Experimental effects of structural enrichment on avian nest survival

Matthew E. Hane [a,1], Andrew J. Kroll [b,*], Josh R. Johnson [c], Mike Rochelle [c], Edward B. Arnett [d]

[a] Weyerhaeuser NR, PO Box 275, Springfield, OR 97477, USA
[b] Weyerhaeuser NR, WTC 1A5, PO Box 9777, Federal Way, WA 98063-9777, USA
[c] Weyerhaeuser NR, Lebanon, OR 97355, USA
[d] Bat Conservation International, Austin, TX 78746, USA

ABSTRACT

Managers of landscapes dedicated to commodity production require information about how alternative practices can promote retention of native biological diversity. Retaining or creating structural features (e.g., snags or downed logs) needed to fulfill life history requirements may benefit populations and communities. However, demographic responses of species to alternative practices have received little research attention. We tested nest survival of cavity-dependent birds in response to experimental structural enrichment by creating snags on 28 plots, Oregon, USA, 2008–2010. Each plot represented one of six combinations of created snag density (0.5, 1, and 2 snags/ha) and spatial dispersion (clumps of 5–7 snags or dispersed individual snags). We monitored 506 nests built by 10 species; three species nested in sufficient numbers for analysis. Chestnut-backed chickadee *Poecile rufescens* nest success was highest in the medium density clumped created snag treatment (average proportion of successful nests = 0.76; 95% CI = 0.61–0.87) and lowest in the low density clumped treatment (average proportion of successful nests = 0.39; 95% CI = 0.20–0.62). We did not find a response of either house wren *Troglodytes aedon* or northern flicker *Colaptes auratus* nest success to the experimental treatments. Period survival rates were 0.57 (95% CL: 0.39–0.72) for CBCH; 0.71 (95% CL: 0.51–0.84) for HOWR; and 0.59 (95% CL: 0.34–0.77) for NOFL. Our study suggests that creating snags in commercial harvest units is an effective practice for increasing structural complexity and supporting nesting communities of cavity-dependent birds. While leaving either clumped or dispersed created snags at a density of ∼1 ha should support nest survival rates that are similar to those reported from unmanaged forests, we emphasize that this type of structural enrichment is not a panacea for species that require very large snags or snags that occur under complex forest canopies. Retention of existing structural features in reserve areas may be an appropriate practice for conserving species with nesting requirements that differ from those we evaluated in our study.

1. Introduction

The rising global demand for commodities and increased rates of resource consumption have necessitated the intensive management of landscapes (Berlik et al., 2002). Intensive management has potentially dire consequences for the maintenance of biological diversity and ecosystem functions, and managers require information to promote positive ecological outcomes and ameliorate deleterious practices where and when they occur (Bunnell et al., 2002; Brockerhoff et al., 2008). For example, intensive forest management often results in simplified habitats, as maximizing woody biomass of favored commercial species is the primary management objective (Bailey and Tappeiner, 1998; Hayes et al., 2005).

In these situations, alternative silvicultural prescriptions may create new, or modify existing, habitat structures to increase retention of native wildlife populations (Chambers et al., 1999; Walter and Maguire, 2005). So-called "structural enrichment" (Rosenvald and Lõhmus, 2008) is generally thought to yield positive conservation outcomes and, in some areas, to be critical for maintaining local populations where intensive management has reduced the amount of natural habitat structures (Franklin et al., 2002; McKenny et al., 2006). However, relatively few structural enrichment prescriptions are directed to yield specific ecological outcomes (e.g., increased productivity or survival of a target species) or monitored over long time frames, thereby limiting confidence in their effectiveness (Rosenvald and Lõhmus, 2008).

Both snags (dead, standing trees) and live trees with cavities are prominent components of forests worldwide, providing nesting, roosting, and foraging substrates for up to one-third of forest species (Thomas et al., 1979; Neitro et al., 1985; Cockle et al., 2011), 11% of which are obligate cavity nesting birds (Newton, 1994).

* Corresponding author. Tel.: +1 253 924 6580.
  E-mail addresses: matt.hane@weyerhaeuser.com (M.E. Hane), aj.kroll@weyerhaeuser.com (A.J. Kroll).
  [1] Tel.: +1 253 924 6753; fax: +1 253 924 4380.

Industrial forest management creates landscapes where snag densities are often far lower than on unmanaged forests (Wisdom and Bate, 2008; Liira and Sepp, 2009; Politi et al., 2010). As a mitigation practice, green trees may be retained after harvest, with the intention that they will develop into large trees and snags (Chambers et al., 1999; Busby et al., 2006).

Alternatively, nest boxes, artificial snags, and cavity construction in live trees may be used to supplement cavity nesting populations when snags are substantially reduced in number and distribution (Gano and Mosher, 1983; Kerr, 1999; Spring et al., 2001). However, these techniques may not accommodate the needs of all species in the cavity-dependent community (Cade and Temple, 1994; Woodley et al., 2006). Also, with the exception of nest boxes, demographic responses to these practices have received little research attention. Our objectives were to examine (1) how experimental structural enrichment of managed forest stands with created snags influenced nest survival and (2) how nest survival varied by nesting stage. We used a general linear model to evaluate main treatment effects (density and dispersion of created snags in experimental units) and a general linear mixed model to evaluate temporal variation in avian nest survival (Grant et al., 2005; Kroll and Haufler, 2009). We expected that nest survival would be highest in the high density treatment, regardless of dispersion, as this prescription will offer more foraging opportunities to provision nestlings.

2. Methods

2.1. Study site and experimental design

We conducted our study on land owned by Weyerhaeuser Company, Fruit Growers Supply Company, and Giustina Resources near Cottage Grove, Oregon, USA (Fig. 1). The study area occurred at the junction of the Western Cascades and Coast Range Physiographic Provinces (Franklin and Dyrness, 1988). Elevations ranged from 180 m to 1375 m. Planted stands of Douglas-fir (*Pseudotsuga menziesii*) dominated the study area but other conifers were present including western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Red alder (*Alnus rubra*) was abundant in riparian areas and disturbed sites. Understory vegetation was typically dominated by Himalayan blackberry (*Rubus armeniacus*), thimbleberry (*Rubus parviflorus*), salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), and swordfern (*Polystichum munitum*). Since the mid 1960s, these forests have been managed primarily for high-yield timber production by planting of nursery-grown seedlings, fertilization, control of competing deciduous vegetation, precommercial and commercial thinning, and clearcutting on 45–60 year rotations. At the landscape level, primary growth and mature 2nd growth conifer forests (aged 40–330 years old) were interspersed with riparian reserves and other inoperable areas, recent clearcuts, and small gaps associated with streams, steep topography, and roads.

We used a completely randomized design with harvest unit as the experimental unit. All scheduled 1997–1999 clearcut harvest units >20 ha and with >50% of the unit available for harvesting with ground-based equipment were considered available for the study. The random distribution of treatments occurred across an elevational gradient of ~1200 m. We defined treatments by snag density [expressed as trees per ha (TPH)] and dispersion (dispersed versus clumped) (Fig. 2). We subjectively defined three different density levels (low, 0.5 TPH; medium, 1 TPH; and high, 2 TPH) based on coordination with operations foresters and compromises based on logistical, safety, and financial considerations. These densities were multiplied by the size (ha) of each harvest unit to derive a target number of created snags. Clumps constituted 5–7 trees/

clump with trees no greater than 10 m apart from one another. For example, a 40 ha unit assigned the high density/dispersed treatment would have 80 individual trees dispersed across the unit; the high density/clumped treatment would have ~14 clumps created in the unit.

Operators used a feller-buncher to create snags by raising the saw and topping a tree as high as the machine could safely extend (generally 5–10 m high). We instructed operators to target trees with minimum dimensions of >30.5 cm diameter at the top of the tree and >6 m high. Operators created 1111 snags on 28 experimental harvest settings ($\bar{x}$ = 34.6 ha; SE = 1.7; range: 21.6–50.2 ha) in the study area from February 1997 to April 1999 (see Arnett et al., 2010 for additional details). Seven hundred and eighty-five snags were Douglas-fir (80%), 111 were western hemlock (11%), 51 were western red cedar (5%), 34 were unknown conifer (3%) and 5 were hardwood (1%). The desired equal replication of all treatment combinations was not quite achieved, resulting in 4 low clumped (LC), 6 low single (LS), 4 medium clumped (MC), 5 medium single (MS), 4 high clumped (HC), and 5 high single (HS) harvest units (n = 28).

2.2. Data collection

We monitored nest survival from April–August in 2008–2010. Daily monitoring began at dawn and continued throughout the day (Ralph et al., 1993). On occasion, monitoring was conducted for several hours prior to dusk if nearby harvest operations created safety concerns or excessive noise. Each stand was visited at least once per week throughout the sampling season. We used audio and visual clues to locate nesting attempts in created snags. An average of 5 min was spent watching each snag to identify active nests. Active nests were visited more frequently (every 4–6 days) and monitored for up to 30 min or until nest stage was determined. Monitoring was not conducted during periods of heavy rain or wind. In order to minimize risk of nest predation, we did not mark snags that contained active nests or observation points.

We viewed contents of cavities up to 10 m above ground with a custom cavity camera (patterned after a design in Huebner and Hurteau, 2007); every nest that we detected was accessible for monitoring, but some cavity openings were too small for the camera to enter. For those nests in cavities that were too small for visual monitoring, we determined nest stage by adult behaviors (e.g., construction of cavity, male feeding female, both adults feeding young). We categorized nest stage as building, laying, incubation, nestlings, or fledged. We attempted to check each nest at least once a week until nest fate was determined. A nest was considered successful if ⩾1 young were observed leaving the nest cavity, if ⩾1 young observed in close proximity to the created snag, or if young were absent from the cavity at the predicted time of fledging and the cavity showed no obvious signs of disturbance or damage. We recorded nests as depredated if all eggs or young were gone before the anticipated time of fledging or if the cavity displayed obvious signs of disturbance and damage.

2.3. Statistical analyses

We conducted two different analyses with the nest monitoring data. First, the experimental unit in our study was a harvest unit, and the individual nests were sub-samples taken from each unit. To remain consistent with the experimental design, we modeled the proportion of successful nests in each harvest unit as a function of the six treatment types with a generalized linear model using a logit link. The binary response was the total number of successful nests out of the total number of nest attempts for each species on each harvest unit in each year. We examined Type III chi-square tests to determine the significance of treatment effects. In addition,
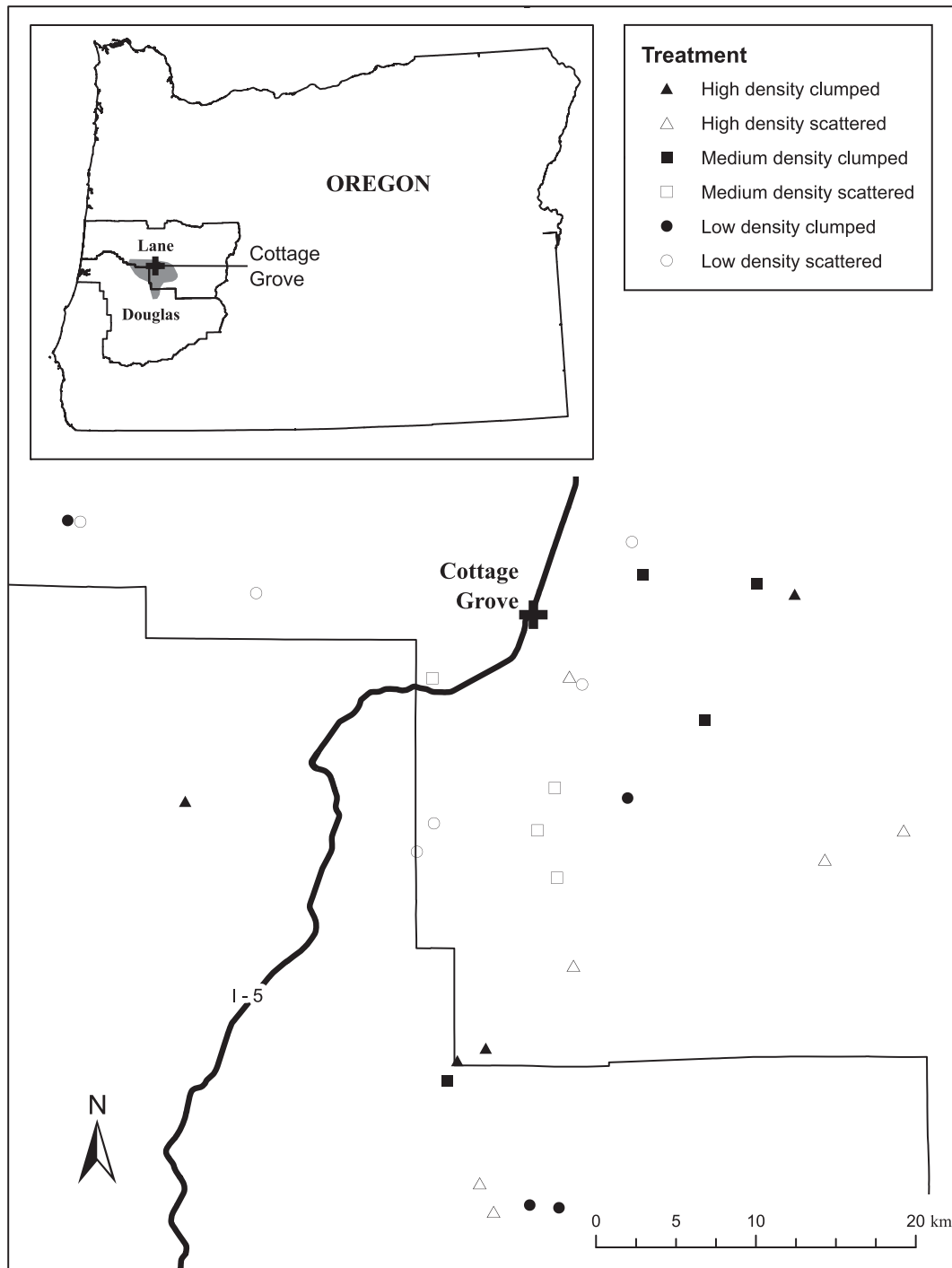
Fig. 1. Location of 28 units with created snags, by treatment type, in Lane and Douglas Counties, Oregon, USA. The shaded area in the inset map shows the general study area location.

we used orthogonal contrasts to further divide the treatment effect into its components of density, distribution, and the interaction between density and distribution. We used least-squares means (SAS Institute, 2004) to estimate means, standard errors, and 95% confidence intervals for the treatment and age effects. We calculated means on the logit scale and back-transformed these to the percent scale. We fit these models with PROC GENMOD (SAS Institute, 2004).

In the second analysis, we treated individual nests as the sample unit in order to examine covariates that influenced daily nest survival rates. We used the logistic-exposure method (Shaffer, 2004) which model estimates daily nest survival probabilities as a logistic function of the values of independent covariates on a given day. The two assumptions of this method are that nest fates are independent of each other (i.e., the fate of a nest is not influenced by the fate of other nests) and that daily nest survival probabilities are equivalent among nest-days that have equal values of explanatory covariates. In this analysis, each interval between visits to a nest was treated as one observation. We calculated period-survival rates (PSR, laying + incubation + nestling stages; Shaffer and Thompson, 2007) and defined period lengths based on the average length for each stage from all successful nests
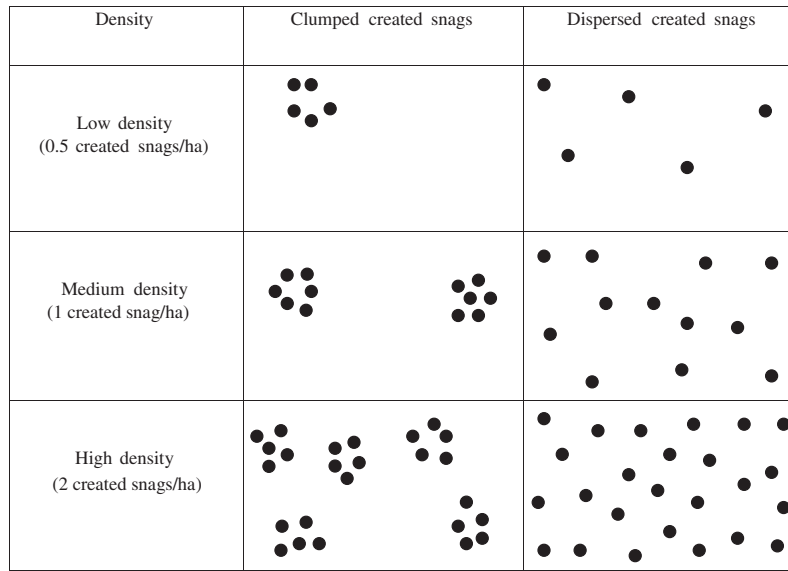
Density	Clumped created snags	Dispersed created snags
Low density (0.5 created snags/ha)		
Medium density (1 created snag/ha)		
High density (2 created snags/ha)		

Fig. 2. Density and spatial arrangement of created snags in each of six treatment types, Cottage Grove, Oregon, USA, 2008–2010.

observed in our study. We incorporated nest stage as a fixed effect in our models as avian behavior can change during the different nesting stages and influence nest survival (Martin et al., 2000). We combined the building and laying stages for analysis. We treated both year and plot as random effects in our model, since both covariates can be considered to have been drawn from larger populations. We fit nest-survival models with PROC GLIMMIX (SAS Institute, 2004) using a logit-link function. We examined confidence intervals for parameter estimates and graphed fitted values as a function of the independent covariates (Hosmer and Lemeshow, 2000; Shaffer and Thompson, 2007).

3. Results

One thousand and twelve of the 1111 (91%) snags created from 1997 to 1999 were standing in 2008. Average diameter at breast height of all 1012 created snags was 49.7 cm (SE = 1.7, range = 17.8–101.1) and average height was 6.5 m (SE = 0.1, range = 3.7–10.1). Diameter at breast height (n = 28, $F_{5,22}$ = 0.79, P = 0.57) and snag height (n = 28, $F_{5,22}$ = 1.12, P = 0.38) did not differ among treatments.

We monitored 506 nests from 10 species (Appendix S1). We found sufficient numbers of nests to conduct survival analysis for chestnut-backed chickadee *Poecile rufescens* (CBCH; n = 235 nests), house wren *Troglodytes aedon* (HOWR; n = 109 nests) and northern flicker *Colaptes auratus* (NOFL; n = 63 nests). We did not find any HOWR nests in the LC treatment. We found only 3 NOFL nests in the LC and LS treatments combined, so we did not include these treatments in the treatment analysis for NOFL. We found less than 20 nests for each of the other seven species and did not consider these for analysis (Hensler and Nichols, 1981). Average interval between nest visits was 6 days (SE = 0.03). Average period lengths (building/laying, incubation, and nestling) were 51 days for CBCH (18, SE = 0.52; 16, SE = 0.48; 17, SE = 0.36); 51 days for HOWR (18, SE = 1.6; 17, SE = 1.04; 16, SE = 0.85), and 49 for NOFL (12, SE = 1.01; 18, SE = 0.78; 19, SE = 0.97).

We found a significant effect of treatment type (χ^2 = 14.12, P = 0.02) on proportion of successful nests for CBCH. The proportion of successful nests was highest in the MC treatment and lowest in the LC treatment (Fig. 3). Using the contrasts for treatment type, we did not find significant effects for the interaction of distribution and density of snags (χ^2 = 6.0, P = 0.05) or distribution of

snags (χ^2 = 1.8, P = 0.18). However, we did find a significant effect of snag density (χ^2 = 8.6, P = 0.01), with the proportion of successful nests highest in the medium density treatment and lowest in the high density treatment.

We did not find a significant effect of treatment type (χ^2 = 5.12, P = 0.27) on proportion of successful nests for HOWR. The proportion of successful nests was highest in the HC treatment and lowest in the MS treatment (Fig. 3). Using the contrasts for treatment type, we did not find significant effects for the interaction of distribution and density of snags (χ^2 = 0.75, P = 0.39), distribution of snags (χ^2 = 0.9, P = 0.34), or density of snags (χ^2 = 4.47, P = 0.11).

We did not find a significant effect of treatment type (χ^2 = 3.87, P = 0.28) on proportion of successful nests for NOFL. The proportion of successful nests was highest in the HS treatment and lowest in the HC treatment (Fig. 3). Using the contrasts for treatment type, we did not find significant effects for the interaction of distribution and density of snags (χ^2 = 2.23, P = 0.14), distribution of snags (χ^2 = 1.82, P = 0.18), or density of snags (χ^2 = 0.08, P = 0.78).

We found significant effects of nest stage for CBCH (n = 235, $F_{2,1444}$ = 12.82, P = 0.0001), but not for HOWR (n = 109, $F_{2,601}$ = 2.45, P = 0.09) or NOFL (n = 63, $F_{2,325}$ = 0.35, P = 0.71). For both CBCH and HOWR, nest survival increased across the nesting cycle (nestling > incubation > building/laying); for NOFL, nest survival was lowest during the incubation stage (Fig. 4). Period survival rates from the nest stage model were 0.57 (95% CL: 0.39–0.72) for CBCH; 0.71 (95% CL: 0.51–0.84) for HOWR; and 0.59 (95% CL: 0.34–0.77) for NOFL (Fig. 4). Average daily and period survival from the constant survival model were 0.989 (95% CL: 0.965–0.996) and 0.58 (95% CL: 0.16–0.85) for CBCH; 0.994 (95% CL: 0.985–0.997) and 0.73 (95% CL: 0.46–0.88) for HOWR; and 0.989 (95% CL: 0.973–0.996) and 0.59 (95% CL: 0.27–0.81) for NOFL.

4. Discussion

Large-scale field experiments can support strong inference about operational practices that balance commercial extraction of resources and conservation of wildlife communities. For example, intensive management of forest stands can reduce the number and distribution of structural features such as snags and downed logs, thereby reducing habitat quality for organisms that rely on these features (Hayes et al., 2005). However, implementing beneficial practices at the landscape scale represents a significant
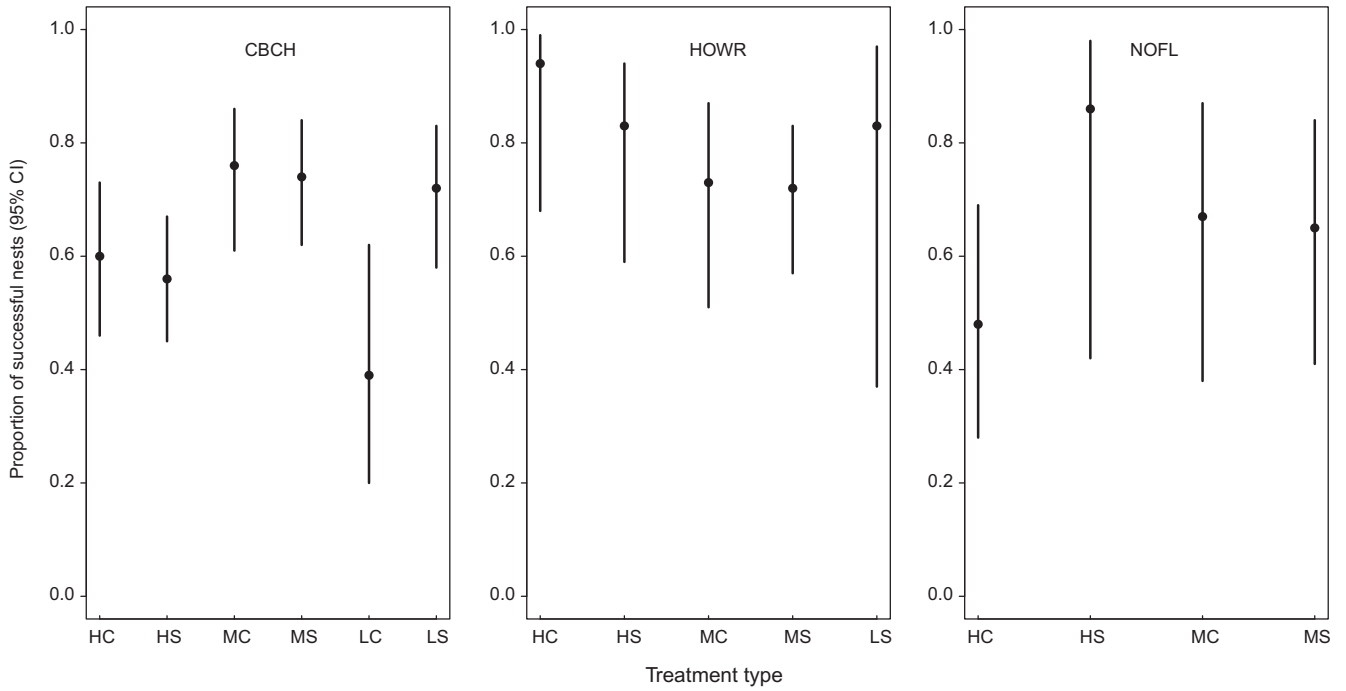
Fig. 3. Estimated proportion of successful nests and 95% confidence intervals for CBCH, HOWR, and NOFL by treatment type, Cottage Grove, Oregon, USA, 2008–2010. Treatment types are high clumped (HC), high single (HS), medium clumped (MC), medium single (MS), low clumped (LC), and low single (LS).
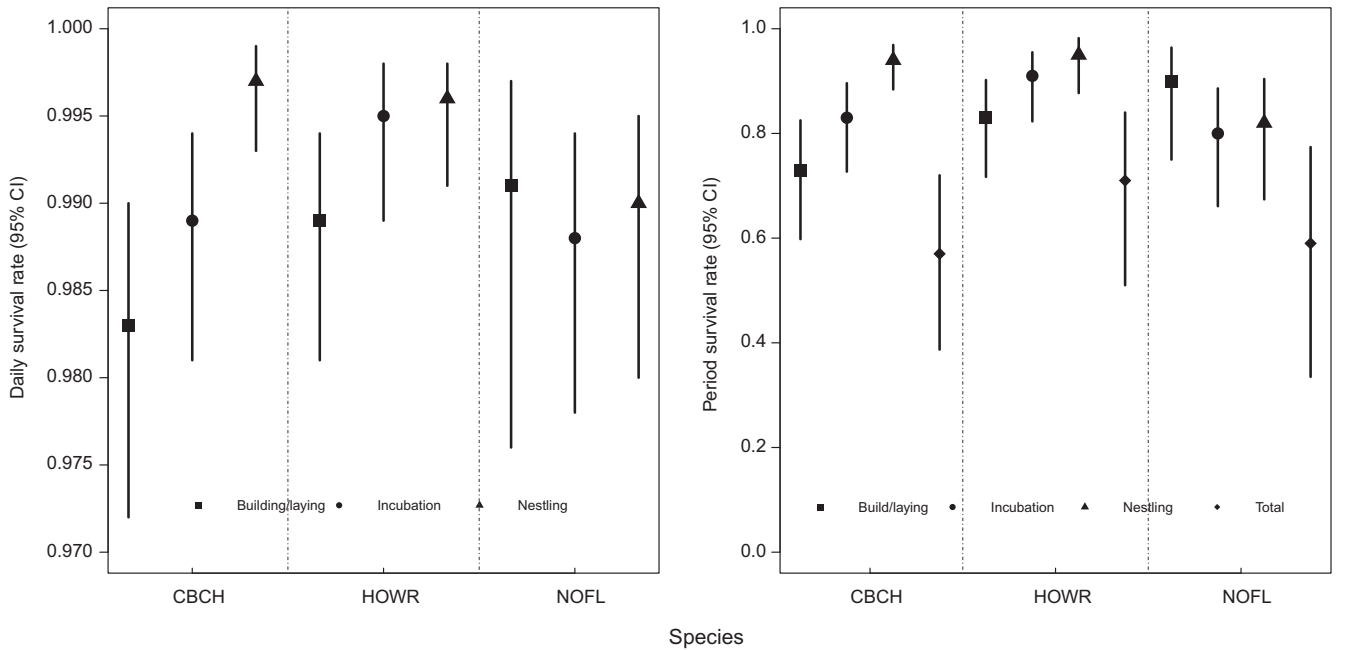

Fig. 4. Estimated daily and period survival rates and 95% confidence intervals for CBCH, HOWR, and NOFL by nest stage and in total, Cottage Grove, Oregon, USA, 2008–2010. Estimates were derived from a mixed-effects model with nest stage as a fixed effect and year and study plot as random effects. Note that scaling of *y*-axis differs on each figure.

logistical challenge because traditional practices (such as nest boxes) are not implemented in conjunction with forestry operations. Also, demographic responses of target populations to these practices are rarely monitored, leading to substantial uncertainty about their ecological benefits, especially in comparison to unmanaged habitats.

In our study, nest survival for the three primary species utilizing created snags was generally similar to or higher than survival rates reported for these species, suggesting that created snags may be equivalent substitutes for natural snags. For example, both Mahon and Martin (2006) and Sperry et al. (2008) reported period survival rates for CBCH that were <50%. While we estimated that period survival rates were <50% for only the low and high density treatments in 2010 (Kroll et al., unpub. data), we note that the 2010 breeding season was characterized by uncommonly low temperatures and high precipitation in our region (Western Regional

Climate Center, 2011) that may have reduced nest survival (Pasinelli, 2001). Published period survival rates for HOWR vary from 0.63 in natural cavities to 0.83 in nest boxes (Finch, 1989, 1990; Li and Martin, 1991; Johnson and Kermott, 1994; Purcell et al., 1997); our estimate fell in the middle of that range. Finally, survival rates of NOFL vary substantially by habitat type and management regime. For example, Saab et al. (2007) reported average nest survival rates of ∼0.65 in both unlogged burned forests and partially logged burned forests; Vierling et al. (2008) reported nest success for NOFL ranging from 50% in a low severity burn to 100% in a high severity burn; Fisher and Wiebe (2007) reported period survival of ∼0.65 in an unmanaged forest; and Kozma and Kroll (2012) reported period survival rates of 0.41 in unburned forests and 0.80 in burned forests. We note that comparison with available estimates is the best way to gauge the effectiveness of created snags, as a relevant control is difficult to define. For example, a control with no created snags is not suitable, as substrates are not available for cavity-nesting birds. The most relevant control is a young stand that was created by a natural disturbance that removed the majority of the forest canopy but left residual structures to be used by cavity-nesting birds (or turned into created snags). However, this type of stand was not available in our study area. Also, natural disturbances cannot be manipulated experimentally, so inclusion of these as controls in experimental designs is challenging.

We did not find strong treatment effects on nest survival. Raphael and Morrison (1987) recommended leaving snags in clumps to meet nesting and foraging requirements, in part because natural snags are typically found in clumps (Bull et al., 1997 although see Harmon et al., 2004). In addition, clumping snags may be more practical when one considers operational factors such as efficiency of creation, equipment operation, and logistics of monitoring (Chambers et al., 1997). However in situations where cavities are limited or clustered, negative interactions can be more evident (Bull et al., 1997; Walter and Maguire, 2005). For example, Kroll et al. (2012) found that the percentage of created snags used for nesting in this study was lower in clumped than dispersed snags. In addition, we note that the territorial nature of cavity-nesting birds may have hindered our ability to gather a sufficient sample size to test treatment effects. Clearly, the sample size was inadequate for 7 of the 10 species that we found nesting in created snags. Given both the territorial nature of cavity-nesting birds and the lack of sufficient samples to test the treatment across all species, we suggest that a conservative approach to implementing the practices that we evaluated is to distribute created snags in both clusters and individually within each harvest unit, and to do so while varying density. As a whole, this application should support nest survival rates similar to what we observed in our study.

Differences in nest survival between (Peak et al., 2004; Grant et al., 2005, this study) and within stages (Cresswell, 1997) may reflect proximate responses to selective pressures (Martin et al., 2000, 2006) that vary across the nesting cycle and nesting season. Past efforts have focused on modeling variation in nesting survival due to vegetation characteristics, although other studies suggest that additional factors, including parental and nestling activity, may have separate and interactive effects with vegetation features (Martin et al., 2000). Habitat conditions, individual responses to current limiting factors including food and predators, and prior experience may influence avian nest survival. Stage-specific covariates may incorporate variation from these factors into nest survival models, but fail to portray the wide array of interactions displayed in avian nest survival patterns.

In a review of structural retention practices, Bunnell et al. (2002) suggested leaving 12–23 snags/ha in managed conifer forests. In our study area, researchers have reported variable snag densities required for maintaining cavity-nesting bird communities, ranging from 0.3 snags/ha (Neitro et al., 1985) to 14 snags/ha (Schreiber and deCalesta, 1992). Although, and not while we evaluated created snags at densities on the lower end of this range, we note that rotation age stands in the landscape where we conducted our study contain an average of 3.4 snags/ha (95% CI: 1.2–5.5) greater than 36 cm in diameter (Kroll et al., unpub. data), an amount ∼70% greater than the highest density that we evaluated experimentally. Clearly, created snags provide relatively high quality (as measured by nest survival) nesting substrates for some species at relatively low densities (although we found an effect of snag density on nest survival for only CBCH). Additional research is needed to determine what densities of created snags are required to support nesting populations of cavity-dependent birds that occur in our study area but which we observed in very low numbers. However, we note that regenerating harvest stands may lack other structural features that are required by these species (e.g., well-developed canopies).

Nest boxes are often used to provide nesting structures for cavity-dependent organisms, and can be critical management tools for target populations (Lalas, 1999; Citta and Lindberg, 2007). However, nest boxes can be expensive to install and maintain (McKenney and Lindenmayer, 1994) and are unlikely to be distributed at spatial and temporal scales required to support communities of cavity-dependent organisms (Lindenmayer et al., 2009). A snag created from a live tree will provide a superior ecological subsidy over time compared to a nest box, as it serves as habitat for a wide range of vertebrates and invertebrates in each stage of decay and as a downed log (Thomas et al., 1979; Maser and Trappe, 1984). Our method also eases operational and economic planning for structural enrichment. Snags are created when a stand is harvested, and managers can emphasize snag creation when log costs are least restrictive (the only lost revenue from a created snag is the bottom log of the tree from which the snag is created).

Finally, the amount of intensively managed forest is increasing to meet the growing global demand for wood products and other ecological services (Binkley et al., 2005; Carnus et al., 2006). Intensive management limits structural complexity and reduces habitat quality for organisms that utilize forest structures to meet life history requirements. Our results suggest that created snags could ameliorate some negative consequences of increased management intensity. However, despite the potentially numerous advantages of this method, created snags are not a panacea. Additional research is needed to determine how created snags can be deployed to provide habitat for diverse communities of snag- and cavity-dependent organisms in plantation forests worldwide (Rosenvald and Lõhmus, 2008; Paquette and Messier, 2010), although options will be necessarily constrained by management regimes implemented to maximize wood production (i.e., rotation age of harvest units). In the most intensively managed landscapes, retention of existing mature forest structures (e.g., in riparian areas or on unstable slopes) will likely be critical for the conservation of intact communities of snag- and cavity-dependent species.

5. Management implications

Structural enrichment is often proposed as a management tool to promote species retention on intensively managed landscapes although relatively little information is available about demographic responses to different practices. Our results indicate that creating snags from harvest age trees will provide nesting substrates that support avian nest survival rates comparable to those in natural snags. We found effects of either created snag distribution (clumped or dispersed) or created snag density on nesting survival for only one species. However, we evaluated a relatively limited range of densities, and additional research is needed to

determine the effect of higher densities of created snags on breeding populations of cavity-dependent birds, as well as other taxa. Creating snags from live trees will provide substantially more benefits than nest boxes or other artificial structures, as created snags will provide habitat throughout their life cycle. Finally, our method has the potential to be applied in the growing number of intensively-managed forests worldwide, many of which are likely to contain limited amounts of habitat for snag-dependent organisms (Nájera and Simonetti, 2010). However, some organisms rely on snags larger than harvest age trees or other forest structural features not found in managed forests, and we note that other practices and policies will be required to maintain the entire community of cavity-dependent organisms (Cockle et al., 2011).

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.06.037.

References

Arnett, E.B., Kroll, A.J., Duke, S.D., 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. Forest Ecology and Management 260, 1773–1779.

Bailey, J.D., Tappeiner, J., 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. Forest Ecology and Management 108, 99–113.

Berlik, M.M., Kittredge, D.B., Foster, D.R., 2002. The illusion of preservation: a global environmental argument for the local production of natural resources. Journal of Biogeography 29, 1557–1568.

Binkley, C.S., Aronow, M.E., Washburn, C.L., New, D., 2005. Global perspectives on intensively managed plantations: implications for the Pacific Northwest. Journal of Forestry 103, 61–64.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17, 925–951.

Bull, E.L., Parks, C.G., Torgersen, T.R., 1997. Trees and Logs Important to Wildlife in the Interior Columbia River Basin. U.S. Department of Agriculture, Forest Service, Portland, OR, p. 55.

Bunnell, F.L., Boyland, M., Wind, E., 2002. How should we spatially distribute dead and dying wood? In: Laudenslayer, W.F. Jr., Shea, P.J., Valentine, B.F., Weatherspoon, C.P., Lisle, T.E. (Eds.), Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests. Gen. Tech. Rep. PSW-GTR-181, Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Albany, CA, USA, pp. 739–752.

Busby, P., Adler, P., Warren, T., Swanson, F., 2006. Fates of live trees retained in forest cutting units, western Cascade Range, Oregon. Canadian Journal of Forest Research 36, 2550–2560.

Cade, T.J., Temple, S.A., 1994. Management of threatened bird species: evaluation of the hands on approach. Ibis 137, S161–S172.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. Journal of Forestry 104, 65–77.

Chambers, C.L., Carrigan, T., Sabin, T.E., Tappeiner, J., McComb, W.C., 1997. Use of artificially created Douglas-fir snags by cavity-nesting birds. Western Journal of Applied Forestry 12, 93–97.

Chambers, C.L., McComb, B.C., Tappeiner II, J.C., 1999. Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. Ecological Applications 9, 171–185.

Citta, J., Lindberg, M.S., 2007. Nest-site selection of passerines: effects of geographic scale and public in personal information. Ecology 88, 2034–2046.

Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Frontiers in Ecology and the Environment 9, 377–382.

Cresswell, W., 1997. Nest predation rates and nest detectability in different stages of breeding in blackbirds Turdus merula. Journal of Avian Biology 28, 296–302.

Finch, D.M., 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. Condor 91, 848–859.

Finch, D.M., 1990. Effects of predation and competitor interference on nesting success of House Wrens and Tree Swallows. Condor 92, 674–687.

Fisher, R.J., Wiebe, K.L., 2007. Nest site attributes and temporal patterns of northern flicker nest loss: effects of predation and competition. Oecologia 147, 744–753.

Franklin, J.F., Dyrness, C.T., 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR, USA.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155, 399–423.

Gano Jr., R.D., Mosher, J.A., 1983. Artificial cavity construction – an alternative to nest boxes. Wildlife Society Bulletin 11, 74–76.

Grant, T.A., Shaffer, T.L., Madden, E.M., Pietze, P.J., 2005. Time-specific variation in passerine nest survival: new insights into old questions. Auk 122, 661–672.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S.V., Lattin, P.D., Andersen, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Leinkaemper, G.W., Cromack Jr., K., Cummins, K.W., 2004. Ecology of coarse woody debris in temperate ecosystems. In: Caswell, H. (Ed.), Advances in Ecological Research, Elsevier, vol. 34. Oxford, UK, pp. 59–234.

Hayes, J.P., Schoenholtz, S.H., Hartley, M.J., Murphy, G., Powers, R.F., Berg, D., Radosevich, S.R., 2005. Environmental consequences of intensively managed forest plantations in the Pacific Northwest. Journal of Forestry 103, 83–87.

Hensler, G.L., Nichols, J.D., 1981. The Mayfield method of estimating nest success: a model, estimators and simulation results. Wilson Bulletin 93, 42–53.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. John Wiley and Sons, New York, New York, USA.

Huebner, D.P., Hurteau, S.R., 2007. An economical wireless cavity nest viewer. Journal of Field Ornithology 78, 87–92.

Johnson, L.S., Kermott, L.H., 1994. Nesting success of cavity-nesting birds using natural tree cavities. Journal of Field Ornithology 65, 36–51.

Kerr, G., 1999. The use of silvicultural systems to enhance the biological diversity of plantation forestry in Britain. Forestry 72, 191–205.

Kozma, J.M., Kroll, A.J., 2012. Woodpecker nest survival in burned and unburned managed ponderosa pine forests of the northwestern USA. The Condor 114, 1–12.

Kroll, A.J., Duke, S.D., Hane, M.E., Johnson, J.R., Rochelle, M., Betts, M.G., Arnett, E.B., 2012. Landscape composition influences avian colonization of experimentally created snags. Biological Conservation 152, 145–151.

Kroll, A.J., Haufler, J.B., 2009. Age and clutch size variation in Dusky Flycatcher nest survival. Journal of Ornithology 150, 409–417.

Lalas, C., 1999. The design and use of a nest box for yellow-eyed penguins megadyptes antipodes – a response to a conservation need. Marine Ornithology 27, 203–204.

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

Liira, J., Sepp, T., 2009. Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46, 208–325.

Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., Macgregor, C., McBurney, L., Montague-Drake, R., Gibbons, P., 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. Biological Conservation 142, 33–42.

Mahon, C.L., Martin, K., 2006. Nest survival of chickadees in managed forests: habitat, predator, and year effects. Journal of Wildlife Management 70, 1257–1265.

Martin, T.E., Bassar, R.D., Bassar, S.K., Fontaine, J.J., Lloyd, P., Mathewson, H.A., Niklison, A.M., Chalfoun, A.D., 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. Evolution 60, 390–398.

Martin, T.E., Scott, J., Menge, C., 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London B 267, 2287–2293.

Maser, C., Trappe, J.M. (Eds.), 1984. The Seen and Unseen World of the Fallen Tree. Gen. Tech Rep. PNW-164, US Department of Agriculture, Pacific Northwest Forest and Range Experimental Station, Portland, OR, USA.

McKenney, D.W., Lindenmayer, D.B., 1994. An economic assessment of a nest-box strategy for the conservation of an endangered species. Canadian Journal of Forest Research 24, 2012–2019.

McKenny, H.C., Keeton, W.S., Donovan, T.M., 2006. Effects of structural complexity enhancement on eastern red-backed salamander (Plethodon cinereus) populations in northern hardwood forests. Forest Ecology and Management 230, 186–196.

Nájera, A., Simonetti, J.A., 2010. Enhancing avifauna in commercial plantations. Conservation Biology 24, 319–324.

Neitro, W., Mannan, R.W., Taylor, D., Binkley, V.W., Marcot, B.G., Wagner, F.F., Cline, S.P., 1985. Snags (wildlife trees). In: Brown, E.R. (Ed.), Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. US Department of Agriculture, Forest Service, Publication Number R6-F&WL-192-1985, Portland, OR, pp. 129–169.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70, 265–276.

Paquette, A., Messier, C., 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment 8, 27–34.

Pasinelli, G., 2001. Breeding performance of the middle spotted woodpecker Dendrocopos medius in relation to weather and territory quality. Ardea 89, 353–361.

Peak, R.G., Thompson III, F.R., Shaffer, T.L., 2004. Factors affecting songbird nest survival in riparian forests in midwestern agricultural landscapes. Auk 121, 726–737.

Politi, N., Hunter Jr., M.L., Rivera, L., 2010. Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. Forest Ecology and Management 260, 893–906.

Purcell, K.L., Verner, J., Oring, L.W., 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114, 646–656.

Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. Handbook of Field Methods for Monitoring Landbirds. Gen. Tech. Rep. PSW-GTR-144, Pacific Southwest Research Station, US Forest Service, US Department of Agriculture, Albany, CA, USA.

Raphael, M.G., Morrison, M., 1987. Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33, 774–783.

Rosenvald, R., Lõhmus, A., 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. Forest Ecology and Management 255, 1–15.

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

SAS Institute, 2004. The SAS System for Windows, Version 9.1. SAS Institute, Inc., Cary, North Carolina, USA.

Schreiber, B., deCalesta, D.S., 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. Forest Ecology and Management 50, 299–316.

Shaffer, T.L., 2004. A unified approach to analyzing nest success. Auk 121, 526–540.

Shaffer, T.L., Thompson III, F.R., 2007. Making meaningful estimates of nest survival with model-based methods. Studies in Avian Biology 34, 84–95.

Sperry, D.M., Kissling, M.K., George, T.L., 2008. Avian nest survival in coastal forested buffer strips on Prince of Wales Island, Alaska. The Condor 110, 740–746.

Spring, D.A., Bevers, M., Kennedy, J.O.S., Harley, D., 2001. Economics of a nest-box program for the conservation of an endangered species: a reappraisal. Canadian Journal of Forest Research 31, 1992–2003.

Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Snags. In: Thomas, J.W. (Ed.), Wildlife Habitat in Managed Forests. US Department of Agriculture Forest Service, Washington, DC, USA, pp. 60–77.

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

Walter, S.T., Maguire, C.C., 2005. Snags, cavity-nesting birds, and silvicultural treatments in western Oregon. Journal of Wildlife Management 69, 1578–1591.

Western Regional Climate Center, 2011. RAWS United States of America Climate Archive, Willow Creek, OR, Sub-Station. <http://www.raws.dri.edu/cgi-bin/rawMAIN.pl?orOWLL>.

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

Woodley, S.J., Johnson, G., Freedman, B., Kirk, D.A., 2006. Effects of timber harvesting and plantation development on cavity-nesting birds in New Brunswick. Canadian Field-Naturalist 120, 298–306.