than for snag height as factors influencing cavity excavation.

Both mean and median diameter ($\bar{x} = 51.0 \pm 1.0$ [SE] cm; median = 49.0 cm) and height ($\bar{x} = 11.5 \pm 0.4$ m; median = 10.0 m) of snags containing excavated cavities exceeded minimum size criteria in all proposed guidelines (see Table 1), suggesting that those criteria were reasonable in light of observed snag use patterns. Nonetheless, relative inclusiveness varied widely among recommendations, and relatively high proportions of cavity snags were smaller in diameter or shorter than the recommended minimum size in some snag guidelines evaluated (Figs. 2 and 3; Table 7). Minimum diameter and height of cavity snags were 21 cm and 2 m, respectively. The 2-m-tall snag was broken, however, and that snag may have been taller at the time of cavity excavation. Minimum height for unbroken cavity snags was 3 m.

DISCUSSION

This study documented that snags were relatively abundant and widely distributed within mixed-conifer and ponderosa pine forest. Despite that abundance, however, densities of

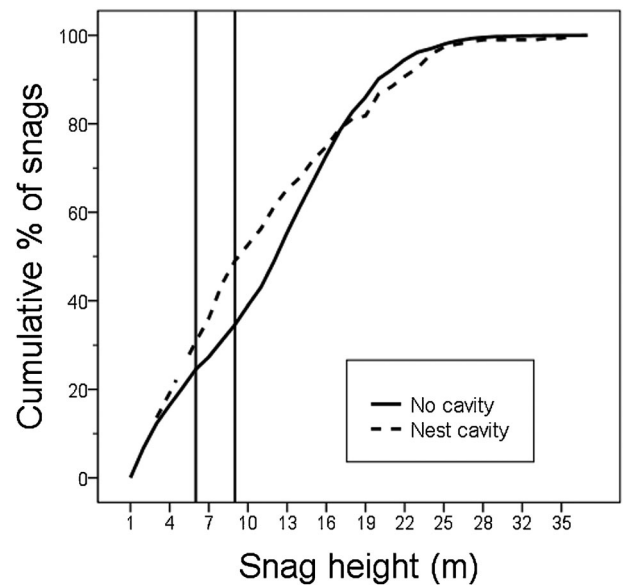


Figure 3. Cumulative percentage of snags sampled in 2007 with and without excavated nest cavities in mixed-conifer and ponderosa pine forest, northern Arizona, USA, by snag height. From left to right, the vertical reference lines indicate minimum snag-height recommendations proposed by Cunningham et al. (1980) and Reynolds et al. (1992). These recommendations would exclude approximately 30% and >45%, respectively, of snags containing excavated cavities from contributing to management targets. Based on 4,779 snags, including 302 snags with excavated nest cavities.

larger snags as defined in some sets of recommendations for snag retention failed to meet the minimum density levels recommended. In large part, that failure was caused by the failure of many snags to meet the minimum diameter and/or height criteria recommended, and failure rates increased as size criteria increased and as multiple criteria (i.e., diam and ht) were included.

Proposed size criteria clearly were intended to ensure that snag retention focused on the larger snags most used by cavity-nesting birds and roosting bats. That intent is entirely appropriate, but the links between specific minimum size criteria proposed and snag use by native wildlife typically were not explicitly stated, and some sets of size criteria may be overly restrictive. For example, although cavity snags typically were large relative to available snags, many cavity snags were smaller in diameter or shorter than some of the recommended minimum size criteria. This suggests that it

Table 6. Percent of snags containing excavated nests cavities in northern Arizona, USA, mixed-conifer and ponderosa pine forest, by selected species. Only snags sampled in 2007 were included here because that was the last year in which I recorded presence-absence of excavated nest cavities.

Species	No. of snags	% containing nest cavity
Ponderosa pine	1,415	13.1
Gambel oak	700	9.1
Quaking aspen	394	4.3
Douglas-fir	426	2.8
White fir	1,739	0.7

Table 7. Selected percentile values for diameter at breast height (dbh) and height of snags containing excavated nest cavities in northern Arizona, USA, mixed-conifer and ponderosa pine forest. Based on 302 snags sampled in 2007, the last year in which presence or absence of excavated nest cavities was recorded. Seventy-nine of these snags were unbroken, ensuring that height did not decrease subsequent to cavity excavation.

Parameter	Percentile			
	5th	10th	25th	50th
dbh (cm)	25	30	38	49
Ht (m) ^a	3	3	6	10
Ht (m) ^b	7	8	13	20

^a Estimate includes all snags containing excavated nest cavities.

^b Estimate includes all unbroken snags containing excavated nest cavities.

may be feasible to reduce these minimum size criteria while still providing nest substrates for cavity-nesting birds.

Empirical data on cavity snags may aid in revising these size criteria, where available. For example, managers could use percentile values from this study to set minimum size criteria, with that determination dependent on how inclusive they wanted those criteria to be. If the goal were to include 95% of cavity snags, minimum snag dbh based on this study would be 25 cm and minimum height would be 3 m (or 7 m if based on unbroken snags; see Table 7). Similarly, a goal of including 90% of cavity snags would result in minimum recommendations for snag diameter and height of 30 cm and 3 m, respectively. Ideally, these determinations would be based on empirical data from local areas and the relevant forest type, to account for potential spatial variation in forest productivity and snag size.

Although reducing minimum snag-size criteria would render minimum targets for snag retention more attainable, that reduction may come with notable costs. Smaller diameter snags may provide nesting substrates of poorer quality for cavity-nesting birds. Such snags tend to break and fall more quickly than larger snags (Chambers and Mast 2005, 2014; Ganey and Vojta 2005; Ganey et al. 2015b), making them a more ephemeral resource; and cavities in smaller diameter snags may undergo greater fluctuations in temperature than cavities in larger diameter snags, providing a less stable thermal environment during the incubation and brooding periods. These smaller snags also may not support the large plates of exfoliating bark that provide cover for roosting bats (Rabe et al. 1998, Solvesky and Chambers 2009). Thus, although reduced minimum snag size criteria may facilitate meeting guidelines for snag density, those guidelines may be met in part by snags of lower quality. This suggests that managers should continue to emphasize recruitment and retention of large snags, and supplement these populations of larger snags with smaller snags only where necessary to provide adequate snag numbers. It also demonstrates a need for studies explicitly linking snag size to demography of cavity-nesting birds.

Also unknown here is what effect past management may have had on the size of snags containing nest cavities. It is generally accepted that tree size distributions in these forest types have become increasingly dominated by smaller trees

following the advent of effective fire suppression (Covington and Moore 1994, Fulé et al. 2009). If these changes have resulted in increased use of smaller snags for excavation of nest cavities, then data from this study may be biased low in terms of size of cavity snags. This again indicates the need for studies linking snag size to snag quality and demographic performance of birds nesting in those snags, as well as the ongoing need to emphasize recruitment of large snags.

Unlike recommendations related to snag size, recommendations for snag density have changed little since the original recommendations by Balda (1975), especially in ponderosa pine forest. Those recommendations were explicitly linked to populations of cavity-nesting birds, and this study does not indicate a pressing need for revision of those recommendations. Given reasonably inclusive minimum size criteria (see above), the recommended maximum density from Balda (1975; 6.7 snags/ha) should be attainable in mixed-conifer forest and the intermediate recommended density (5.4 snags/ha; Balda 1975) generally should be attainable in ponderosa pine forest, although not on every hectare (see Tables 1 and 2). Snag abundance should be assessed at larger spatial scales, however, and should be allowed to vary spatially across heterogeneous landscapes (Balda 1975, Stephens 2004, Hutto 2006). As with snag size, studies explicitly evaluating links between snag density and demography of cavity-nesting birds should be conducted to ensure that these densities are adequate to support viable populations of these birds.

This study did not evaluate some important characteristics of snags that influence snag use by native wildlife, including bark cover and decay class. As noted, some roosting bats rely on large plates of exfoliating bark (Rabe et al. 1998, Solvesky and Chambers 2009), and these plates are an ephemeral resource. Similarly, decay class influences suitability for cavity excavation and use, with many snags becoming unsuitable for excavation or for repeated use of existing cavities as decay increases. Despite their potential importance, however, I do not recommend incorporating specific criteria for these characteristics in snag retention guidelines. If managers ensure a steady supply of snags over time, the resulting snag populations should include snags in various decay classes and with varying amounts of retained bark cover.

Finally, studies also are needed on sustainable densities of snags in these forest types. We know little about historical snag levels in these forest types, although some information on historical densities is available from relatively similar forest types. For example, Harrod et al. (1998) estimated that historical densities of snags >15 cm dbh ranged from 14.5 to 34.6 snags/ha in dry forests (ponderosa pine and mixed-conifer) east of the Cascade Mountains in Oregon and Washington, USA, and Stephens (2004) estimated mean snag densities of 3.95 and 5.1 snags/ha in 1998 and 2002, respectively, in a Jeffrey pine (*P. jeffreyi*)–mixed-conifer forest in northwestern Mexico that had not experienced systematic fire suppression. Better information on historical densities of snags in southwestern mixed-conifer and

ponderosa pine forests clearly would be beneficial because it is pointless to recommend minimum densities of snags that are not ecologically sustainable.

CONCLUSIONS

Guidelines for snag retention should be ecologically sustainable while ensuring the provision of adequate numbers of snags of sufficient quality to support viable populations of snag-dependent wildlife. My results suggest that many guidelines proposed for snag management are not readily attainable in these forest types, largely because of size criteria that limit the number of qualifying snags. Those size criteria were not strongly data-based and may be overly restrictive. Empirical data on snag use by native wildlife can guide revision of size criteria, but studies explicitly linking snag size and density to demography of cavity-nesting birds are badly needed, as are studies documenting ecologically sustainable snag levels. Until such data are available, managers should continue to emphasize snag recruitment and retention, with the focus on providing a steady supply of the larger snags most useful to native wildlife. Managers also should ensure that snags are well-distributed, but not uniformly distributed, across the landscape; retain both hardwood and coniferous trees and snags; sustain a range of size, age, and decay classes of trees and snags; and limit salvage logging following disturbance events (Li and Martin 1991; Chambers and Mast 2005, 2014; Hutto 2006; Bunnell 2013).

ACKNOWLEDGMENTS

I thank J. Jenness, G. Martinez, M. Stoddard, B. Strohmeier, R. White, and especially A. and J. Iniguez for their assistance in establishing plots; and L. Doll, D. and N. Ganey, C. Vojta, and especially S. Vojta for assistance with plot sampling. For assistance with initial plot selection, I thank J. Ellenwood, B. Higgins, K. Menasco, C. Nelson, and G. Sheppard (Kaibab National Forest) and C. Beyerhelm, A. Brown, H. Green, T. Randall-Parker, C. Taylor, and M. Whitney (Coconino National Forest). This article was improved by comments from D. Donner and 2 anonymous reviewers. Dedicated to R. P. Balda for his work on snags and cavity-nesting birds.

LITERATURE CITED

Balda, R. P. 1975. The relationship of secondary cavity nesters to snag densities in western coniferous forests. U.S. Forest Service, Southwestern Region, Wildlife Habitat Technical Bulletin 1, Albuquerque, New Mexico, USA.

Brawn, J. D., and R. P. Balda. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? *Condor* 90:61–71.

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. Forest Service General Technical Report PNW-GTR-391, Portland, Oregon, USA.

Bunnell, F. L. 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. *ISRN Forestry* 2013: Article ID 457698, 33 pp. doi: 10.1155/2013/457698

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

Calcagno, V. 2013. Glmulti: model selection and multimodel inference made easy. R package version 1.0.7. <http://CRAN.R-project.org/package=glmulti>. Accessed 15 Nov 2014.

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.

Chambers, C. L., and J. N. Mast. 2014. Snag dynamics and cavity excavation after bark beetle outbreaks in southwestern ponderosa pine forests. *Forest Science* 60:713–723.

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.

Covington, W. W., and M. M. Moore. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153–181.

Cunningham, J. B., R. P. Balda, and W. S. Gaud. 1980. Selection and use of snags by secondary cavity-nesting birds of the ponderosa pine forest. U.S. Forest Service Research Paper RM-222, Fort Collins, Colorado, USA.

Davis, J. W., G. A. Goodwin, and R. A. Ockenfels, technical coordinators. 1983. Snag habitat management: proceedings of the symposium. U.S. Forest Service General Technical Report RM-99, Fort Collins, Colorado, USA.

Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152-(Supplement 2):S317–S323.

Fulé, P. Z., J. E. Korb, and R. Wu. 2009. Changes in forest structure of a mixed-conifer forest, southwestern Colorado. *Forest Ecology and Management* 258:1200–1210.

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., B. J. Bird, L. S. Baggett, and J. S. Jenness. 2015a. Density of large snags and logs in northern Arizona mixed-conifer and ponderosa pine forests. *Forest Science* 61:353–362.

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.

Ganey, J. L., and S. C. Vojta. 2005. Changes in snag populations in northern Arizona mixed-conifer and ponderosa pine forests, 1997–2002. *Forest Science* 51:396–405.

Ganey, J. L., and S. C. Vojta. 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona. *Forest Ecology and Management* 261:162–168.

Ganey, J. L., G. C. White, J. S. Jenness, and S. C. Vojta. 2015b. Mark-recapture estimation of snag standing rates in northern Arizona mixed-conifer and ponderosa pine forests. *Journal of Wildlife Management* 79:1369–1377.

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

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

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

Laudenslayer, W. F. Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. 2002. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Forest Service General Technical Report PSW-GTR-181, Albany, California, USA.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Second edition. Elsevier, Amsterdam, Netherlands.

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

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.

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

- Mellen, K., B. G. Marcot, J. L. Ohmann, K. L. Waddell, E. A. Wilhite, B. B. Hostetler, S. A. Livingston, and C. Ogden. 2002. DecAID: a decaying wood advisory model for Oregon and Washington. Pages 527–533 *in* W. F. Laudenslayer Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, technical coordinators. Proceedings of the symposium on the ecology and management of dead wood in western forests. U.S. Forest Service General Technical Report PSW-GTR-181, Albany, California, USA.
- 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? *Western Journal of Applied Forestry* 1:38–40.
- 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.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. Accessed 15 Nov 2014.
- Reynolds, R. T., R. T. Graham, M. H. Reiser, R. L. Bassett, P. L. Kennedy, D. A. Boyce Jr., G. Goodwin, R. Smith, and E. L. Fisher. 1992. Management recommendations for the northern goshawk in the southwestern United States. U.S. Forest Service General Technical Report RM-217, Fort Collins, Colorado, USA.
- Scott, V. E. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds. *Journal of Forestry* 76:26–28.
- Scott, V. E. 1979. Bird response to snag removal in ponderosa pine. *Journal of Forestry* 77:26–28.
- Scott, V. E., and J. L. Oldemeyer. 1983. Cavity-nesting bird requirements and responses to snag cutting in ponderosa pine. Pages 19–23 *in* J. W. Davis, G. A. Goodwin, and R. A. Ockenfels, technical coordinators. Snag habitat management: proceedings of the symposium. U.S. Forest Service General Technical Report RM-99, Fort Collins, Colorado, USA.
- 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. 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in northwestern Mexico. *Forest Ecology and Management* 199:103–113.

Associate Editor: Donner.