ELSEVIER

Forest Ecology and Management 117 (1999) 169–178

Forest Ecology and Management

Snag density and composition of snag populations on two National Forests in northern Arizona

Joseph L. Ganey*

USDA Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll, Flagstaff, AZ 86001, USA

Received 4 June 1998; accepted 20 August 1998

Abstract

Snags (standing dead trees) provide important habitat for forest wildlife, as well as a source of coarse woody debris important in forest succession. Because of their importance, some land-management agencies have standards for snag retention on lands under their jurisdiction (e.g. U.S. Forest Service, British Columbia Ministry of Forestry). Despite these guidelines, however, little information is typically available on snag numbers or dynamics on these lands. As part of a long-term effort to monitor snag dynamics, snag populations were sampled on 114 1-ha plots randomly located across six Ranger Districts on two National Forests in northern Arizona. Sixty plots were located in ponderosa pine forest, with the remainder in mixed-conifer forest. Small snags and snags in later decay classes numerically dominated snag populations. Because large snags are most useful to forest wildlife, this suggests a need to retain large trees as future snags. Only 6.7 and 16.7% of plots in ponderosa pine and mixed-conifer forest, respectively, met or exceeded current U.S. Forest Service standards for retention of large snags (defined as snags $\geq$46 cm in diameter at breast height and 9 m in height) in this geographic region. Even plots with no evidence of timber or fuelwood harvest seldom met targets for retention of large snags, however. Only 30 and 32% of unlogged plots met or exceeded standards in ponderosa pine and mixed-conifer forest, respectively. This suggests that current standards for snag retention may be unrealistic, and that those standards may need to be reconsidered. Snag guidelines should be based on an understanding of both, snag dynamics and the requirements of snag-dependent wildlife species.

Keywords: Snags; Standing dead trees; Ponderosa pine; Mixed-conifer; Arizona; Cavities; Cavity-nesting birds

1. Introduction

Snags (standing dead trees) are important components of forest ecosystems that provide habitat for numerous species of wildlife (Balda, 1975; Scott et al., 1977; Thomas et al., 1979; Bull et al., 1997). Snags provide both nest and roost sites for cavity-nesting birds (Scott et al., 1977; Scott, 1978; Cunningham et al., 1980; Sydeman and Guntert, 1983; Raphael and White, 1984; Horton and Mannan, 1988; Ohmann et al., 1994; Bull et al., 1997), foraging substrates, perches, and song posts for many species of birds (Bull et al., 1997), and roost sites for many species of bats (Chung-Maccoubrey, 1996; Rabe et al., 1998; Bull et al., 1997). Snags also provide homes, escape cover, and foraging sites for terrestrial small mammals when they fall (Maser et al., 1978; Bull et al., 1997), as well as

---

*Tel.: +1-520-556-2156; fax: +1-520-556-2130; e-mail: Joe.Ganey@nau.edu

PII: S0378-1127(98)00476-9

coarse woody debris important in stand succession (Harmon et al., 1986; Moir, 1992; Bull et al., 1997).

Snags may be particularly important to bird communities in mixed-conifer and especially ponderosa pine (*Pinus ponderosa*) forests in the southwestern United States, because cavity-nesting birds comprise a large and important component of the avifauna in these forests (Balda, 1975; Cunningham et al., 1980). Most work in this region has focused on secondary cavity nesters. This group of birds, which includes such common species as the pygmy nuthatch (*Sitta pygmaea*), white-breasted nuthatch (*S. carolinensis*), mountain chickadee (*Poeale gambeli*), western bluebird (*Sialia mexicana*), and violet-green swallow (*Tachycineta thalassina*), uses existing cavities rather than excavating cavities themselves. They are often highly dependent on cavities in snags not only for nest sites (Balda, 1975; Cunningham et al., 1980), but in some cases for winter roosts as well (Sydeman and Guntert, 1983). Collectively, secondary cavity nesters comprised an estimated 33% of the breeding species and 32–45% of the breeding pairs in Arizona's ponderosa pine forests (Balda, 1975). Eighty-two percent of these secondary cavity nesters nested in snags (Balda, 1975). Densities of secondary cavity nesters in Arizona ponderosa pine forests were three times greater in mature forest than in snag-depauperate areas (Balda, 1975, see also Scott, 1979; Balda et al., 1983). Brawn et al. (1987) were able to artificially increase densities of cavity-nesting birds in several areas by providing nest boxes, suggesting that available cavities limit bird populations in some (but not all; see Brawn and Balda, 1988) areas. Although suitable cavities are not limited to snags exclusively (e.g. Cunningham et al., 1980; Bull et al., 1997), they tend to be most abundant in snags. Available evidence suggests that large snags are preferred to smaller snags (Scott, 1978; Cunningham et al., 1980; Horton and Mannan, 1988; Bull et al., 1997), and snags with >40% bark cover are selectively used by nesting birds (Scott, 1978; Cunningham et al., 1980).

Cavity-nesting birds probably play an important role in the ecology of ponderosa pine forests. Numerous authors (see reviews by Holmes, 1990; Machmer and Steeger, 1995) have noted that birds play an important role in regulating numbers of forest insects. Bird predation appears to be particularly effective at regulating insect numbers when populations of insects are low (Holmes, 1990). Most of the cavity nesters in Arizona's ponderosa pine forest are permanent residents (i.e. nonmigratory). Balda (1975) estimated that secondary cavity nesters alone contributed 63–73% of the total density of wintering birds in these forests. Cavity-nesting birds are the primary insectivores in these forests during the winter and early spring (Balda, 1975), when insect numbers are presumably low, and thus may be important in controlling populations of forest insects.

In view of the demonstrated importance of snags, some land-management agencies have management standards requiring the retention of specified numbers and kinds of snags to provide habitat for wildlife (e.g. U.S. Forest Service, British Columbia Ministry of Forestry). Current standards in the southwestern region (Arizona and New Mexico) of the U.S. Forest Service (USFS; USDA Forest Service, 1996) are based on recommendations in Reynolds et al. (1992). These recommendations call for retention of 4.9 and 7.4 snags/ha in ponderosa pine and mixed-conifer forests, respectively, with minimum diameter at breast height (DBH) of 46 cm and minimum height of 9 m. Reynolds et al. (1992) stated the size requirements should "meet the minimum requirements for the majority of prey species" for northern goshawks (*Accipiter gentilis*). No empirical basis was provided for the recommended snag densities.

Despite the existence of standards, data on existing densities and composition of snag populations are scarce in many areas. Further, there is evidence that snag-retention standards are not being met in several areas (Ffolliott, 1983; Morrison et al., 1986). As part of a long-term study of snag dynamics, snags were sampled in ponderosa pine and mixed-conifer forests on two National Forests in northern Arizona. This paper reports on current snag densities and the composition of snag populations on these forests, and compares existing densities of snags to current standards for snag retention on these forests.

2. Methods

2.1. Plot location

Snags were sampled on a study area of ≈7300 ha, located around Flagstaff in north-central Arizona (latitude 35°11′, longitude 111°39′). The study area included six Ranger Districts, two on the Kaibab National Forest (Challender and Williams) and four on the Coconino National Forest (Blue Ridge, Long Valley, Mormon Lake, and Peaks). Because of its size and variation in topography, the study area included a wide range of ecological conditions. As a result of this ecological variability, coupled with differences in land-use history, forests on the study area varied greatly in density, size-class distribution, and species composition, and spanned the range of conditions typically encountered in this geographic area.

Snags were sampled on square 1-ha plots. Plots were located using a stratified random sampling procedure with forest type and forest district as strata. Forest types recognized were ponderosa pine (dominated by ponderosa pine) and mixed-conifer (dominated by Douglas-fir [*Pseudotsuga menziesii*]and/or white fir [*Abies concolor*]) forest. Forest districts were included as strata to ensure adequate geographic representation throughout the study area. Stands were selected by:

(1) querying the stand data base for the Coconino and Kailbab National Forests to generate a list of stands by forest type and Ranger District;
(2) selecting all stands from this list with stand area >10 ha (to facilitate locating plots within stands while avoiding stand boundaries); and
(3) randomly selecting 10 stands from this list in each forest type (ponderosa pine, mixed-conifer) on each Ranger District.

Boundaries of selected stands were then plotted on 1 : 24 000 topographic maps.

To establish plots in the field, the approximate centers of mapped stands were located in the field, using topography, visual landmarks, and/or a global positioning system (GPS) unit (Trimble Geo Explorer). A compass was then used to select a random azimuth and number of paces (number of paces=azimuth/10, and thus ranged from 1 to 36), and the first plot corner was located by walking the indicated number of paces in the indicated direction. From this corner, another random azimuth was selected as above, and one side of the plot was laid out along that azimuth (plot dimensions=100 m× 100 m). Upon reaching the second plot corner, a coin flip was used to determine whether to turn left or right, then the second plot boundary was laid out on an azimuth perpendicular to the original azimuth. The square was then closed to complete plot layout. The GPS unit was used to obtain a series of locations at the first plot corner, and these locations were differentially corrected using location files obtained from a base station at the Colorado Plateau Research Station, Flagstaff, AZ. The mean Universal Transverse Mercator coordinates for this corner were recorded, along with the compass azimuths to the second and third plot corners, to monument the plot for future resampling.

2.2. *Plot sampling*

In view of the fact that a number of factors might influence abundance and dynamics of snags, data on land and management status, accessibility, and overall terrain were recorded for each plot. Land status was recorded as reserved (wilderness, Research Natural Area) or unreserved. Timber status was recorded as logged or unlogged. Unlogged indicated that no stumps were observed, so logged stands included stands subject to thinning or fuelwood harvest as well as timber harvest. Fire status was recorded as unburned, lightly burned (i.e. understory burn), or severely burned (i.e. evidence of recent crown fire). All plots were categorized as either accessible (i.e. plot contained or was immediately adjacent to a road) or inaccessible by road. Terrain on the plot was characterized as flat (mean slope <10%), moderate (mean slope >10% and ≤30%), or steep (mean slope >30%). Elevation (m) was recorded as the mean value from the differentially corrected corner location.

All snags ≥2 m in height and ≥20 cm DBH within plot boundaries were sampled. Snags <20 cm DBH were not sampled to save time, and because they were suspected to be less valuable as wildlife habitat than larger snags (Thomas et al., 1979). Signs of woodpecker foraging activity were observed on numerous snags <20 cm DBH, however. For all snags sampled, species, DBH (or diameter at root crown [DRC] for oaks [*Quercus* spp.] and junipers [*Juniperus* spp.]), height, percent bark cover, and decay class were recorded. DBH was recorded to the nearest cm using a DBH tape. Height was estimated to the nearest m using a clinometer. Percent bark cover was estimated

Table 1
Criteria used to classify snags into decay classes in ponderosa pine and mixed-conifer forests, northern Arizona (after Raphael and White, 1984)

Decay class	Needles	Twigs	Limbs
1	present	present	intact
2	absent	present	intact
3	absent	absent	mostly intact
4	absent	absent	mostly broken
5	absent	absent	gone

visually to the nearest 5%. Decay classes (Table 1) followed Raphael and White (1984).

2.3. Data analysis

Data on plot characteristics and composition of snag populations were summarized by forest type. Because distributions of snag numbers across plots were highly skewed and could not be normalized using standard transformations, medians and interquartile ranges (IQR; the range between the values representing the 25th and 75th percentiles; Conover, 1980) are reported rather than means and standard deviations. For simplicity, all species of snags were pooled for analyses, I recognize, however, that all species may not be equally valuable to forest wildlife (e.g. see Bull et al., 1997).

Current snag densities were compared with USFS standards for snag retention using two approaches. First, for each forest type, a 95% confidence interval was computed around the median density (Conover, 1980) of snags meeting USFS size requirements (hereafter large snags). If this confidence interval included the target density of large snags for that forest type, I concluded that snag standards were met. This served as an estimate of whether or not snag standards are being met across the landscape as a whole. Second, I computed the percentage of plots within a forest type that contained target densities of large snags. This served as a crude estimate of the proportion of the landscape on which snag standards are being met. Where snag standards were not met within a forest type based on analyses using all plots, I repeated the analysis using only unlogged plots to determine whether or not standards were met in plots not subject to timber or fuelwood harvest.

3. Results

3.1. Plot characteristics

Snags were sampled on 114 plots: 60 in ponderosa pine and 54 in mixed-conifer forest. Six selected mixed-conifer stands were not sampled, two because they included large cliffs that could not be sampled safely, one because snags had already been marked in the area by unknown parties, and three because of time constraints.

Sample plots were widely scattered across the study area, and covered a broad elevational gradient (1778–2561 m on ponderosa pine plots; 1886–3050 m on mixed-conifer plots). This gradient included the entire elevational range of both forest types.

Few plots fell on administratively reserved lands in either forest type (3.3 and 7.4% of plots in ponderosa pine and mixed-conifer forest, respectively; Table 2). Most plots (83.3%) in the ponderosa pine type showed evidence of past logging, whereas 46.3% of mixed-conifer plots showed no evidence of prior logging (Table 2). Most plots in both forest types showed obvious evidence of past fires (65.0 and 72.2% of plots in ponderosa pine and mixed-conifer forest, respectively). More ponderosa pine than mixed-conifer plots were accessible by road (55.0 vs. 29.6%), and ponderosa pine plots were located on the flat terrain more often than were mixed-conifer plots (55.0 vs. 5.6%; Table 2).

3.2. Composition of snag populations

Only four plots, all in ponderosa pine, lacked any snags $\geq$20 cm DBH. Density ranged from 0 to 45 snags/ha (median=5.0; IQR=3–11) for ponderosa pine forest and from 6 to 117 snags/ha (median=29.0; IQR=17–46) for mixed-conifer forest. I summarized snag numbers across levels of plot variables (Table 2), but caution that these variables are not independent. For this reason, and because of the unbalanced design and large number of empty cells, I did not attempt to model snag numbers across levels of plot variables.

Snag populations were dominated numerically by small snags in both forest types, with relatively few snags in the largest size classes (Fig. 1). Snag populations in ponderosa pine forest were comprised almost entirely of ponderosa pine (76.4%), Gambel oak (*Q.*

Table 2
Density (snags/ha) of snags $\geq$20 cm in diameter [a] on 1-ha plots sampled in ponderosa pine and mixed-conifer forest, Coconino and Kaibab National Forests, northern Arizona, 1997

Plot variable	Forest type					
	ponderosa pine			mixed-conifer		
	No.	median	IQR [b]	No.	median	IQR [b]
Land status						
reserved	2	30.0	—	4	36.0	56.8
unreserved	58	5.0	7.3	50	29.0	26.0
Timber status						
logged	50	5.0	6.3	29	24.0	23.0
unlogged	10	8.0	21.5	25	33.0	32.0
Terrain						
flat	33	4.0	5.0	3	21.0	—
moderate	24	6.0	7.0	25	24.0	19.5
steep	3	31.0	—	26	35.0	33.5
Road access?						
yes	33	5.0	5.5	16	23.5	25.0
no	27	5.0	10.0	38	31.5	30.8

[a] Diameter sampled at root crown for oaks and junipers, at breast height for all others.

[b] Interquartile range (range between the 25th and 75th percentiles). Missing values means the IQR was not defined, due to small sample size.

gambelii, 18.0%), and alligator juniper (*J. deppeana*, 2.3%). Snag populations were more diverse in mixed-conifer forest. Dominant species included white fir (25.1%), ponderosa pine (24.9%), Gambel oak (24.3%), Douglas-fir (8.3%) and quaking aspen (*Populus tremuloides*, 8.3%).

Snags in decay classes 4 and 5 dominated snag populations in both forest types when all snags were considered (Table 3). Relatively few large snags occurred in decay Class 5 (Table 3), probably because breakage reduced many Class-5 snags to <9 m tall (Fig. 2). Median bark cover was >40% for all decay classes when all snags were considered (Fig. 3(a)), but less than 40% for decay Class 5 when only large snags were considered (Fig. 3(b)), Percent bark cover also tended to be lower for decay classes 3 and 4 when only large snags were considered (Fig. 3(b)).

3.3. Comparisons to current snag standards

Median densities of large snags were 1.0 and 4.0 snags/ha in ponderosa pine and mixed-conifer

Table 3
Percent of snags in five decay classes in two forest types in northern Arizona, 1997. Snags were sampled on 54 and 60 1-ha plots in mixed-conifer and ponderosa pine forest, respectively. Large snags refer to snags $\geq$46 cm in DBH and $\geq$9 m in height (after USDA 1996). Decay classes follow Raphael and White (1984), n=number of snags sampled

Decay class	Mixed-conifer forest		Ponderosa pine forest	
	All snags (n=1851)	Large snags (n=273)	All snags (n=480)	Large snags (n=80)
1	10.0	13.2	16.5	20.0
2	17.2	26.0	16.7	22.5
3	15.9	24.9	12.1	22.5
4	25.5	30.4	23.5	26.3
5	31.4	5.5	31.3	8.8

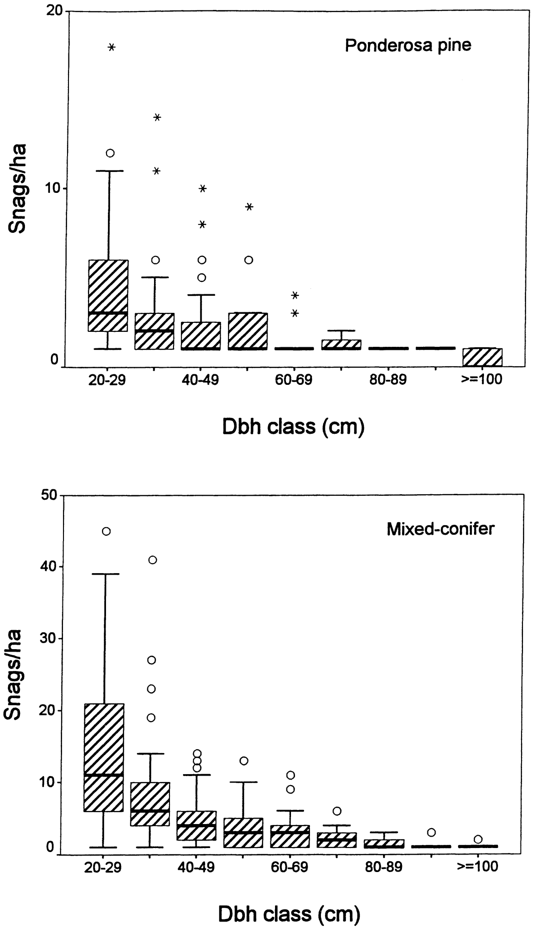

Fig. 1. Box plots of diameter distributions of snags (n=2331) sampled in ponderosa pine and mixed-conifer forest on two National Forests in northern Arizona, 1997. The box shows the interquartile range (25th–75th percentile). The horizontal line within the box indicates the median. Circles and asterisks denote outliers and extremes, respectively. Outliers are observations more than 1.5 box-lengths from the box; extremes are more than three box-lengths from the box. The vertical bars indicate the range of observations excluding outliers and extremes. (A) Ponderosa pine (n=60 plots); and (B) mixed-conifer (n=54 plots).

forest, respectively. The 95% confidence intervals (1.0–2.0 snags/ha and 2.0–5.0 snags/ha for ponderosa pine and mixed-conifer forest, respectively) did not contain the target density of snags (4.9 and 7.4 snags/ha) in either type. Only 6.7 and 16.7% of plots met or exceeded standards for snag density in ponderosa pine and mixed-conifer forest, respectively.

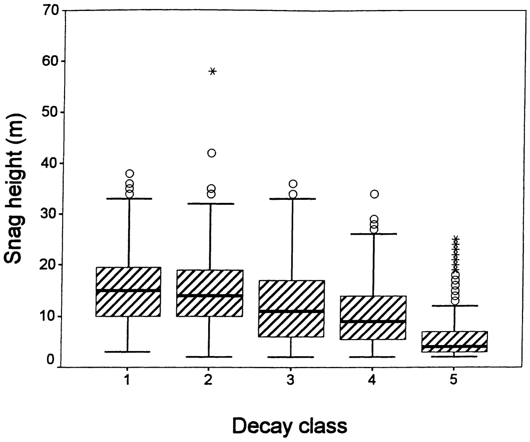

Fig. 2. Box plot of snag height by decay class for snags on two National Forests in northern Arizona, 1997. Decay classes follow Raphael and White (1984). Snags (n=2331) were sampled in 60 and 54 1-ha plots in ponderosa pine and mixed-conifer forest, respectively. The box shows the interquartile range (25th–75th percentile). The horizontal line within the box indicates the median. Circles and asterisks denote outliers and extremes, respectively. Outliers are observations more than 1.5 box-lengths from the box; extremes are more than three box-lengths from the box. The vertical bars indicate the range of observations excluding outliers and extremes.

Median densities of large snags on unlogged plots were 2.0 and 6.0 snags/ha in ponderosa pine and mixed-conifer forest, respectively. The 95% confidence interval for unlogged mixed-conifer forest (4–7 snags/ha; n=25 plots) approached but did not contain the target density for large snags. Sample size for unlogged ponderosa pine (n=10 plots) was too small to compute a meaningful confidence interval. Only 30 and 32% of unlogged plots met or exceeded standards in ponderosa pine and mixed-conifer forest, respectively.

4. Discussion

Although snags appeared to be relatively abundant in the study area, USFS standards for retention of large snags were rarely met. This was largely because snag populations were dominated by small snags (Fig. 1). Because large snags are used more by wildlife than small snags (Bull et al., 1997), these small snags are not the most valuable to wildlife. With respect to bird

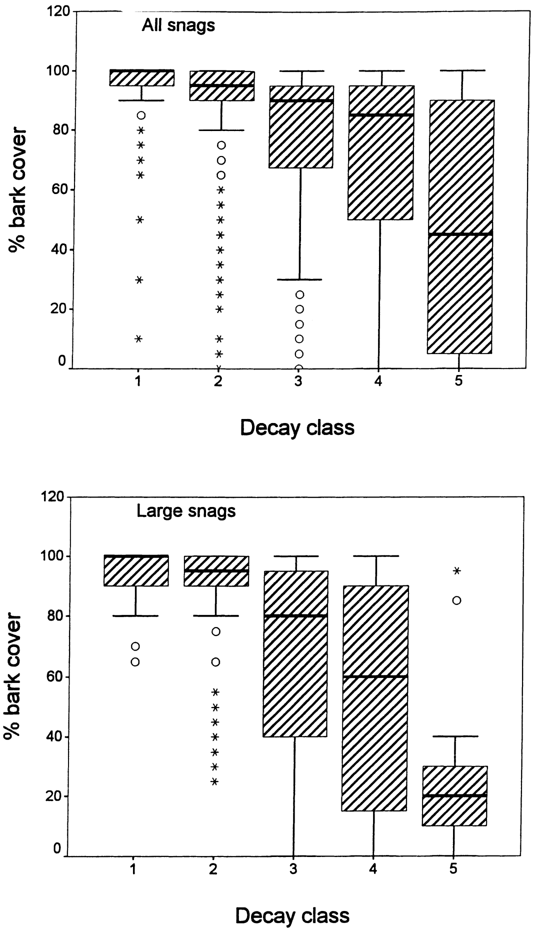

Fig. 3. Box plots of % bark cover by decay class within snag populations on two National Forests in northern Arizona, 1997. Decay classes follow Raphael and White (1984). Snags were sampled in 60 and 54 1-ha plots in ponderosa pine and mixed-conifer forest, respectively. The box shows the interquartile range (25th–75th percentile). The horizontal line within the box indicates the median. Circles and asterisks denote outliers and extremes, respectively. Outliers are observations more than 1.5 box-lengths from the box; extremes are more than three box-lengths from the box. The vertical bars indicate the range of observations excluding outliers and extremes. (A) All snags (n=2331); and (B) large snags (DBH$\geq$46 cm, height $\geq$9 m; n=353 snags).

use of snags in the southwest, Scott (1978) documented greatest rates of use of snags $\geq$38 cm DBH and $\geq$23 m tall, Cunningham et al. (1980) recommended retention of snags >33 cm DBH and >6 m tall, and Horton and Mannan (1988) noted that cavity-nesting birds preferred snags $\geq$50 cm dbh. Rabe et al. (1998) also noted that roosting bats selected large snags. These large snags typically last longer than small snags, and thus probably provide wildlife habitat over a longer time period than small snags (Bull et al., 1997).

This does not necessarily mean that small snags are unimportant, however. Although small snags are probably less valuable as nesting substrates for cavity-nesting birds than large snags, small snags provide important habitat components such as foraging sites, perching sites, and song posts. Results of this study suggest that small snags are relatively common in the study area, but they should still be considered in planning. Smaller snags may be particularly important where numbers of large snags are limited.

Snag populations in the study area were also dominated by snags in the later decay classes (Table 3). These snags appeared to be very susceptible to breakage, resulting in reduced snag height (Fig. 2) that might reduce their attractiveness to nesting birds. They also generally retained less bark cover than snags in earlier decay classes, particularly when large snags are considered (Fig. 3). This may also reduce their value to wildlife such as bats or Brown Creepers (*Certhia americana*) that nest or roost under loose bark (Rabe et al., 1998; Bull et al., 1997), or birds that nest preferentially in snags retaining considerable bark cover (Scott, 1978). Snags in the later decay classes are also closer to the end of their useful life as foraging, nesting, and roosting substrates than are snags in earlier decay classes. Thus, the relative dominance of classes 4 and 5 snags may indicate that many of these snags have passed their period of maximum value to wildlife. It may also indicate an unbalanced age structure in snag populations, with snag density possibly decreasing as many of these older snags fall. That hypothesis cannot be tested at present, however, because of uncertainty about how long snags remain in a particular decay class and what factors may influence transition rates between classes.

Perhaps the most significant finding in this study was that USFS snag standards were seldom met even in unlogged forest. If snag densities in these areas represent 'natural' conditions, these data suggest that current standards for retention of large snags may be unrealistic and difficult to attain. Unfortunately, historic forest inventories in this area (e.g. see Woolsey, 1911) typically did not include data on snags, and little is known about 'natural' snag densities in southwestern forests. There is some reason to speculate that snag densities in these unlogged plots may be as high or higher than densities occurring under natural conditions, however.

Unlogged plots, by definition, showed no evidence or fuelwood harvest that might have removed snags. These areas have been subject to effective fire suppression for many decades, however. Fire can both create and destroy snags, and the net effect of fire suppression on snag densities is unknown. Historical fire regimes in southwestern ponderosa pine forests were characterized by relatively frequent, low-intensity, stand-maintaining fires (Moir et al., 1997). This was probably true for many mixed-conifer forests as well, although fire frequency decreases along a gradient from ponderosa pine to mesic mixed-conifer forest (Swetnam and Baisan, 1996). These low-intensity fires generally did not cause much mortality of large trees (Woolsey 1911; Moir et al., 1997), but may have resulted in loss of snags, which are susceptible to damage or loss even in low-intensity fires (e.g. Horton and Mannan, 1988; Gordon, 1996). Consequently, densities in unlogged forests, subject to fire suppression, may exceed those expected under natural fire regimes, although this conclusion remains speculative.

5. Conclusions

The goal of retaining snags to provide habitat for wildlife is admirable and should be continued. However, my results suggest that current standards for snag retention may be unrealistic, and that those standards should be reconsidered. Ideally, guidelines for snag management should be based on a thorough understanding of both snag population dynamics and the ecology of the wildlife species dependent on the snag resource (e.g. see Bull et al., 1997). This would require, at minimum, information on nesting, roosting, and foraging requirements of cavity-nesting birds and other wildlife species linked to snags, tree mortality rates, and longevity of snags. Additional information that would be useful includes: how snags contribute to forest structure, how useful different species and sizes of snags are to wildlife, the effects of fire, both natural and prescribed, on snag density and longevity, and the importance of partially dead trees to wildlife.

We currently lack most of this information for southwestern forests, pointing out the great need for additional work in these areas (see also Bull et al., 1997; Rabe et al., 1998). Until better information is available, my results suggest that retention of large trees would be appropriate in most areas. These large trees would not only provide large snags in the future, but could also benefit cavity-nesting birds and other wildlife before these trees die. Dead wood in dead tops and/or lightning scars can provide foraging and nesting sites for birds (e.g. Cunningham et al., 1980; Bull et al., 1997) or roosting sites for bats (Bull et al., 1997). Live trees with dead wood often stand much longer than snags, and so may be useful to wildlife over a longer time period than a typical snag. Many large old trees are injured by lightning during their lifespan in this region, suggesting that these trees could provide a significant source of cavities for use by wildlife. Indeed, if snags did occur in lower numbers under natural fire regimes, many species of cavity-nesting birds may have formerly relied heavily on cavities in live trees containing dead wood.

Snag management should also consider the effects of snag distribution and juxtaposition on use by wildlife. The patchy distribution of snags observed in this and other studies (e.g. Ohmann et al., 1994) argues against the application of uniform targets for snag retention across the landscape. Balda (1975) implicitly recognized this patchiness when he proposed standards for a 40-ha area, rather than per hectare. Thus, a more reasonable goal might be to maintain high snag densities across portions of the landscape, while allowing density to vary in other areas. This would acknowledge that snags (and the animals that depend on them) are, and probably always will be, patchily distributed.

Acknowledgements

Special thanks to A. and J. Iníguez for their conscientious and dedicated assistance in the field. G. Martinez, M. Stoddard, B. Strohmeyer, and R. White also assisted in the field. Numerous USFS personnel assisted with plot selection, including 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). R.P. Balda, W.M. Block, C. Chambers, and two anonymous reviewers commented on earlier drafts of this paper.

References

Balda, R.P., 1975. The relationship of secondary cavity nesters to snag densities in western coniferous forests. Wildl. Habitat Tech. Bull 1. USDA For. Serv. Southwestern Region. Albuquerque, NM.

Balda, R.P., Gaud, W.S., Brawn, J.D., 1983. Predictive models for snag nesting birds. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Technical Coordinators). Snag habitat management: Proceeding of the symposium. USDA For. Serv. Gen. Tech. Rep. RM-99. Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO. pp. 216–222.

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

Brawn, J.D., Boecklen, W.J., Balda, R.P., 1987. Investigations of density interactions among breeding birds in ponderosa pine forests: correlative and experimental evidence. Oecologia 72, 348–357.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and logs important to wildlife in the interior Columbia River Basin. USDA For. Serv. Gen. Tech. Rept. PNW-GTR-391. Pacific Northwest Res. Stn. Portland, OR.

Chung-Maccoubrey, A., 1996. Bat species composition and roost use in pinyon–juniper woodlands of New Mexico. In: Barclay, M.R., Brigham, R.M. (Eds.), Bats and Forests Symposium. Work Pap. 23/1996. Research Branch, B.C. Min. For., Victoria, British Columbia. Canada. pp. 118–123.

Conover, W.J., 1980. Practical Nonparametric Statistics, 2nd edn. John Wiley & Sons, New York.

Cunningham, J.B., Balda, R.P., Gaud, W.S., 1980. Selection and use of snags by secondary cavity-nesting birds of the ponderosa pine forest. USDA For. Serv. Res. Pap. RM-222. Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO.

Ffolliott, R.F., 1983. Implications of snag policies for southwestern forests. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A., (Technical Coordinators). Snag Habitat Management: Proceedings of the Symposium. USDA For. Serv. Gen. Tech. Rep. RM-99. Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO, pp. 28–32.

Gordon, J.V., 1996. Effects of prescribed fire on snags and logs in northern Arizona ponderosa pine forests. M.S. thesis. Northern Arizona Univ., Flagstaff.

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

Holmes, R.T., 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. Studies in Avian Biology 13, 6–13.

Horton, S.P., Mannan, R.W., 1988. Effects of prescribed fire on snags and cavity-nesting birds in southeastern Arizona pine forests. Wildl. Soc. Bull. 16, 37–44.

Machmer, M.M., Steeger, C., 1995. The Ecological Role of Wildlife Tree Users in Forest Ecosystems. British Columbia Ministry of Forests. Victoria, British Columbia, Canada.

Maser, C., Trappe, J.M., Nussbaum, R.A., 1978. Fungal–small mammal interrelationships with emphasis on Oregon forests. Ecology 59, 799–809.

Moir, W.H., 1992. Ecological concepts in old-growth definition. In: Kaufmann, M.R., Moir, W.H., Bassett, R.L. (Technical Coordinators). Old-growth forests in the Southwest and Rocky Mountain regions: Proceedings of a workshop. USDA For. Serv. Gen. Tech. Rep. RM-213. Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO. pp. 18-23.

Moir, W.H., Geils, B., Benoit, M.A., Scurlock, D., 1997. Ecology of southwestern ponderosa pine forests. In: Block, W.M., Finch, D.M. (Technical Eds.), Songbird Ecology in Southwestern Ponderosa Pine Forests: A Literature Review. USDA For. Serv. Gen. Tech. Rep. RM-GTR-292. Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO. pp. 3–27.

Morrison, M.L., Dedon, M.F., Raphael, M.G., Yoder-Williams, M.P., 1986. Snag requirements of cavity-nesting birds: are USDA Forest Service guidelines being met?. West. J. Appl. For. 1, 38–40.

Ohmann, J.L., McComb, W.C., Zumrawi, A.A., 1994. Snag abundance for primary cavity-nesting birds on nonfederal forest lands in Oregon and Washington. Wildl. Soc. Bull. 22, 607–620.

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

Raphael, M.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86, 1–66.

Reynolds, R.T., Graham, R.T., Reiser, M.H., Bassett, R.L., Kennedy, P.L., Boyce Jr., D.A., Goodwin, G., Smith, R., Fisher, E.L., 1992. Management recommendations for the Northern Goshawk in the Southwestern United States. USDA For. Serv. Gen. Tech. Rep. RM-217. Rocky Mtn. For. and Range Exper. Stn. Fort. Collins, CO.

Scott, V.E., Evans, K.E., Patton, D.R., Sone, C.P., 1977. Cavity-nesting birds of North American forests. USDA Agricultural Handbook 511. Washington, D.C.

Scott, V.E., 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. J. For. 76, 26–28.

Scott, V.E., 1979. Bird response to snag removal in ponderosa pine. J. For. 77, 26–28.

Swetnam, T.W., Baisan, C.H., 1996. Historical fire regime patterns in the southwestern United State since AD 1700 In: C.D. Allen (Technlcal Ed.), Fire Effects in Southwestern Forests: Proc. 2nd La Mesa Fire Symp. USDA For. Serv. Gen. Tech. Rep. RM-GTR-286, Rocky Mtn. For. and Range Exper. Stn., Fort Collins, CO. pp. 11–32.

Sydeman, W.J., Guntert, M., 1983. Winter communal roosting in the Pygmy Nuthatch. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Technical Coordinators), Snag Habitat

Management: Proceedings of the symposium, USDA For. Serv. Gen. Tech. Rep. RM-99, Rocky Mtn. For and Range Exper. Stn., Fort Collins, CO. pp. 121–124.

Thomas, J.W., Anderson, R.G., Master, C., Bull, E.L., 1979. Snags. In: Thomas, J.W. (Technical Ed.), Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington, USDA Agricultural Handbook 553, 60–77, Washington, D.C.

USDA Forest Service, 1996. Record of Decision for amendment of Forest Plans: Arizona and New Mexico, USDA For. Serv. Southwestern Region, Albuquerque, New Mexico.

Woolsey Jr., T.S., 1911. Western yellow pine in Arizona and New Mexico, USDA For. Serv. Bull. 101, Washington, D.C.