Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 255 (2008) 99–105
Forest Ecology and Management
www.elsevier.com/locate/foreco

Prescribed fire, snag population dynamics, and avian nest site selection

Karen E. Bagne[a,b,*], Kathryn L. Purcell[b], John T. Rotenberry[a]

[a] *Department of Biology, University of California, Riverside, CA 92521, USA*
[b] *USDA Forest Service, Pacific Southwest Research Station, 2081 East Sierra Avenue, Fresno, CA 93710, USA*

Received 30 March 2007; received in revised form 25 August 2007; accepted 30 August 2007

Abstract

Snags are an important resource for a wide variety of organisms, including cavity-nesting birds. We documented snag attributes in a mixed-conifer forest dominated by ponderosa pine in the Sierra Nevada, California where fire is being applied during spring. A total of 328 snags were monitored before and after fire on plots burned once, burned twice, or left unburned to assess the effects of prescribed fire on snag populations. The greatest loss of snags (7.1 snags ha^{-1} or 43%) followed the first introduction of fire after a long fire-free period. On plots burned a second time 21% of snags (3.6 snags ha^{-1}) were lost, whereas 8% (1.4 snags ha^{-1}) were lost on unburned control plots in the same time period. New snags replaced many of those lost reducing the net snag losses to 12% (2.0 ha^{-1}) for plots burned once, and 3% (0.5 ha^{-1}) for plots burned twice and unburned plots. We also examined snags used by cavity-nesting birds. Snags preferred for nesting were generally ponderosa pine (*Pinus ponderosa*), larger diameter, and moderately decayed as compared to available snags. For monitored snags that met the preferred criteria, there was a net loss (1.7 snag ha^{-1} or 34%) after the first burn, while the loss of useable snags was less than 1 snag ha^{-1} following the second burn (15%) or on unburned controls (8%). We recommend protection of preferred snags, in particular large ponderosa pines, especially during primary fire applications on fire-suppressed landscapes.

Keywords: Habitat selection; Prescribed fire; Breeding biology; Sierra Nevada; Snags; Cavity-nesting birds

1. Introduction

Ecologists have long recognized the important role of standing dead trees, or snags, in the life cycle of a wide variety of organisms (Bull, 2002). Additionally, snags have their own ‘‘life cycle,’’ beginning with their creation due to the death of a tree, subsequent decay, and eventual termination (though not of their ecological role) after falling to the ground. Due to the nature of disease, weather, and fire, all of which are factors influencing this cycle, the transition of snags from one stage to the next is often episodic (Morrison and Raphael, 1993). In addition, tree species differ in wood structure and decay pattern in ways that can also influence snag dynamics (Parks et al., 1997). Thus, snag availability for wildlife is the result of a complex of biotic and abiotic factors.

A number of studies have investigated how bird populations interact with snag populations. As studies move beyond a simple numerical association between snag and bird populations, researchers are finding complex ecological relationships (Bednarz et al., 2004). The process of excavating cavities in snags by primary cavity-nesting birds forms the basis of a web that connects a wide variety of species (Martin et al., 2004). Furthermore, cavity or snag choice may be influenced by competition and can also vary as bird populations fluctuate in abundance (Nilsson, 1984). Snag characteristics, such as decay, influence cavity creation and thus snag suitability (Jackson and Jackson, 2004). Additionally, fungi that promote wood decay are spread by foraging woodpeckers, which are further influenced by presence of prey such as bark-boring beetles, another creator of snags (Farris et al., 2004).

Tree mortality following prescribed fire is generally low, is not always immediate, and is influenced by tree species, tree size, season of burn, and fire intensity (Harrington, 1996; Schwilk et al., 2006). Prescribed fire, which is generally of lower severity, does not have the same potential as wildfires to create large

---

* Corresponding author. Current address: U.S. Forest Service, Rocky Mountain Research Station, 333 Broadway SE, Suite 115, Albuquerque, NM 87102-3407, USA. Tel.: +1 505 724 3684; fax: +1 505 724 3688.
E-mail address: kebagne@fs.fed.us (K.E. Bagne).

0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2007.08.024

continuous stands of snags. On the other hand, loss of existing snags following prescribed fire can be relatively high (Horton and Mannan, 1988) and season of burning may differ from natural fire regimes (McKenzie et al., 2004). Fall rates of snags created by prescribed fire may be higher than fall rates in the absence of fire, because snags in burn areas can attract wood-boring insects that reduce structural integrity. In addition, fall rates may differ with season of burn where rates following prescribed fire in the spring may be higher than rates in the dormant season, possibly due to lower allocation of resin during the growing season to fight insect attack (Harrington, 1996; McHugh et al., 2003).

With wildfires increasing in severity and frequency, prescribed fire is being used more frequently (Kauffman, 2004), but we know little about the role of this type of fire in snag population dynamics or its effect on cavity-nesting birds (Bock and Lynch, 1970; Saab et al., 2004; Saab and Powell, 2005). Thus, the focus of our study is the immediate role of spring prescribed fire in the snag cycle, and how it relates to snags used for breeding by a suite of avian species in the Sierra Nevada of California.

2. Methods

2.1. Study area

We conducted our study in Sierra National Forest, Fresno County, CA (37°02′N, 119°15′W). The study area was dominated by ponderosa pine (*Pinus ponderosa*), but other common tree species included incense cedar (*Calocedrus decurrans*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), California black oak (*Quercus kelloggii*), and canyon live oak (*Quercus chrysolepis*). The study plots experienced fires in the 1930s or 1940s, with the last wildfire in the area recorded in 1947. None had been recently logged. The study area was comprised of nine 40-ha plots of mature coniferous forest at elevations ranging from 1000 to 1400 m (Fig. 1). Our study consisted of three types of treatments, each with three replicate plots: (1) unburned plots that continued to have fire excluded, (2) similar plots that were burned in early April 2002, and (3) plots that had controlled burn applications in April 1997, February 1998, and May 1998 prior to the initiation of the study, with two of these plots burned a second time in June 2003. Thus, prescribed fire was applied to two types of plots: plots that were previously burned (burned twice) and plots that started with a fire history similar to the unburned plots (burned once). Each plot was burned separately, although plots burned in the same year were burned within a few weeks. Prescribed fire was applied to plots as well as surrounding areas, depending on locations of roads or natural fuel breaks. Burning was part of a fuels reduction program implemented by the Sierra National Forest, High Sierra Ranger District, and plots chosen for burning were within burn units based on the burn management plan, where fire is applied through a rotation for up to three fire applications in 10 years.

2.2. Snag availability

On each of the nine plots, we inventoried available snags using a 50-m wide belt transect that was placed randomly along a permanently marked line also used for surveying bird populations. All snags greater than 20 cm dbh (diameter at breast height, 1.3 m from the ground) along the transect were marked with aluminum tags and measured until 35–44 snags were recorded on each plot. Additionally, geographic coordinates of each snag were recorded with a Garmin GPS unit to aid in relocating snags. Because we were primarily interested in snag characteristics and snag fate following prescribed fire, we focused on number of snags rather than sampling a uniform area. We calculated snag density (number ha^{-1}) based on the transect length on each plot. Tree species of the snag was recorded when possible and measurements included height and dbh. Classifications were made for state of branches (five categories, size and amount of remaining branches), bark (three categories, tight to bole or loose), surface wood hardness (four categories, sound to crumbling), and overall decay class (five categories; based on Cline et al., 1980). These classifications were combined into a single summary measure of snag age or decay (higher numbers indicate greater decay). This summary measure (range 4–17) is referred to as ‘‘decay’’ hereafter. Snags known to contain bird nests that fell within the transect were included in both the available snag dataset and the used snag dataset described below. The snag measurements were taken before sites were burned in 2002. Snags were reassessed on all plots by September 2003.

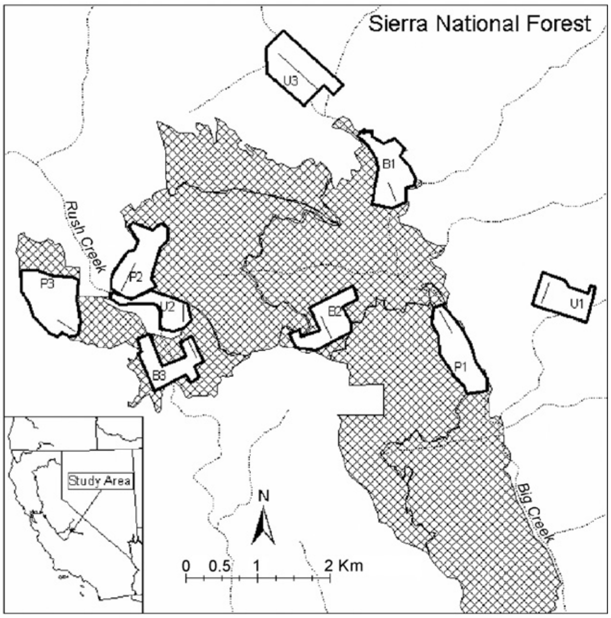

Fig. 1. Locations of nine 40-ha study plots and transects used to track available snags. Plots are identified as U for unburned, B for burned once in 2002, and P for burned previous to study and again in 2003 (except for P3, which was not re-burned). Cross-hatching represents area managed with prescribed fire 1997–2003.

2.3. Bird choice

Data were also obtained from snags used for breeding by cavity-nesting bird species throughout the entire 40 ha of each plot collected as part of two studies from 1995 to 2003. Snag use was established based on confirmed nesting activity rather than inferred from cavity presence. Cavity-nesting species included primary cavity nesters, secondary cavity nesters, and the brown creeper (*Certhia americana*), which uses the natural "cavity" created when bark peels away from the trunk but remains attached to the bole. We collected the same measurements as those taken for snags on the transects, but because some snag characteristics change over time, measurements were taken in the same year the nest was active.

We used canonical discriminant function analysis (DFA; Tabachinick and Fidell, 1996) to determine which snag characteristics best distinguished between used and available snags ("bird choice"). Snag species was dummy-coded using incense cedar as the reference group (coded "0"), because this species is generally avoided by cavity-nesting species. Besides incense cedar, snag species included ponderosa pine, white fir, and sugar pine, and a fourth group that combined the remaining snag species used. Loadings of snag species, height, dbh, and decay on canonical variates and class means were obtained using PROC DISCRIM (SAS Ver. 8.2 for personal computer, SAS Institute and Inc., 2000). Loadings, or the correlation of each variable with the canonical discriminant axis, were considered important if >0.33 (10% of the variance) (Tabachinick and Fidell, 1996).

Based on the estimated discriminant function of bird choice, snags sampled within the transects were classified into predicted "used" or "unused." This classification was made using a nonparametric method based on the Mahalanobis distance of the pooled covariance matrix (SAS Institute and Inc., 2000). Using these distances, classifications were assigned from nearest neighbors. The number of nearest neighbors (k) was chosen to maximize the correct classification into the "useable" snag group.

2.4. Snag fate and creation

Tagged snags were revisited in 2003 following burning and significant alterations, such as falling or consumption by fire, noted. New (untagged) snags within the transects were recorded and measured. These data were used to estimate the numbers of new and fallen snags. The specific cause of death was not determined for each tree, but burning was assumed to be a contributor to mortality following fire. Burned snags that were wholly or mostly consumed were included with fallen snags as they were equally unavailable as nesting substrates.

3. Results

3.1. Snag availability

From the transects, we collected information on 328 snags. Six snags in the transects were also known to contain active nests and were repeated in the "used" dataset. Snag species included ponderosa pine (35% of total), incense cedar (32%), white fir (13%), sugar pine (10%), black oak (5%), and white alder (*Alnus rhombifolia*, 0.6%). Sixteen snags were too decayed to determine tree species. Area surveyed in the transects used to assess available snags ranged from 1.2 to 3.7 ha (Table 1). When combined across replicates, the density of available snags before burning was 16.2 snags ha^{-1} on unburned plots, 16.5 snags ha^{-1} on plots to be burned once, and 16.6 snags ha^{-1} on plots to be burned twice.

3.2. Bird choice

Bird species recorded nesting in snags ($n = 240$ nests) were red-breasted nuthatch (*Sitta canadensis*; $n = 75$), brown creeper ($n = 61$), white-headed woodpecker (*Picoides albolarvatus*; $n = 37$), northern flicker (*Colaptes auratus*; $n = 26$), acorn woodpecker (*Melanerpes formicivorus*; $n = 15$), downy woodpecker (*Picoides pubescens*; $n = 8$), hairy woodpecker (*Picoides villosus*; $n = 7$), mountain chickadee (*Poecile gambeli*; $n = 4$), red-breasted sapsucker (*Sphyrapicus ruber*; $n = 3$), pileated woodpecker (*Dryocopus pileatus*; $n = 1$), northern pygmy owl (*Glaucidium gnome*; $n = 1$), northern saw-whet owl (*Aegolius acadicus*; $n = 1$), and great gray owl (*Strix nebulosa*; $n = 1$). Snag species used, in order of frequency, were ponderosa pine, white fir, incense cedar, sugar

Table 1
Numbers of available snags surveyed on transects and changes following re-measurement after ~2 years on each of nine experimental plots

Treatment	Plot	Transect area (ha)	Number of snags				Change in available snags (number ha^{-1})	Change in useable snags (number ha^{-1})
			2001		2003			
			On transect	Useable	Fallen (useable)	New (useable)		
Unburned	U1	1.7	35	10	7 (3)	3 (2)	−2.4	−0.6
	U2	1.2	35	7	1 (1)	1 (0)	0.0	−0.8
	U3	3.7	37	9	1 (0)	2 (0)	+0.3	0.0
Burned 2002	B1	1.4	36	15	18 (8)	2 (0)	−11.4	−5.7
	B2	1.7	36	5	8 (4)	29 (7)	+12.4	+1.8
	B3	1.4	35	12	20 (6)	2 (0)	−12.9	−4.3
Burned 1997–1998, again in 2003	P1	1.9	35	11	11 (5)	9 (4)	−1.1	−0.5
	P2	2.3	35	9	4 (2)	4 (0)	0.0	−0.9
	P3[a]	1.5	44	10	9 (1)	4 (1)	−3.3	0

Designation as "useable" for nesting by cavity-nesting birds is based on classification from the discriminant function model of available vs. used snags.

[a] This postburn site did not have fire reapplied in 2003.

Table 2
Means (S.D.) for characteristics of snags and percent of snag species used by cavity-nesting birds for nesting and unused snags on unburned and burned plots

Attribute	Used		Unused	
	Unburned ($n = 155$)	Burned ($n = 85$)	Unburned ($n = 215$)	Burned ($n = 115$)
Height (m)	13.7 (12.9)	17.5 (13.7)	9.8 (8.0)	12.7 (8.4)
Dbh (cm)	54.5 (26.4)	46.7 (21.8)	37.5 (16.9)	32.9 (12.7)
Decay	8.5 (2.5)	8.4 (2.3)	9.0 (3.5)	7.0 (2.8)
Species (%)				
Ponderosa pine (*Pinus ponderosa*)	80.7	60.0	37.7	28.7
White fir (*Abies concolor*)	3.9	22.4	7.9	22.6
Incense cedar (*Calocedrus decurrens*)	6.5	8.2	33.5	27.8
Sugar pine (*Pinus lambertiana*)	2.6	7.1	7.9	13.9
Other	6.5	2.4	13.0	7.0

For unused, only snags >20 cm dbh (diameter at breast height) were sampled. Higher values of decay (range 4–17) indicate greater decay. "Other" includes snags of unknown tree species.

pine, white alder, California black oak, and canyon live oak, which was used once. Not only did snags selected differ from those sampled on the transects, but selection varied with availability on burned and unburned plots (Table 2). Ponderosa pine was used proportionally more than it was available, but use was relatively lower on burned plots where it was less available than on unburned plots. This pattern was similar for dbh with an overall preference for larger snags.

Discriminant function analysis was successful at distinguishing between snags used for nesting and unused snags (Wilks' lambda = 0.86, $F = 89.96$, $p < 0.001$). The mean of used snags on the canonical axis was 0.68 and the mean for available snags was −0.50. The DFA identified ponderosa pine (canonical loading = 0.74) and substrate dbh (0.73) as the most important variables differentiating between used and unused snags. Correlations of the remaining variables with the canonical axis were all less than 0.33 (sugar pine = −0.20, white fir = −0.09, decay = 0.07, other species = −0.05). Increased diameter and ponderosa pine were associated with greater probability of use. Snag species other than ponderosa pine were, along with decay, relatively nonpredictive of use.

The discriminant function for snag use was used to classify available snags inventoried in the transects. A k (number of nearest neighbors) of two was chosen for classification of available snags as used or unused as this maximized correct classification of the used group (94% correct for used, 74% correct for unused). That the proportion of correct classifications for unused is less than that for used is expected, as that category contains snags that are suitable but that have not been used. The six snags that contained active nests within the transects were correctly classified as useable.

The plots differed in numbers of snags classified as suitable for use (Table 1). Proportion of snags useable ranged from 14% to 42% at the beginning of the study. On average, 24% and 29% of snags were predicted to be suitable for use on unburned and previously burned transects, respectively.

3.3. *Snag fate and creation*

Conditions during burning were moist and fire left a mosaic of burned and unburned patches, though no transect was left with substantial unburned area. On all transects, including those that were unburned, existing snags fell. Though there was variation among plots, proportion of snags lost tended to be higher for transects burned once and also for those snags that were predicted for use by cavity-nesting birds (Table 1). In the absence of fire, 8% (9 or 1.4 ha^{-1}) of snags fell though 15% (4 or 0.6 ha^{-1}) of useable snags fell. For transects burned once, 43% (46 or 7.1 ha^{-1}) of all snags fell and 56% (18 or 2.8 ha^{-1}) of useable snags fell. For transects burned twice, 21% (15 or 3.6 ha^{-1}) of all snags fell and 35% (7 or 1.7 ha^{-1}) of useable snags fell after burning. The remaining transect, which was burned at the start of the study but not re-burned, had a 20% (9 or 6.0 ha^{-1}) loss of all snags and only one useable snag fell (0.7 ha^{-1}).

New snags were created on all transects though few were classified as useable except on one burned transect, "B2" (Table 1). There were six new snags (0.9 ha^{-1}) on unburned transects and 33% (0.3 ha^{-1}) of these were classified as useable. For transects burned once, there were 33 new snags (5.1 ha^{-1}) and 21% (1.1 ha^{-1}) of these were useable. After burning twice there were 13 new snags (3.1 ha^{-1}) and 31% (1.0 ha^{-1}) were useable. The remaining transect, which was burned at the start of the study but not re-burned, had four new snags with one useable.

Once snag losses were balanced with snag gains, the net loss of snags was similar for unburned plots and plots burned twice with a 3% or 0.5 ha^{-1} loss, while there was a net loss of 12% (13 or 2.0 ha^{-1}) on plots burned once. For useable snags the pattern was similar, with a net loss of 2 (2% or 0.3 snags ha^{-1}) for unburned plots, 11 (34% or 1.7 snags ha^{-1}) for plots burned once, and 3 (15% or 0.7 snags ha^{-1}) for plots burned twice (Fig. 2).

Those snags that fell tended to be larger than average dbh on burned plots (Table 3). The species of snags vulnerable to falling differed between burned and unburned plots. Ponderosa pines were most vulnerable. Incense cedar snags were vulnerable to burning, but none fell on unburned plots where sugar pine and white fir were more likely to fall (Table 3).

New snags were dominated by ponderosa pine, with a large number of these from a single burned site (Table 1) where the transect "B2" included a stand infested by bark beetles

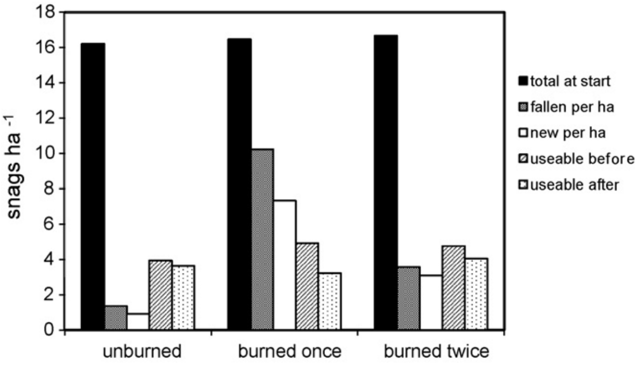

Fig. 2. Total snags ha^{-1} in 2001 and changes by 2003 following burning of plots once or twice, and unburned plots. Useable snags are based on classification by the discriminant function based on snag selection by cavity-nesting species.

following burning (∼20 of 25 new ponderosa pines). This was the only plot with a net gain of ‘‘useable’’ snags. On unburned plots half the new snags were sugar pine, but sample sizes were small. The newly created snags were of slightly smaller average dbh (seven of nine sites) than available snags, with size being similar between new snags on unburned plots and on burned plots (Table 3).

4. Discussion

Birds selected specific snag types for nesting. Relative to available snags, cavity-nesting species selected large ponderosa pine snags, although even very small snags were used on occasion by red-breasted nuthatch (four snags <20 cm dbh, minimum = 14 cm dbh). On average, 27% of snags >20 cm were predicted to be useable for nesting. Though all bird species were combined in the reported analysis, the same snag selection pattern was seen when a DFA was run on the four most abundant species individually. Selection of larger snags for nesting is consistent with other research (Horton and Mannan, 1988; Ganey and Vojta, 2004; Blewett and Marzluff, 2005; Spiering and Knight, 2005). Additionally, preference for particular snag species, including for ponderosa pine, has been found by other studies (Conway and Martin, 1993; Bevis and Martin, 2002; Ganey and Vojta, 2004; Martin et al., 2004). Greater use of ponderosa pine for cavity construction is thought to be due to the relatively greater proportion of sapwood, which decays more readily, as compared to other conifer species (Parks et al., 1997).

Table 3
Average (S.D.) attributes and percent of tree species comprising snags leaving or entering the sample on unburned plots and following prescribed fire

Snag status	Attributes	Unburned plots[a]	Burned plots
Fallen or burned		*n* = 18	*n* = 61
	Height (m)	13.3 (8.4)	11.6 (9.8)
	dbh (cm)	30.0 (7.8)	42.8 (19.4)
	Decay	8.4 (3.5)	9.3 (3.7)
	Ponderosa pine	61.1	59.7
	White fir	16.7	3.2
	Incense cedar	0	21.0
	Sugar pine	16.7	3.2
	Other	5.6	12.9
New		*n* = 10	*n* = 46
	Height (m)	17.8 (6.9)	17.1 (8.8)
	dbh (cm)	33.7 (11.7)	30.4 (10.0)
	Ponderosa pine	30	70.2
	White fir	20	2.1
	Incense cedar	0	19.2
	Sugar pine	50	4.3
	Other	0	4.3

Dbh is diameter at breast height. For decay (range 4–17) higher values indicate greater decay and new snags by definition are undecayed. ‘‘Other’’ includes snags of unknown tree species.

[a] Unburned includes one previously burned site not burned during the study.

The role of fire in snag population dynamics is complex and historic populations are largely unknown. Evidence from repeat photography and unmanaged forests indicates snags in the past were less numerous, but mostly of large diameter and less decayed (Minnich et al., 2000; Gruell, 2001; Stephens, 2004). Studies of contemporary wildfire have found increased bird use of snags in the first years following fire (Linder and Anderson, 1998; Saab et al., 2004), and studies of prescribed fire have reported an overall loss of snags (Horton and Mannan, 1988; Randall-Parker and Miller, 2002). However, variation in burning intensities and existing forest structure complicates comparison of results, not just from wildfires, but also from prescribed fire. In our study, initial burning of plots after a long period of fire exclusion resulted in the greatest turnover in snags, with turnover after the second burn more similar to that from unburned plots where snag losses and gains were smaller and mostly balanced. A study of multiple wildfires in New Mexico similarly found most changes in snags after the first fire (Holden et al., 2006). This trend likely results because the most vulnerable snags are removed during the first burn, leaving more resistant ones behind.

We found that in the first years following prescribed burning, many existing snags were lost, but this was offset to some extent by creation of new snags (Fig. 2). On plots burned once, 43% of snags were lost although taking into consideration the creation of new snags yielded a net loss of only 12%. We found proportionally more useable snags lost after fire on plots burned once with 56% (2.8 ha^{-1}) of useable snags lost and, after adding new snags, 34% (1.7 ha^{-1}) lost. Following prescribed fire, Horton and Mannan (1988) found smaller losses of preferred snags (0.5 ha^{-1}) and proportionally fewer preferred snags lost. All our results are confined to within 2 years of burning and over time more snags may replace those lost, but more snags may fall as well. Harrington (1996) found 75–80% of new snags fell within 10 years after prescribed fire. We found most snags lost were ponderosa pine and/or of larger than average diameter, a finding consistent with Horton and Mannan (1988), though under natural conditions larger diameter snags generally have lower fall rates (Keen, 1955).

A net loss of 1.7 preferred nesting snags ha^{-1}, while not insignificant, should be considered in the context of bird population densities and local snag populations. The density of cavity-nesting species in the Sierra Nevada may range from 0.5 to 1.6 pairs ha^{-1} (Raphael and White, 1984); thus, on average, an individual pair may experience the loss of two snags potentially useable for nesting immediately following fire. The effects of this loss will depend on local snag and tree availability as well as the local suite of cavity-nesting birds.

While net losses of all snags in our study were ≤2 snags ha^{-1}, there was considerable variation among plots burned once and most of the new snags were from one plot that experienced a large increase in number of snags (all ponderosa pine) due to attack by bark beetles. Without this event, prescribed fire would have resulted in a much larger overall loss of snags including those preferred by cavity-nesting birds (52% net loss on the remaining two plots burned once). While it is likely that the infestation was related to burning, a single patch of snags, regardless of the number of snags within the patch, will benefit birds only within a limited area. In addition, snags created through insect outbreaks are sometimes removed for forest management purposes and so, despite the potential benefits, are additionally vulnerable to loss from the ecosystem.

5. Management implications

Despite the patchy distribution and the dynamic nature of snag populations, researchers and forest managers have created guidelines for recommended density of snags for wildlife (e.g. Balda, 1975; Raphael and White, 1984; Brawn et al., 1987). The amended Sierra Nevada Forest Plan calls for retention of 10 of the largest snags ha^{-1} in the vegetation type of the study area (USDA Forest Service, 2003). Schreiber and DeCalesta (1992) recommend 14 snags ha^{-1} of types preferred by cavity nesters. While we found an average of 19.5 snags ha^{-1} (>20 cm dbh) across all sites, there were only 5.2 snags ha^{-1} overall that had characteristics chosen by snag-nesting species, and thus only a portion of the available snags will be suitable for nesting at any one time. We agree with others who have criticized the snag density approach for managing wildlife (Morrison and Raphael, 1993; Zack et al., 2002; Spiering and Knight, 2005), and instead emphasize the process of snag selection as well as dynamics of snag populations. Forest management strategies that affect tree species composition, tree mortality, and tree size will affect snag availability and, consequently, snag-nesting species. Our results suggest that forest managers can improve availability of useable snags by retaining large trees (both living and dead), and preferred species (ponderosa pine in our area). In addition, because we found the largest losses of snags on plots burned once, protection of preferred snags may be warranted during proposed burning after long fire-free intervals, particularly in areas where snags are limited.

Acknowledgments

Financial support for this project was provided by the USDA Forest Service, Pacific Southwest Research Station, the Joint Fire Sciences Program, a U.S. Dept. of Education GAANN fellowship, and the University of California Chancellor's Distinguished Fellowship. Sandpiper Technologies, Inc. generously provided use of an extendible video camera system (TreePeeper©). The manuscript was improved by suggestions from W. Laudenslayer, Jr., M. Morrison, M.G. Raphael, and four anonymous reviewers. S. Mori provided statistical advice. Field assistance was provided by K. Bush, C. Caris, S. Deal, D. Drynan, S. Ebrahim, A. Fogg, C. Gustavarow, J. Hartwig, E. Keenan, J. Lindsey, K. Mazzocco, R. Miller, S. Moore, L. Nason, L. Nicolas, S. Moore, R. Olsen, L. Nicolas, C. Seck, M. Seeley, D. Smith, S. Sutton-Mazzocco, R. Swanberg, K. Thumlert, J. Turner, and V.Wible.

References

Balda, R., 1975. The Relationship of Secondary Cavity Nesters to Snag Densities in Western Coniferous Forests. Forest Wildlife Habitat Technical Bulletin 1. U.S. Department of Agriculture, Forest Service, Southwest Region, Albuquerque, NM.

Bednarz, J., Ripper, D., Radley, P., 2004. Emerging concepts and research directions in the study of cavity-nesting birds: keystone ecological processes. Condor 106, 1–4.

Bevis, K., Martin, S., 2002. Habitat preferences of primary cavity excavators in Washington's East Cascades. In: Laudenslayer, Jr., W., Shea, P., Valentine, B., Weatherspoon, C., Lisle, T. (Technical coordinators), Proceedings of the Symposium on the Ecology and Management of Coarse Woody Debris in Western Forests. USDA Forest Service General Technical Report, PSW-GTR-181, pp. 207–221.

Blewett, C., Marzluff, J., 2005. Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. Condor 107, 678–693.

Bock, C., Lynch, J., 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72, 182–189.

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

Bull, E., 2002. The value of coarse woody debris to vertebrates in the Pacific Northwest. In: Laudenslayer, Jr., W., Shea, P., Valentine, B., Weatherspoon, C., Lisle, T. (Technical coordinators), Proceedings of the Symposium on the Ecology and Management of Coarse Woody Debris in Western Forests. USDA Forest Service General Technical Report, PSW-GTR-181, pp. 171–178.

Cline, S., Berg, A., Wight, H., 1980. Snag characteristics and dynamics in Douglas-fir forest, Western Oregon. J. Wildl. Manage. 44, 773–786.

Conway, C., Martin, T., 1993. Habitat suitability for Williamson's Sapsuckers in mixed conifer forests. J. Wildl. Manage. 57, 322–328.

Farris, K., Huss, M., Zack, S., 2004. The role of foraging woodpeckers in the decomposition of ponderosa pine snags. Condor 106, 50–59.

Ganey, J., Vojta, S., 2004. Characteristics of snags containing excavated cavities in Northern Arizona mixed-conifer and ponderosa pine forests. Forest Ecol. Manage. 199, 323–332.

Gruell, G., 2001. Fire in the Sierra Nevada: A Photographic Interpretation of Ecological Change since 1849. Mountain Press, Missoula, MT.

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

Holden, Z., Morgan, P., Rollins, M., Wright, R., 2006. Ponderosa pine snag densities following multiple fires in the Gila Wilderness, New Mexico. Forest Ecol. Manage. 221, 140–146.

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

Jackson, J., Jackson, B., 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor 106, 37–49.

Kauffman, J., 2004. Death rides the forest: perceptions of fire, land use, and ecological restoration of Western forests. Conserv. Biol. 18, 878–882.

Keen, F., 1955. The rate of natural falling of beetle-killed ponderosa pine snags. J. Forest. 53, 720–723.

Linder, K., Anderson, S., 1998. Nesting habitat of Lewis' woodpeckers in southeastern Wyoming. J. Field Ornithol. 69, 109–116.

Martin, K., Aitken, K., Wiebe, K., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia Canada: nest characteristics and niche partitioning. Condor 106, 5–19.

McHugh, C., Kold, T., Wilson, J., 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ. Entomol. 32, 510–522.

McKenzie, D., Gedalof, A., Peterson, D., Mote, P., 2004. Climatic change, wildfire, and conservation. Conserv. Biol. 18, 890–902.

Minnich, R., Barbour, M., Burk, J., Sosa-Ramirez, J., 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. J. Biogeo. 27, 105–129.

Morrison, M., Raphael, M., 1993. Modeling the dynamics of snags. Ecol. Appl. 3, 322–330.

Nilsson, S., 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15, 167–175.

Parks, C., Conklin, D., Bednar, L., Maffei, H., 1997. Field guide for the identification of snags and logs in the interior Columbia River Basin. USDA Forest Service Research Paper, PNW-RP-515.

Randall-Parker, T., Miller, R., 2002. Effects of prescribed fire in ponderosa pine on key wildlife habitat components: preliminary results and a method for monitoring. In: Laudenslayer, Jr., W., Shea, P., Valentine, B., Weatherspoon, C., Lisle, T. (Technical coordinators), Proceedings of the Symposium on the Ecology and Management of Coarse Woody Debris in Western Forests. USDA Forest Service General Technical Report, PSW-GTR-181, pp. 823–834.

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

Saab, V., Powell, H., 2005. Fire and avian ecology in North America: process influencing pattern. Stud. Avian Biol. 30, 1–13.

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

SAS Institute, Inc., 2000. SAS/STAT User's Guide. SAS Institute, Cary, NC.

Schreiber, B., DeCalesta, D., 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. For. Ecol. Manage. 50, 299–316.

Schwilk, D., Knapp, E., Ferrenberg, S., Keeley, J., Caprio, A., 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. Forest Ecol. Manage. 232, 36–45.

Spiering, D., Knight, R., 2005. Snag density and use by cavity-nesting birds in managed stands of the Black Hills National Forest. Forest Ecol. Manage. 214, 40–52.

Stephens, S., 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in Northwestern Mexico. Forest Ecol. Manage. 199, 103–113.

Tabachinick, B., Fidell, L., 1996. Using Multivariate Statistics, 3rd ed. Harper Collins College Publishers, New York.

USDA Forest Service, 2003. Sierra Nevada Forest Plan Amendment. Pacific Southwest Region R5-MB-019.

Zack, S., George, T., Laudenslayer, Jr., W., 2002. Are there snags in the system? Comparing cavity use among nesting birds in "snag-rich" and "snag-poor" Eastside pine forests. In: Laudenslayer, Jr., W., Shea, P., Valentine, B., Weatherspoon, C., Lisle, T. (Technical coordinators), Proceedings of the Symposium on the Ecology and Management of Coarse Woody Debris in Western Forests. USDA Forest Service General Technical Report, PSW-GTR-181, pp. 207–221.