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NEST DENSITIES OF CAVITY-NESTING BIRDS IN RELATION TO POSTFIRE SALVAGE LOGGING AND TIME SINCE WILDFIRE

VICTORIA A. SAAB[1,3], ROBIN E. RUSSELL[1], AND JONATHAN G. DUDLEY[2]
[1] *USDA Forest Service, Rocky Mountain Research Station, 1648 S. 7th Ave., MSU Campus, Bozeman, MT 59717*
[2] *USDA Forest Service, Rocky Mountain Research Station, 322 E. Front St., Suite 401, Boise, ID 83702*

Abstract. We monitored the nest densities and nest survival of seven cavity-nesting bird species, including four open-space foragers (American Kestrel [*Falco sparverius*], Lewis's Woodpecker [*Melanerpes lewis*], Western Bluebird [*Sialia mexicana*], and Mountain Bluebird [*S. currucoides*]) and three wood-foragers (Hairy Woodpecker [*Picoides villosus*], Black-backed Woodpecker [*P. arcticus*], and Northern Flicker [*Colaptes auratus*]), after two wildfires (one partially salvage-logged and one unlogged) in western Idaho from 1994–2004. We estimated the relationship between nest density and time since fire, tested for statistical differences in nest densities and nest survival in the partially salvage-logged vs. unlogged wildfires, and tested for differences in nest survival between early (1–4 years after fire) and late (5–12 years after fire) postfire periods. Nest densities of open-space foragers and Northern Flickers generally increased with time since fire, whereas nest densities of Black-backed and Hairy Woodpeckers peaked 4–5 years postfire. Nest densities of wood-foraging species and Mountain Bluebirds were significantly higher in the unlogged burn, whereas Lewis's Woodpeckers had significantly higher nest densities in the partially logged burn. Kestrels tended to favor the partially logged burn, while Western Bluebird nest densities were nearly equal in both burned areas. For most species, postfire period and treatment (partially logged vs. unlogged) had little influence on nest survival. However, Hairy Woodpecker nest survival was significantly lower in the partially logged burn versus the unlogged wildfire in the early postfire period, and Lewis's Woodpecker nest survival was significantly reduced in the later postfire period versus the early postfire period in the partially logged burn. Importantly, the salvage logging was designed to retain more than half of the snags over 23 cm in diameter, which provided suitable nesting habitat for open-space foragers during the decade following fire.

Key words: cavity-nesting birds, nest densities, nest survival, ponderosa pine forests, postfire salvage logging, wildfire.

Densidades de Nidos de Aves que Nidifican en Cavidades con Relación a las Actividades Forestales Después de las Quemas y al Tiempo Transcurrido desde los Incendios Naturales

Resumen. Monitoreamos las densidades y la sobrevivencia de los nidos de siete especies de aves que nidifican en cavidades, incluyendo cuatro especies que se alimentan en zonas abiertas (*Falco sparverius*, *Melanerpes lewis*, *Sialia mexicana* y *S. currucoides*) y tres que se alimentan sobre troncos (*Picoides villosus*, *P. arcticus*, y *Colaptes auratus*), después de dos incendios naturales (uno en una zona con actividades forestales y otro en una zona sin talar) en el oeste de Idaho de 1994 a 2004. Estimamos la relación entre la densidad de los nidos y el tiempo transcurrido desde las quemas, evaluamos estadísticamente las diferencias en la densidad y la sobrevivencia de los nidos entre la zona con actividades forestales y la no talada y evaluamos las diferencias en la sobrevivencia de los nidos entre los períodos tempranos (1–4 años después de las quemas) y los tardíos (5–12 años después de las quemas) posteriores a las quemas. Las densidades de los nidos de las especies que se alimentan en zonas abiertas y de *C. auratus* se incrementaron, de manera general, con el tiempo transcurrido desde las quemas, mientras que las densidades de *P. villosus* y *P. arcticus* alcanzaron su máximo entre cuatro y cinco años después de las quemas. Las densidades de los nidos de las especies que se alimentan sobre troncos y de *S. currucoides* fueron significativamente más altas en zonas no taladas, mientras que *M. lewis* tuvo una densidad de nidos significativamente más alta en las zonas con actividades forestales posteriores a las quemas. *F. sparverius* prefirió las zonas con actividades forestales posteriores a las quemas, mientras que las densidades de los nidos de *S. mexicana* fueron casi iguales en ambas zonas quemadas. Los períodos posteriores a las quemas y el tratamiento (parcialmente talado y no talado) tuvieron poca influencia sobre la sobrevivencia de los nidos de la mayoría de las especies. Sin embargo, la sobrevivencia

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[3] E-mail: vsaab@fs.fed.us

de los nidos de *P. villosus* fue significativamente más baja en las áreas parcialmente taladas que en las no taladas durante los períodos tempranos posteriores a las quemas. La sobrevivencia de los nidos de *M. lewis* fue significativamente menor en los períodos tardíos posteriores a las quemas en comparación con los períodos tempranos en la zona parcialmente talada. Es importante señalar que la zona con actividades forestales posteriores a las quemas fue diseñada para preservar más de la mitad de los tocones de 23 cm de diámetro, lo que proporcionó un hábitat adecuado para la nidificación de las especies que se alimentan en zonas abiertas durante la década subsiguiente a los incendios naturales.

INTRODUCTION

The importance of recently burned forests to breeding cavity-nesting birds is well known (Bock et al. 1978, Raphael and White 1984, Saab and Powell 2005) and densities of cavity-nesters in burned forests change with time since fire (Bock et al. 1978, Apfelbaum and Haney 1981, Hannon and Drapeau 2005). Species that obtain their insect prey from wood, such as the Black-backed Woodpecker (*Picoides arcticus*), rapidly colonize postfire forests and then experience population declines as time since fire increases, presumably due to declines in bark and wood-boring beetles (Bock et al. 1978, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). In contrast, Lewis's Woodpecker (*Melanerpes lewis*), an aerial insectivore, is abundant in both recent burns (2–4 years postfire) and older burns (10–25 years postfire; Bock and Lynch 1970, Linder and Anderson 1998, Saab and Vierling 2001). Other aerial insectivores and open-space foragers (e.g., bluebirds [*Sialia* spp.], flycatchers [*Empidonax* spp.], and swallows [*Tachycineta* spp.]) often use burned forests 10–20 years after fires, potentially in response to improved conditions for aerial foraging following decreases in canopy cover and increases in flying arthropods associated with shrub regrowth (Lowe et al. 1978, Hobson and Schieck 1999, Hannon and Drapeau 2005).

Little is known about the combined effects of postfire salvage logging and time since wildfire on nesting densities of cavity-nesting birds (Hutto 2006). Postfire salvage logging removes snags that provide critical breeding, roosting, and foraging habitat for many taxa (Kotliar et al. 2002, Morissette et al. 2002, Lindenmayer et al. 2004). Studies indicate that wood- and bark-foraging species (e.g., Black-backed and Hairy Woodpeckers [*Picoides villosus*]) favor unlogged burned forests (Haggard and Gaines 2001, Morissette et al. 2002, Saab et al. 2002), whereas some aerial insectivores and other open-space foragers (e.g., Lewis's Woodpecker, Western Bluebird [*Sialia mexicana*], and American Kestrel [*Falco sparverius*]) can use partially logged postfire forests (Saab and Dudley 1998, Haggard and Gaines 2001, Johnson and Anderson 2002). Such relationships might be explained by greater foraging opportunities for wood- and bark-foraging species in unlogged forests due to high snag densities, and more space for aerial foraging maneuvers in openings created by partial salvage-logging.

We examined trends in nest densities of cavity-nesting birds over an 11-year period (1994–2004) after two wildfires in Idaho, one of which was primarily unlogged and one that was partially salvage-logged. We hypothesized that postfire nest densities of cavity-nesting birds would change with time according to expected availability of their primary prey species. We identified three possible trajectories for trends in nest densities: 1) linear (numbers increase over the study period); 2) pseudothreshold (numbers reach a carrying capacity; Franklin et al. 2000); and 3) peaked (numbers peak at four to five years postfire). We expected nest densities of aerial insectivores and open-space foragers (Lewis's Woodpecker, Mountain Bluebird [*Sialia currucoides*], Western Bluebird, and American Kestrel) to increase linearly with time over the 11-year period (Hobson and Schieck 1999, Saab et al. 2004, Hannon and Drapeau 2005), corresponding with increases in shrubs and associated arthropods after fire (Hermann et al. 1998, McCullough et al. 1998). We anticipated that the Northern Flicker (*Colaptes auratus*), a foraging generalist, would increase linearly or exhibit a pseudothreshold trend over the same period, because this species frequently uses logs as a foraging substrate (Moore 1995) and log volumes increase with time since disturbance as snags fall (Mellen and Ager 2002). In contrast, we predicted that nest densities of bark- and wood-foraging specialists

(Black-backed and Hairy Woodpeckers) should closely resemble a peaked pattern, with the peak occurring approximately 4–5 years postfire, corresponding to peaks in beetle densities (Apfelbaum and Haney 1981, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Werner 2002). We predicted that aerial insectivores would prefer the more open partially logged burn, where aerial maneuvers and capture of flying insects might be more efficient, and that bark- and wood-foraging species would prefer the unlogged burn, where higher snag densities should provide greater foraging opportunities.

METHODS

STUDY AREAS AND SURVEY METHOD

We conducted nest surveys at two wildfire sites in western Idaho (43°35′N, 115°42′W) over an 11-year period, during May–June in 1994–1999 and in 2002–2004, representing 1–12 years after fire. Study site elevation ranged from 1120 to 2300 m and the perimeters of the burns were separated by 10 km on average. The Foothills burn was created in 1992 by a mixed-severity fire and about 40% of snags over 23 cm diameter at breast height (dbh) were harvested after the fire (see below). The 1994 Star Gulch fire was also of mixed severity and the burned area was principally unlogged following the wildfire: two survey units (each 1000 ha in size) in the Star Gulch burn were excluded from logging for our research purposes. Prefire vegetation in both wildfire sites was similar and dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with lesser amounts of quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), and buckbrush (*Ceanothus* spp.; Saab et al. 2004).

We assessed the similarities in prelogging snag densities, prefire crown closure, and burn severity of the two study sites. We tested for these similarities to strengthen evidence that any differences in population parameters between the two burns would be more likely attributable to postfire salvage logging than other factors. Snag densities were measured at 60 random plots without nest sites within the partially logged (n = 30) and unlogged (n = 30) burns. We recorded snags >1.4 m height within 11.3 m radius plots (0.04 ha) centered on the random points. Prelogging snag densities were estimated from cut stumps during the year logging was completed (1994) in the salvage-logged area; large snag (>23 cm dbh) densities averaged 73.4 ± 9.3 (SE) snags per ha. After salvage logging, large snag densities were reduced to 45.0 ± 5.1 snags per ha and small snags (≤23 cm dbh) averaged 129.6 ± 19.8 snags per ha. In the unlogged Star Gulch burn, large snag densities (67.8 ± 11.5 snags per ha) one year after the fire (1995) were similar to those reported for the Foothills fire before logging ($t_{58} = 0.4$, $P = 0.71$), and small snags averaged 100.4 ± 19.7 snags per ha.

Prefire crown closure was derived from Landsat Thematic Mapper (TM) images and characterized as low (<40%), moderate (>40%–70%), and high (>70%; Johnson et al. 2000, Saab et al. 2002). The Foothills site consisted of 56% low, 32% moderate, and 12% high prefire crown closures, while the Star Gulch site was composed of 46% low, 41% moderate, and 13% high prefire crown closures. Composition of prefire crown closures at the two sites was not statistically different ($\chi^2_2 = 4.3$, $P = 0.11$).

Landsat TM imagery was also used to quantify burn severity by calculating the change in the normalized burn ratio (ΔNBR) between pre- and postfire conditions (Key and Benson 2006). The ΔNBR was described as a continuous variable (between −500 and +1200) to classify burn severity at the 30 m × 30 m pixel resolution. Burn severity (ΔNBR) was characterized as unburned (−500 to 99), low severity (100 to 269), and moderate–high severity (270 to 1200; Key and Benson 2006, Russell et al. 2006). The Foothills fire was comprised of 17% unburned, 51% low, and 32% moderate–high burn severities, while the Star Gulch fire consisted of 14% unburned, 47% low, and 39% moderate–high burn severities. Composition of burn severities at the two burned sites was not statistically different ($\chi^2_2 = 1.9$, $P = 0.38$).

We conducted belt transect surveys (0.4 km × 1 km) to identify occupied nest cavities (Dudley and Saab 2003). The area surveyed annually averaged 832 ± 67 ha (SE) in the Star Gulch burn, and 846 ± 224 ha (SE) in the Foothills burn. When a nest cavity was located, occupancy was determined by observing the cavity for a minimum of two 20-min visits between early May and late June each year (Saab et al. 2004). Nests were monitored every 3–4 days to record nest stage (laying, incubating, nestling, fledgling), evidence of predation, and nest fate (success or failure). We used behavioral cues to determine nest status and, when possible, a treetop-peeper (video camera) to aid in nest monitoring (TreeTop II System, Sandpiper Technologies, Inc., Manteca, California; Dudley and Saab 2003).

STATISTICAL ANALYSIS

We tested for statistical differences in nest densities between the logged and unlogged wildfire locations using a mixed model ANOVA with year postfire and treatment as fixed effects and calendar year as a random effect (PROC MIXED; SAS Institute 2003). Least-square mean nest densities in the logged and unlogged site were considered statistically different at $P \leq 0.05$.

We conducted regressions of nest densities versus year postfire for seven species of cavity-nesting birds to evaluate trends in density over the 11-year study period (which includes up to 12 years postfire; PROC REG; SAS Institute 2003). Analyses were conducted separately for the salvage-logged and unlogged wildfire sites. We compared results of regression models for linear ($\beta_0 + \beta_1 x$), pseudothreshold ($\beta_0 + \beta_1(\log[x])$), and peak trends (based on a partial sine wave, $\beta_0 + \beta_1 * \sin[20 * x]$; Wickerhauser 1994), representing the three hypothesized trends in nest densities.

We estimated the daily nest survival rate for all species except the American Kestrel for early (1–4 years after fire) and late (5–12 years after fire) postfire periods within each wildfire site using PROC NLMIXED (SAS Institute 2003), as described by Rotella et al. (2004). We then calculated overall nest survival by raising the average daily nest survival rate to a power equal to the number of days in the nesting cycle (length of nesting cycle derived from Dudley and Saab [2003]). Confidence limits on predicted nest survival were estimated using the delta method (Seber 1982). Early and late postfire periods were defined because of expected biological and physical changes between four and five years following fire. Numerical responses by bark- and wood-foraging bird species usually occur 1–2 years after fire, numbers remain high for 2–4 years (Bock et al. 1978, Apfelbaum and Haney 1981, Dixon and Saab 2000), then decline as bark and wood-boring beetle (Scolytidae, Cerambycidae, and Buprestidae) abundances decline (Murphy and Lehnhausen 1998; Covert-Bratland et al., in press). Habitat structure also changes 4–5 years postfire because snag falling rates increase rapidly during this time period (Russell et al. 2006).

RESULTS

NEST DENSITIES IN LOGGED VERSUS UNLOGGED

We surveyed 7611 ha in the unlogged burn and 6657 ha in the partially logged burn, and found 2483 occupied nest cavities of seven species during the 11-year period (Table 1). Results of the mixed-model ANOVA indicated that mean nest densities were significantly different between the logged and unlogged burns for five of seven species (Table 1). For Hairy Woodpeckers and Western Bluebirds there was no solution for the random effect of calendar year, therefore this effect was removed from these models and a fixed-effect ANOVA was conducted. Black-backed Woodpecker, Hairy Woodpecker, Northern Flicker, and Mountain Bluebird nest densities were significantly higher in the unlogged burn ($P < 0.01$), whereas Lewis's Woodpecker densities were significantly higher in the partially logged burn ($P = 0.04$; Table 1). American Kestrel nest densities were higher in the partially salvage-logged area, however the difference between the logged and unlogged sites was not statistically significant ($P = 0.16$). Western Bluebird densities were nearly equal in both the unlogged and partially logged burns.

TRENDS IN NEST DENSITIES

Trends in nest densities generally followed our predictions (Fig. 1 and 2, Table 2). The bark- and wood-foraging specialists, Black-backed and Hairy Woodpeckers, showed a peaked pattern, particularly in the unlogged Star Gulch burn (Fig. 1, Table 2A). For Black-backed Woodpeckers, the peaked trend was stronger in the unlogged burn ($r^2 = 0.65$) than the partially logged burn ($r^2 = 0.43$), where their nest densities were more than five times lower (Table 1). Similarly, nest densities of Hairy Woodpeckers were 2.5 times lower in the partially logged burn, where they did not follow

TABLE 1. Number of nests found and nest densities (number of nests per 40 ha ± SE) of seven cavity-nesting species in two wildfire locations in western Idaho. Least-square means of nest densities per year were calculated from ANOVA and are reported for unlogged and partially logged sites. No. of nests = the total number of nests found over the entire study in the two wildfires (not all nests found were monitored for nest survival), and numbers in parentheses are the number of nests found by postfire period; early represents 1–4 years after fire, and late represents 5–12 years after fire. Test statistics are reported for the lsmeans contrast between nest densities in the logged and unlogged burns.

	Unlogged		Logged			
	No. of nests (early, late)	Mean density ± SE	No. of nests (early, late)	Mean density ± SE	*t*-value	*P*-value
American Kestrel (*Falco sparverius*)	103 (20, 83)	0.89 ± 0.16	150 (47, 103)	1.18 ± 0.17	1.5	0.159
Lewis's Woodpecker (*Melanerpes lewis*)	253 (50, 208)	2.03 ± 0.32	483 (203, 280)	3.03 ± 0.30	2.3	0.041
Hairy Woodpecker (*Picoides villosus*)	181 (135, 46)	0.98 ± 0.15	61 (34, 27)	0.39 ± 0.14	−2.9	0.012
Black-backed Woodpecker (*Picoides arcticus*)	43 (29, 14)	0.22 ± 0.04	8 (5, 3)	0.04 ± 0.03	−3.9	0.003
Northern Flicker (*Colaptes auratus*)	253 (50, 203)	1.77 ± 0.15	166 (65, 101)	1.05 ± 0.14	−3.6	0.004
Western Bluebird (*Sialia mexicana*)	201 (60, 141)	1.52 ± 0.26	221 (85, 136)	1.48 ± 0.24	−0.1	0.907
Mountain Bluebird (*Sialia currucoides*)	283 (132, 151)	1.81 ± 0.19	85 (30, 55)	0.46 ± 0.18	−5.2	0.001

any of the hypothesized trends as indicated by low r^2 values (Fig. 2, Table 2B).

Nest densities of aerial insectivores and open-space foragers generally increased with time since fire in the unlogged burn. American Kestrel and Lewis's Woodpecker nest densities most closely reflected a linear trend (Fig. 1, Table 2A). Changes through time in nest densities of Western and Mountain Bluebirds most closely resembled linear or pseudothreshold trends (Fig. 1, Table 2A). However, r^2 values for trends in Mountain Bluebird nests were low for both models (Fig. 1, Table 2A).

In the salvage-logged burn, nest density trends of aerial insectivores were less certain (Fig. 2, Table 2B). Both linear and pseudothreshold trends were plausible for Lewis's Woodpeckers and Western Bluebirds (Fig. 2, Table 2B). Mountain Bluebird nest densities did not appear to follow any of the hypothesized trends, whereas American Kestrel densities most closely resembled a negative peaked trend with a low point 4–5 years postfire (Fig. 2, Table 2B).

Nest densities of the wood-foraging generalist, the Northern Flicker, increased with time since fire at both burn locations. In the unlogged burn, linear and pseudothreshold trends were equally plausible and had similar r^2 values (Fig. 1, Table 2A). In the partially logged burn, trends in nest density most closely resembled a concave pattern (minimum density at 4–5 years after fire), with sharp increases occurring roughly ten years postfire (Fig. 2, Table 2B).

Regression analysis identified significant increasing trends in nest densities for American Kestrels, Lewis's Woodpeckers, Northern Flickers, and Western Bluebirds in both the logged and unlogged wildfire areas. The proportion of the variance explained by the models (r^2 values) was significant and similar for pseudothreshold and linear trends in nest densities of Lewis's Woodpeckers and Western Bluebirds in the partially logged Foothills burn. In comparison, nest density trends of Northern Flickers and American Kestrels followed an S-shaped curved increase in this area.

NEST SURVIVAL

Nonoverlapping confidence limits for estimates of nest survival indicate significant differences in survival. For most species, postfire period and treatment (partially logged vs. unlogged) had little influence on nest survival, based on overlapping confidence limits (Fig. 3). The Hairy Woodpecker was the only species whose nest survival was clearly affected by treatment,

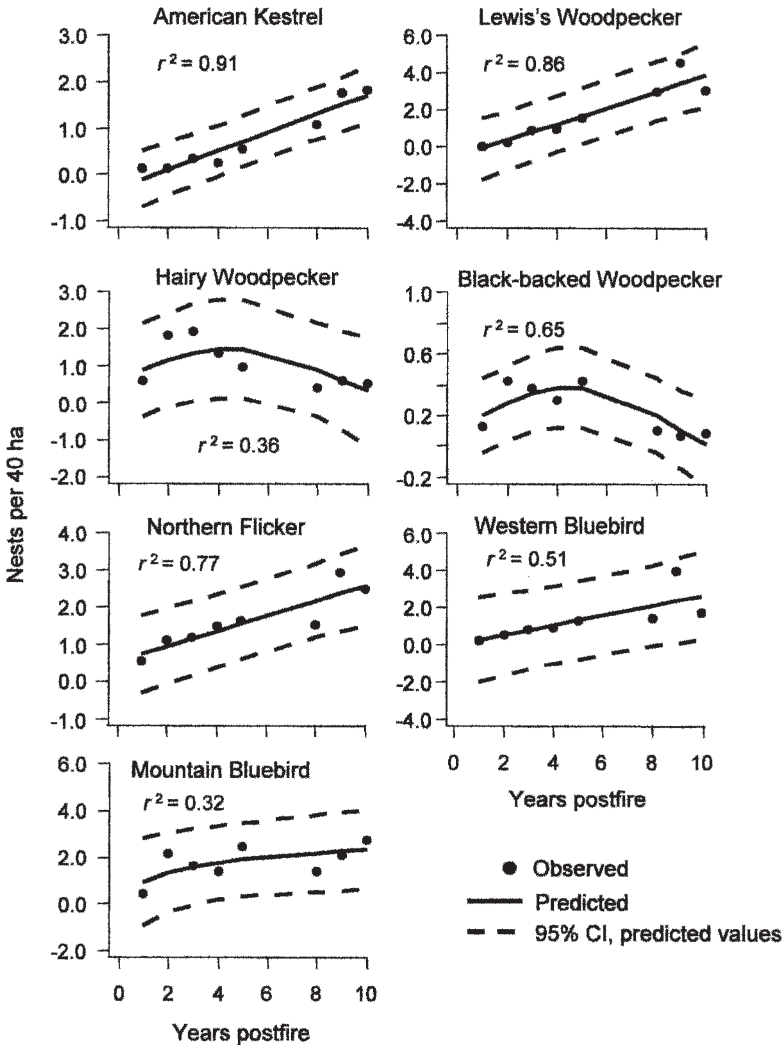

FIGURE 1. Observed and predicted nest densities (nests per 40 ha) for seven species of cavity-nesting birds in the unlogged Star Gulch burn in western Idaho 1–10 years after fire. The wildfire occurred in 1994 and nest densities were monitored from 1995–2004. Predicted values were generated from the best-fitting regression model for each species (linear, peak, or pseudothreshold). For sample sizes see Table 1. Note that the vertical axes differ in scale by species. Nest densities of American Kestrels, Lewis's Woodpeckers, Northern Flickers, and Western Bluebirds increased linearly. Black-backed and Hairy Woodpecker nest densities peaked at roughly 4–5 years postfire.

and its survival was significantly reduced in the partially logged burn vs. the unlogged burn, but only during the early postfire period. Although most species (four of six) tended to have higher nest survival in the early vs. late postfire period, Lewis's Woodpecker was the only species whose survival was significantly higher in the early vs. late postfire period in the partially logged burn (Fig. 3). Nest survival of Hairy Woodpeckers and Mountain Bluebirds increased in the late postfire period, but these differences were not statistically significant. A small sample size and no nest failures precluded the estimation of confidence limits for estimates of nest survival for Black-backed Woodpeckers in the partially logged burn. Estimates of daily survival rate (excluding Black-backed Woodpeckers in the logged site) ranged from a low of 0.980 for Mountain Bluebirds in the unlogged burn in the early postfire period to a high of

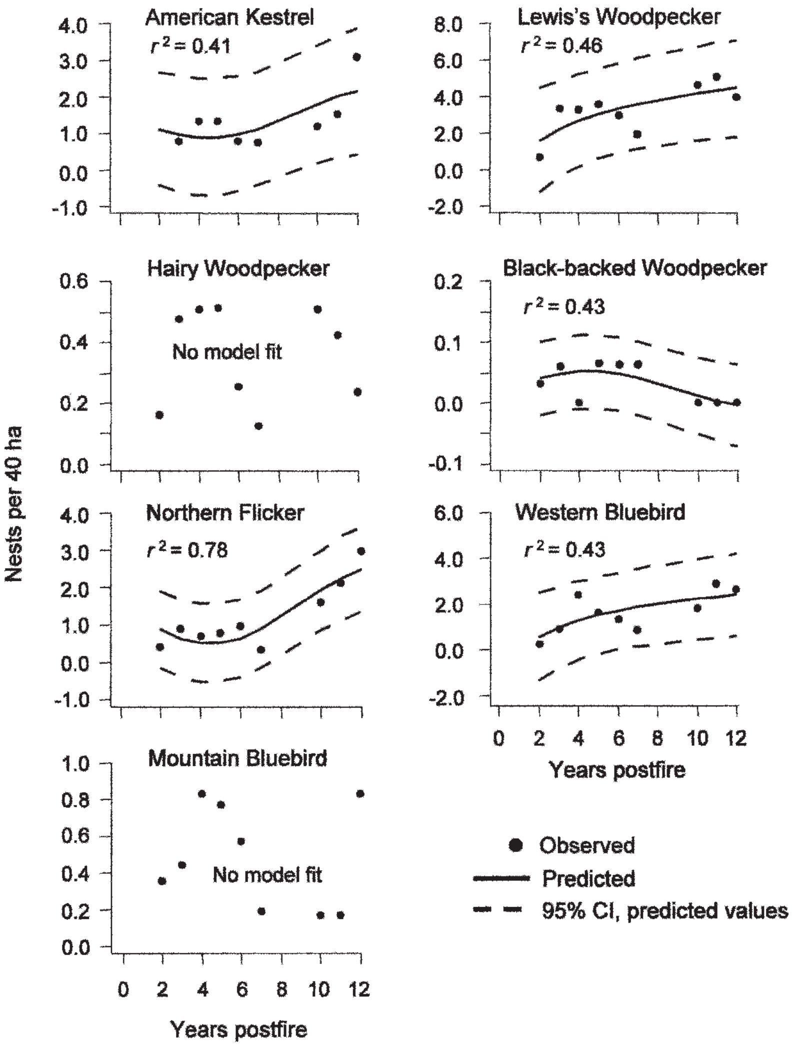

FIGURE 2. Observed and predicted nest densities (nests per 40 ha) for seven species of cavity-nesting birds in the partially salvage-logged Foothills burn in western Idaho 2–12 years after fire. The wildfire occurred in 1992 and nest densities were monitored from 1994–2004. Predicted values were generated from the best-fitting model (linear, peak, or pseudothreshold). For sample sizes see Table 1. Note that the vertical axes differ in scale by species. No linear trends were identified for nest densities of any species in this wildfire. Lewis's Woodpecker and Western Bluebird nest densities reached pseudothreshold levels.

0.998 for Hairy Woodpeckers in the late postfire period in the unlogged burn.

DISCUSSION

Although postfire treatments (i.e., partially logged and unlogged) were not replicated in this study, trends in nest densities at these two wildfire locations in western Idaho closely resembled responses reported at other wildfire locations (Raphael et al. 1987, Imbeau et al. 1999, Smucker et al. 2005), strongly mirrored responses in other logged and unlogged burns (Haggard and Gaines 2001, Johnson and Anderson 2002, Morissette et al. 2002), and generally followed our predicted trends. Nesting densities of wood- and bark-foraging species (Black-backed Woodpecker, Hairy Woodpecker, and Northern Flicker) were significantly higher in the unlogged burn. Two

TABLE 2. Results of model regressions for trends in nest densities in relation to time since fire for seven cavity-nesting bird species in (A) the unlogged Star Gulch burn, and (B) the partially salvage-logged Foothills burn of western Idaho. Model indicates the hypothesized trend (linear, peaked at four years, or pseudothreshold [a declining slope]). Adjusted r^2 indicates model fit, slope = the parameter estimate for the slope of the trend and indicates the direction of the trend (positive = increasing, negative = decreasing), and t-value and P-value indicate the test statistics for the hypothesis that slope = 0.0.

	Model	Adjusted r^2	Slope ± SE	t-value	P-value
A. Unlogged Star Gulch burn					
American Kestrel	Linear	0.91	0.20 ± 0.02	8.5	< 0.001
	Peaked	0.60	−1.18 ± 0.35	−3.4	0.01
	Pseudothreshold	0.69	1.73 ± 0.43	4.0	0.01
Lewis's Woodpecker	Linear	0.86	0.44 ± 0.07	6.6	< 0.001
	Peaked	0.29	−2.06 ± 1.04	−2.0	0.10
	Pseudothreshold	0.76	4.05 ± 0.84	4.8	< 0.001
Hairy Woodpecker	Linear	0.12	−0.11 ± 0.06	−1.9	0.10
	Peaked	0.36	0.87 ± 0.38	2.2	0.07
	Pseudothreshold	0.05	−0.75 ± 0.64	−1.2	0.29
Black-backed Woodpecker	Linear	0.28	−0.03 ± 0.01	−1.9	0.10
	Peaked	0.65	0.27 ± 0.07	3.8	0.01
	Pseudothreshold	0.01	−0.18 ± 0.17	−1.1	0.34
Northern Flicker	Linear	0.77	0.20 ± 0.04	4.9	< 0.001
	Peaked	0.23	−0.93 ± 0.53	−1.8	0.13
	Pseudothreshold	0.73	1.93 ± 0.30	4.4	< 0.001
Western Bluebird	Linear	0.51	0.51 ± 0.26	2.9	0.03
	Peaked	0.14	−1.23 ± 0.84	−1.5	0.19
	Pseudothreshold	0.45	2.41 ± 0.93	2.6	0.04
Mountain Bluebird	Linear	0.21	0.13 ± 0.07	1.7	0.14
	Peaked	−0.11	−0.34 ± 0.61	−0.6	0.59
	Pseudothreshold	0.32	1.38 ± 0.66	2.1	0.08
B. Partially logged Foothills burn					
American Kestrel	Linear	0.34	0.15 ± 0.07	2.1	0.08
	Peaked	0.41	−0.68 ± 0.28	−2.4	0.05
	Pseudothreshold	0.22	2.02 ± 1.17	1.7	0.14
Lewis's Woodpecker	Linear	0.41	0.26 ± 0.10	2.5	0.04
	Peaked	0.23	−1.02 ± 0.56	−1.8	0.11
	Pseudothreshold	0.46	3.66 ± 1.31	2.8	0.03
Hairy Woodpecker	Linear	−0.14	0.00 ± 0.02	0.0	0.98
	Peaked	−0.14	0.01 ± 0.08	0.2	0.88
	Pseudothreshold	−0.14	0.03 ± 0.23	0.1	0.90
Black-backed Woodpecker	Linear	0.20	0.00 ± 0.00	−1.8	0.12
	Peaked	0.43	0.03 ± 0.01	2.7	0.03
	Pseudothreshold	0.07	−0.05 ± 0.00	−1.3	0.25
Northern Flicker	Linear	0.69	0.21 ± 0.05	4.3	< 0.001
	Peaked	0.78	−1.06 ± 0.19	−5.5	< 0.001
	Pseudothreshold	0.51	2.48 ± 0.80	3.0	0.02
Western Bluebird	Linear	0.42	0.17 ± 0.07	2.6	0.03
	Peaked	0.28	−0.72 ± 0.36	−2.0	0.08
	Pseudothreshold	0.43	2.35 ± 0.89	2.6	0.03
Mountain Bluebird	Linear	−0.11	−0.01 ± 0.03	−0.5	0.66
	Peaked	−0.07	0.09 ± 0.14	0.7	0.52
	Pseudothreshold	−0.12	−0.14 ± 0.39	−0.4	0.73

open-space-foraging species (Lewis's Woodpecker and American Kestrel) had higher nesting densities in the partially logged burn, although only densities of Lewis's Woodpecker nests were significantly higher.

Contrary to our predictions that the bluebird species would favor the open habitat of the partially logged burn, Mountain Bluebird nesting densities were significantly higher in the unlogged burn, while densities of Western Bluebird nests were nearly equal in the two burned sites. A similar pattern in abundance of these two species was reported in burned forests of central Washington, where Mountain Blue-

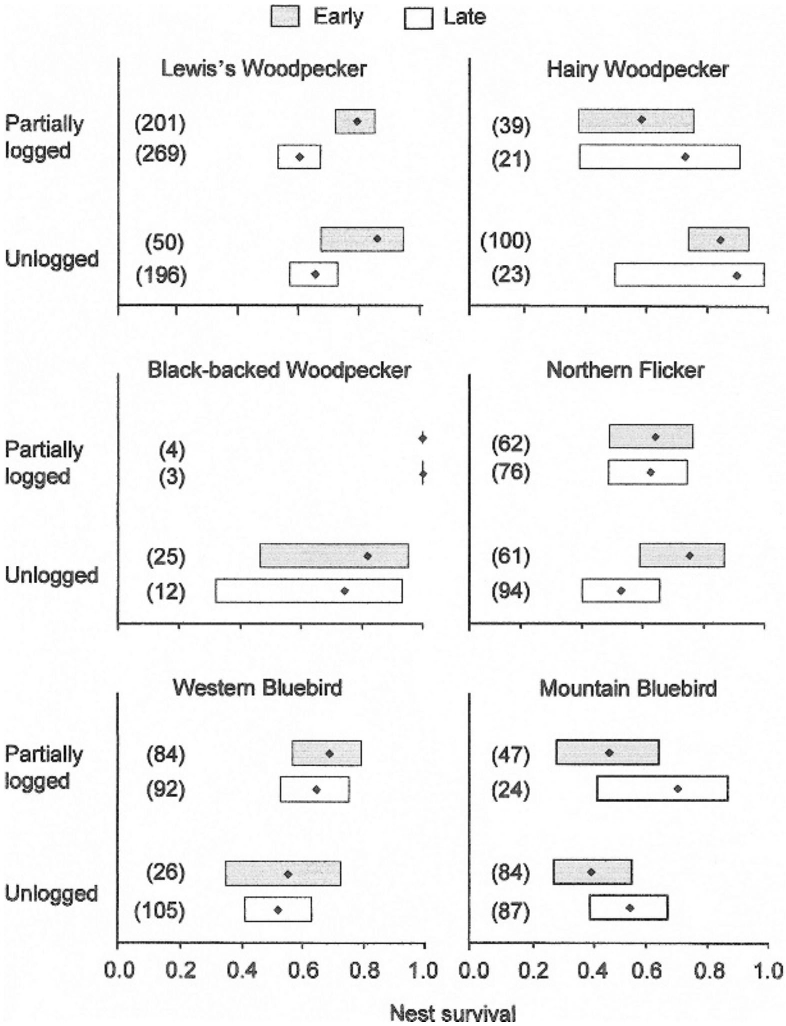

FIGURE 3. Overall nest survival estimates (diamonds) and confidence limits (bars) for early (1–4 years) and late (5–12 years) postfire periods for six species of cavity-nesting birds in the partially logged Foothills burn and the unlogged Star Gulch burn in western Idaho. Numbers in parentheses are the sample sizes of nests for each period and treatment (partially logged and unlogged). Treatment and postfire period did not affect nest survival for most species.

bird numbers were greatest in stands of moderate snag densities, and Western Bluebirds were most abundant in salvage-logged stands of relatively low snag densities (Haggard and Gaines 2001). Perhaps these two similar-sized, congeneric bluebird species were separated in space because of predator avoidance or competition for food and nest sites.

Trends in nesting densities of Mountain Bluebirds were not as apparent compared to other aerial insectivores. Though nest densities were 2–3 times higher for this species in the unlogged Star Gulch burn, average nest densities at both locations remained relatively constant from the early to the late postfire periods. Increasing or constant nest densities in the Star Gulch burn were consistent with Mountain Bluebird nest survival rates, which increased between early and late postfire periods. This observation suggests that Mountain Bluebirds may persist in both environments for more than 10 years after fire.

Trends in nesting densities of aerial insectivores and open-space foragers generally increased in both burns over the 11-year study period. Vegetation regrowth after fire often results in increases in arthropod populations (Hermann et al. 1998, McCullough et al. 1998) that likely provide food and subsequent increased nesting densities of open-space foragers (American Kestrel, Lewis's Woodpecker, and Western Bluebird). Clearly, increases in nest densities will decline at some point when nesting habitat is saturated and snag falling rates increase (Russell et al. 2006). Pseudothreshold trends were also significant for American Kestrels, Northern Flickers, and Western Bluebirds, and perhaps these species have begun to reach a saturation point at 9–10 years postfire in the unlogged burn. Despite increasing trends in nest densities with time, nest survival declined for Lewis's Woodpeckers, Northern Flickers, and Western Bluebirds, suggesting that nest densities were not a good indicator of habitat quality during the later years after fire (cf. van Horne 1983).

Declining nest survival in the later postfire period may be a result of increasing predation pressure or declining food abundance (Saab and Vierling 2001, Saab et al. 2004), as small mammalian predators, such as red squirrels (*Tamiasciurus hudsonicus*), recolonize wildfire areas (Fisher and Wilkinson 2005). An increase in nest predation may also contribute to nest densities reaching a constant value in later postfire years. The exception to this overall trend was the Hairy Woodpecker, whose nest densities declined in the later years after fire, while their nest survival remained high. Their primary food resources were likely diminished by the start of the late postfire period, perhaps causing declines in nest numbers (cf. Covert-Bratland et al., in press).

Inferences from our study are limited because the treatments were not replicated. However, the two burns were similar in prefire crown closure, prelogging snag densities, and burn severity. We also accounted for calendar year effects when testing for differences in nest densities between the partially logged and unlogged burns. This strongly suggests that differences detected between the two burned areas were likely the result of salvage logging and not other factors.

While individuals of every species in the cavity-nesting bird assemblage nested in both the logged and unlogged burns, more species favored the unlogged burn. Black-backed and Hairy Woodpeckers were most strongly associated with the unlogged burn, and both are resident species that may be more at risk from salvage-logging practices than Neotropical migrants (Imbeau et al. 2001, Morissette et al. 2002). Migrants evolved under highly variable abiotic and biotic conditions (Cox 1985), which may explain why they are less vulnerable than residents to habitat changes created by salvage logging. Black-backed Woodpeckers are considered "burn specialists" and may be especially vulnerable to population declines due to habitat loss from postfire salvage logging or fire suppression (Hutto 1995, Dixon and Saab 2000, Hoyt and Hannon 2002).

In contrast, American Kestrels, Lewis's Woodpeckers, and Western Bluebirds, all Neotropical migrants, persisted in the partially logged burn over the 11-year period that we monitored nests. Importantly, the salvage logging was not designed to create clearcuts, but rather to retain more than half the snags over 23 cm dbh, which provided suitable nesting and foraging habitat for aerial insectivores during the decade following fire. However, nest survival for Lewis's Woodpeckers (and, to a lesser extent, Western Bluebirds) declined during the later postfire period, indicating that habitat quality was reduced compared to the earlier years after fire.

Examining postfire trends in nest densities of cavity-nesting birds in logged and unlogged areas is important for determining the time period over which cavity-nesters occupy these forests, identifying factors responsible for their continued use, and providing management direction on habitat conditions needed for the long-term persistence of species at risk. Future research should focus on quantifying postfire changes in vegetation, prey availability, predation pressure, and potential competitive interactions between cavity-nesting species. Prey availability and predation pressure likely differ between salvage-logged and unlogged areas and may influence the extent of interspecific competitive interactions. Replication of study sites is difficult as severity and timing of wildfires create opportunistic study sites, rather than controlled experiments. However, elucidating the relationships among these factors would improve understanding of trends in nest densities and survival through time.

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LITERATURE CITED

APFELBAUM, S., AND A. HANEY. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83:347–354.

BOCK, C. E., AND J. F. LYNCH. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

BOCK, C. E., M. RAPHAEL, AND J. H. BOCK. 1978. Changing avian community structure during early post-fire succession in the Sierra Nevada. Wilson Bulletin 90:119–123.

COVERT-BRATLAND, K. A., W. M. BLOCK, AND T. THEIMER. In press. Hairy Woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. Journal of Wildlife Management.

COX, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist 126: 451–474.

DIXON, R. D., AND V. A. SAAB. 2000. Black-backed Woodpecker (*Picoides arcticus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 509. The Birds of North America, Inc., Philadelphia, PA.

DUDLEY, J., AND V. SAAB. 2003. A field protocol to monitor cavity-nesting birds. USDA Forest Service Research Paper RMRS-RP-44.

FISHER, J. T., AND L. WILKINSON. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

HAGGARD, M., AND W. L. GAINES. 2001. Effects of stand replacement fire and salvage logging on a cavity-nesting bird community in eastern Cascades, Washington. Northwest Science 75: 387–396.

HANNON, S. J., AND P. DRAPEAU. 2005. Bird responses to burning and logging in the boreal forest of Canada. Studies in Avian Biology 30: 97–115.

HERMANN, S. M., T. VAN HOOK, R. W. FLOWERS, L. A. BRENNAN, J. S. GLITZENSTEIN, D. R. STRENG, J. L. WALKER, AND R. L. MYERS. 1998. Fire and biodiversity: studies in vegetation and arthropods. Transactions of the North American Wildlife and Natural Resources Conference 63:384–401.

HOBSON, K. A., AND J. A. SCHIECK. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecological Applications 9:849–863.

HOYT, J. S., AND S. J. HANNON. 2002. Habitat associations of Black-backed and Three-toed Woodpeckers in the boreal forest of Alberta. Canadian Journal of Forest Research 32: 1881–1888.

HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (USA) conifer forests. Conservation Biology 9:1041–1058.

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

IMBEAU, L., M. MÖNKKÖNEN, AND A. DESROCHERS. 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. Conservation Biology 15:1151–1162.

IMBEAU, L., J.-P. L. SAVARD, AND R. GAGNON. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Canadian Journal of Zoology 77: 1850–1860.

JOHNSON, A. S., AND S. H. Anderson [ONLINE]. 2002. Conservation assessment for the American Kestrel in the Black Hills National Forest, South Dakota and Wyoming. USDA Forest Service Rocky Mountain Region. <http://www.fs.fed.us/r2/blackhills/projects/planning/assessments/kestrel.pdf> (19 September 2005).

JOHNSON, V., V. A. SAAB, D. VANDERZANDEN, H. LACHOWSKI, R. BRANNON, AND C. CRIST. 2000. Using landsat satellite imagery to assess fire-created habitat for cavity-nesting birds. CD-ROM. *In* J. D. Greer [ED.], Remote sensing and geospatial technologies for the new millennium, proceedings of the eighth Forest Service remote sensing applications conference, Albuquerque, New Mexico. American Society for Photogrammetry and Remote Sensing, Bethesda, MD.

KEY, C., AND N. BENSON. 2006. Landscape assessment, ground measure of severity, the composite burn index, and remote sensing of severity, the normalized burn ratio. CD-ROM. *In* D. C. Lutes, R. E. Keane, J. F. Caratti, C. H. Key, N. C. Benson, and L. J. Gangi [EDS.], FIREMON, fire effects monitoring and inventory system. USDA Forest Service General Technical Report RMRS-GTR-164-CD.

KOTLIAR, N. B., S. HEJL, R. L. HUTTO, V. A. SAAB, C. P. MELCHER, AND M. E. MCFADZEN. 2002. Effects of wildfire and post-fire salvage logging on avian communities in conifer-dominated forests of the western United States. Studies in Avian Biology 25:49–64.

LINDENMAYER, D. B., D. R. FOSTER, J. F. FRANKLIN, M. L. HUNTER, R. F. NOSS, F. A. SCHMIEGELOW, AND D. PERRY. 2004. Salvage harvesting policies after natural disturbance. Science 303:1303.

LINDER, K. A., AND S. H. ANDERSON. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69: 109–116.

LOWE, P. O., P. E. FOLLIOTT, J. H. DIETERICH, AND D. R. PATTON. 1978. Determining potential benefits from wildfire in Arizona ponderosa pine forests. USDA Forest Service General Technical Report RM-GTR-52.

MCCULLOUGH, D. G., R. A. WERNER, AND D. NEUMANN. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43:107–127.

MELLEN, K., AND A. AGER. 2002. A coarse wood dynamics model for the western cascades, p. 503–516. *In* W. F. Laudenslayer Jr., B. Valentine, C. P. Weatherspoon, and T. E. Lisle [TECH. COORDS.], Proceedings of the symposium on the ecology and management of dead wood in western forests. November 2–4 1999; Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-181.

MOORE, W. S. 1995. Northern Flicker (*Colaptes auratus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 166. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

MORISSETTE, J. L., T. P. COBB, R. M. BRIGHAM, AND P. C. JAMES. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research 32:2169–2183.

MURPHY, E. C., AND W. A. LEHNHAUSEN. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62:1359–1372.

RAPHAEL, M. G., M. L. MORRISON, AND M. P. YODER-WILLIAMS. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. Condor 89:614–626.

RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27:187–204.

RUSSELL, R. E., V. A. SAAB, J. DUDLEY, AND J. J. ROTELLA. 2006. Snag longevity in relation to wildfire and postfire salvage logging. Forest Ecology and Management 232:179–187.

SAAB, V. A., R. BRANNON, J. DUDLEY, L. DONOHOO, D. VANDERZANDEN, V. JOHNSON, AND H. LACKOWSKI. 2002. Selection of fire-created snags at two spatial scales by cavity-nesting birds, p. 835–848. *In* W. F. Laudenslayer Jr., B. Valentine, C. P. Weatherspoon, and T. E. Lisle [TECH. COORDS.], Proceedings of the symposium on the ecology and management of dead wood in western forests. November 2–4 1999; Reno, Nevada. USDA Forest Service General Technical Report PSW-GTR-181.

SAAB, V. A., AND J. G. DUDLEY. 1998. Responses of cavity-nesting birds to stand replacement fire and salvage logging in ponderosa pine/Douglas-fir forests of southwestern Idaho. USDA Forest Service Research Paper RMRS-RP-11.

SAAB, V. A., J. DUDLEY, AND W. L. THOMPSON. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106: 20–36.

SAAB, V. A., AND H. D. POWELL. 2005. Fire and avian ecology in North America: process influencing pattern. Studies in Avian Biology 30: 1–13.

SAAB, V. A., AND K. VIERLING. 2001. Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests. Condor 103: 491–501.

SAS INSTITUTE. 2003. SAS (9.1) SAS/STAT user's guide. Version 9. SAS Institute, Inc., Cary, NC.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan, New York.

SMUCKER, K. M., R. L. HUTTO, AND B. M. STEELE. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. Ecological Applications 15:1535–1549.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

WERNER, R. A. 2002. Effect of ecosystem disturbance on diversity of bark and wood-boring beetles (Coleoptera: Scolytidae, Buprestidae, Cerambycidae) in white spruce (*Picea glauca* (Moench) Voss) ecosystems of Alaska. USDA Forest Service General Technical Report PNW-GTR-546.

WICKERHAUSER, M. V. 1994. Adapted wavelet analysis from theory to software. A. K. Peters, Ltd., Boston, MA.