The Journal of Wildlife Management 75(4):794–804; 2011; DOI: 10.1002/jwmg.111

Research Article

Modeling Nest Survival of Cavity-Nesting Birds in Relation to Postfire Salvage Logging

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ABSTRACT Salvage logging practices in recently burned forests often have direct effects on species associated with dead trees, particularly cavity-nesting birds. As such, evaluation of postfire management practices on nest survival rates of cavity nesters is necessary for determining conservation strategies. We monitored 1,797 nests of 6 cavity-nesting bird species: Lewis's woodpecker (*Melanerpes lewis*), hairy woodpecker (*Picoides villosus*), black-backed woodpecker (*P. arcticus*), northern flicker (*Colaptes auratus*), western bluebird (*Sialia mexicana*), and mountain bluebird (*S. currucoides*) from 1994 to 2004 in ponderosa pine (*Pinus ponderosa*), mixed-severity burned forests (partially logged and unlogged) of Idaho, USA. Based on a priori hypotheses, we modeled daily survival rate (DSR) of nests as a function of abiotic (temperature, precipitation), temporal (time since fire, calendar year) and biotic factors (distance to unburned forest, nest height, and tree harvest [partial-salvage logging vs. unlogged]). Multiple abiotic and biotic factors, other than direct effects of salvage logging, affected daily survival rates of breeding cavity-nesting birds. Hairy woodpecker was the only species in which partial-salvage logging had a measurable, negative impact on DSR. Managers implementing carefully planned salvage logging prescriptions that include both unlogged reserves and partially logged areas can expect to maintain habitat for successfully breeding cavity-nesting birds of the interior northwestern United States. Our results also suggest that nest survival for some species of cavity-nesting birds could be improved if unlogged reserves are located centrally in postfire forests, distant from unburned habitats that potentially serve as sources of nest predators.

KEY WORDS cavity-nesting birds, *Colaptes auratus*, *Melanerpes lewis*, nest survival, *Picoides* spp., *Pinus ponderosa*, salvage logging, *Sialia* spp., wildfire.

The practice of postfire salvage logging has become increasingly prevalent as the amount of forested area burned by wildfire has increased over the past 2 decades (McIver and Starr 2001, Beschta et al. 2004, Stephens and Ruth 2005, Lindenmayer et al. 2008). In addition to tree mortality caused by wildfire, significant increases in tree mortality from bark beetle (*Dendroctonous pondorosae*) infestations are expected as a result of changing climates (Bentz et al. 2010). Increased tree mortality from fire and insects will create more opportunities for salvage logging (cf. Lindenmayer and Noss 2006). Salvage logging removes dead, dying, or weakened trees that provide nesting and foraging habitat for woodpeckers and other cavity-nesting species (Hutto and Gallo 2006, Saab et al. 2007). Thus, land managers face significant challenges implementing fire management policies, while concurrently maintaining wildlife habitat for species associated with dead trees.

Temporal changes in nest densities as time since fire increases, and preferences of species for nesting in logged or unlogged areas, have been documented for cavity-nesting birds (Hutto and Gallo 2006; Saab et al. 2007, 2009; Vierling et al. 2008). Studies modeling nest survival in relation to postfire salvage logging, however, appear to be lacking from the literature. The general patterns of nest site preferences follow that beetle—(e.g., Buprestidae, Cerambycidae, Curculionidae) foraging species (e.g., black-backed [*Picoides arcticus*] and hairy woodpeckers [*P. villosus*]) are associated with unlogged burned forests (Murphy and Lehnhausen 1998, Haggard and Gaines 2001, Morissette et al. 2002, Saab et al. 2009), whereas partially salvage-logged areas provide nesting habitat for other species such as Lewis's woodpecker (*Melanerpes lewis*) and western bluebird (*Sialia mexicana*; Haggard and Gaines 2001, Saab et al. 2007).

Nesting preferences for cavity-nesting species in western Idaho were previously reported (Saab et al. 2009). Among seven cavity-nesting bird species, only Lewis's woodpecker and western bluebird demonstrated an association with the partially salvage logged forest (Saab et al. 2007, 2009). Other species (hairy and black-backed woodpeckers, mountain bluebirds [*S. currucoides*], and northern flickers [*Colaptes auratus*]) favored unlogged burned forests, as indicated by higher nesting densities or nest site selection in an unlogged study area.

Received: 17 March 2010; Accepted: 16 September 2010

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Ecologists have long recognized that the relationship between density and survival or productivity is not always clear (Van Horne 1983, Bock and Jones 2004). Despite documented preferences for logged and unlogged forests, Saab et al. (2007) found nesting pairs of cavity-nesting species in both habitats, and all species except black-backed woodpeckers were found in both early and late postfire years. Due to the controversy surrounding the management of postfire landscapes (Lindenmayer et al. 2004, 2008), determining whether nesting preferences for logged or unlogged areas reflect differences in nest survival is necessary for the long-term persistence of cavity nesters associated with recently burned forests.

Nest survival of cavity-nesting birds is affected by biotic factors, such as predation risk and foraging habitat (Martin 1993, Saab and Vierling 2001, Mahon and Martin 2006, Wightman et al. 2010), and by abiotic variables such as temperature, precipitation, and temporal factors (e.g., nest initiation date; Neal et al. 1993, Conway and Martin 2000). Predation risk can have significant impacts on nest placement and success (Martin 1993, Mahon and Martin 2006). Previous studies of cavity-nesting birds have demonstrated that nests placed at greater heights are often more successful (Nilsson 1984, Rendell and Robertson 1989, Li and Martin 1991).

In burned forests, time since fire potentially influences risks of predation by recolonizing nest predators such as tree squirrels (*Tamiasciurus* spp.; Fisher and Wilkinson 2005). Recently burned forests may provide nesting habitat with a reduced risk of predation for cavity-nesting birds (Saab and Vierling 2001, Saab et al. 2004). In a patchy burn, nests placed farther from potential source populations of predators (i.e., unburned forests) might have higher success rates. Lower tree densities as a result of postfire logging could also reduce habitat for potential nest predators such as squirrels and other small mammals (Sullivan and Moses 1986, Fisher and Bradbury 2006, Holloway and Malcolm 2006).

Fire destroys seed sources and den sites of red squirrels (*Tamiasciurus hudsonicus*), in addition to ground cover used as shelter from predators (Fisher and Wilkinson 2005). Red squirrels were absent from recently burned pine forests affected by wildfires in Colorado (Roppe and Hein 1978). Burned habitat conditions, as well as nest cavity height, potentially influence probabilities of predation by known nest predators in our study area, including gopher snakes (*Pituophis catenifer*), red squirrels, yellow-pine chipmunks (*Tamias amoenus*), and black bears (*Ursus americanus*).

By removing large snags that provide critical foraging habitat for many beetle-foraging species (Hutto 1995, 2006; Morissette et al. 2002; Lindenmayer et al. 2004), postfire salvage logging may negatively impact nest survival. However, lower tree densities could improve foraging opportunities for species that forage in open habitats, such as western bluebirds (Wightman and Germaine 2006).

Foraging options for cavity-nesting birds may also be affected by time since fire. As snags fall, foraging opportunities decrease for beetle-foraging species. Concurrently after fire, shrub and herbaceous regrowth attracts arthropods (Swengel 2001), potentially increasing availability of insect prey for aerial insectivores (Saab et al. 2007).

Large, living trees provided stable and moderate temperatures, whereas smaller, dead trees showed more extreme temperatures inside nest cavities (Wiebe 2001). Reduced forest cover in salvage-logged areas may lead to increased ambient temperatures, potentially affecting nest survival of cavity-nesting birds (Neal et al. 1993, Wachob 1996, Conway and Martin 2000). The influence of ambient temperature on incubation behavior and ultimately reproductive effort likely differs in cold versus hot environments (Conway and Martin 2000). Ambient temperatures could affect nest cavity microclimates differently in burned trees than live trees. Increasing ambient temperatures could likely cause heat stress to eggs and young, particularly in snags of burned forests where little shade is available.

We monitored nests of 6 cavity-nesting bird species (Lewis's woodpecker, western bluebird, mountain bluebird, hairy woodpecker, black-backed woodpecker, and northern flicker) from 1994 to 2004 in ponderosa pine forests of Idaho recently burned by mixed-severity wildfire. Our goal was to evaluate nesting survival in postfire landscapes affected by salvage logging that would lead to decision support tools for guiding management of cavity-nesting bird habitat. Unlike previous work on categorical comparisons of nest success in relation to postfire salvage logging (Saab et al. 2007), our focus here was modeling nest survival in the context of competing hypotheses regarding effects of salvage logging and other environmental factors. Our specific objectives were: 1) to develop nest survival models for cavity-nesting birds that can be used to evaluate their responses to salvage logging after wildfire and 2) to identify key habitat and environmental conditions influencing nest survival in relation to biotic, abiotic, and temporal factors.

We hypothesized that higher air temperatures in burned forests would decrease daily survival rates through heat stress to eggs and young and that higher precipitation would decrease nest survival of species feeding on flying arthropods through decreased insect activity, in accordance with a reduced ability to acquire food, and increased risk of nest abandonment (Neal et al. 1993, Conway and Martin 2000, Wiebe 2001, Dinsmore et al. 2002, Jehle et al. 2004). We expected nest survival of beetle-foraging species to be highest during the early years after fire, when beetles are most numerous, and higher in unlogged forests, where abundant snags provide greater foraging opportunities (Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006, Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Saab et al. 2007). In contrast, we hypothesized that nest survival of aerial-ground insectivores would increase with time since fire in accordance with increases in their nesting densities, and that partial-salvage logging would have little effect on their nest survival because increased space between trees might facilitate foraging maneuvers and therefore their ability to obtain food (Haggard and Gaines 2001, Wightman and Germaine 2006, Saab et al. 2007). Last, we hypothesized that nests placed at greater heights from the ground and farther from unburned forests would have higher survival because those nests would be more difficult to access by nest predators (Nilsson 1984, Li and Martin 1991, Saab et al. 2004, Fisher and Wiebe 2006).

STUDY AREA

We conducted nest surveys at two wildfire locations in western Idaho, USA (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. Elevation ranged from 1,120 to 2,300 m and the perimeters of the two burns were separated by 10 km on average. The Foothills burn (89,159 ha) was created in 1992 by a mixed-severity fire and about 40% of snags >23 cm diameter at breast height were harvested after the fire (Saab et al. 2007). The 1994 Star Gulch burn (12,467 ha) was also mixed severity and principally unlogged following the wildfire. Two survey units (each approximately 400 ha in size) similarly managed for partial logging were selected in the Foothills burn for searching and monitoring nests, along with two survey units (each about 400 ha in size) in the Star Gulch burn that were excluded from logging for our research purposes.

Prefire vegetation in both wildfire locations was similar and descriptive of dry conifer forest dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), with quaking aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), and buckbrush (*Ceanothus* spp.; Saab et al. 2004). A mixed-severity fire regime consists of frequent nonlethal fire (most trees survive) and infrequent stand-replacement fire (most trees die; Arno et al. 2000, Saab and Powell 2005). This regime is characteristic of dry conifer forests in the northern Rocky Mountains (Arno et al. 2000, Schoennagel et al. 2004, Saab et al. 2005).

The two study locations were created by fires that occurred 2 years apart, but both had similar ecological conditions that provided for an observational study with minimal replication in space but excellent samples of years (11-yr period) and nests ($n = 1{,}797$). As reported elsewhere, we assessed prefire similarity of the two study locations (see Saab et al. 2007 for details). Before logging, large (>23 cm dbh) snag densities in the Foothills fire averaged 73.4 $\pm$ 9.3 (SE) snags/ha. After salvage logging, large snag densities were reduced to 45.0 $\pm$ 5.1 snags/ha and small snags ($\leq$23 cm dbh) averaged 129.6 $\pm$ 19.8 snags/ha. In the unlogged Star Gulch burn, large snag densities (67.8 $\pm$ 11.5 snags/ha) 1 year after the fire (1995) were similar to those reported for the Foothills Fire before logging, and small snags averaged 100.4 $\pm$ 19.7 snags/ha. The amount of area in three categories of pre-fire crown closure (<40%, 40–70%, and >70%) and three categories of burn severity (unburned, low, and moderate-high severity) were statistically indistinguishable in both logged and unlogged locations (Saab et al. 2007).

METHODS

Nest Surveys

We characterized cavity-nesting bird species as either wood probers or aerial-ground insectivores based on their dominant foraging behavior. We considered the beetle-foraging species, black-backed and hairy woodpeckers, and northern flicker to be wood probers, although flickers feed often on the ground and on a variety of substrates other than wood (Villard and Beninger 1993, Moore 1995, Dixon and Saab 2000, Jackson et al. 2002, Koivula and Schmiegelow 2007). We characterized Lewis's woodpecker, western bluebird, and mountain bluebird as aerial-ground insectivores (Power and Lombardo 1996, Tobalske 1997, Guinan et al. 2000).

We conducted rectangular belt-transect surveys (0.2 km $\times$ 1 km) to identify occupied nest cavities (Dudley and Saab 2003) during early May until late June, the time when most nests were initiated. We placed belt-transect surveys 200 m apart, and we surveyed transects for 100 m on either side of the center line. The area surveyed annually averaged 832 $\pm$ 67 ha (SE) in the Star Gulch burn and 846 $\pm$ 224 ha (SE) in the Foothills burn. Annual area surveyed depended on field personnel availability. When we located a nest cavity, we determined occupancy by observing the cavity for $\geq$2 20-min visits (Saab et al. 2004). We monitored nests 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 inform nest status and a treetop-peeper (TreeTop II System, Sandpiper Technologies, Inc., Manteca, CA) when nests were $\leq$12 m in height to aid in nest monitoring (Dudley and Saab 2003).

Covariates in Nest Survival Models

We evaluated the influence of eight variables on daily survival rate (DSR) of cavity-nesting birds (Table 1). We grouped the variables into three categories: abiotic, biotic, or temporal factors. Abiotic factors included data for maximum daily temperature and daily total precipitation from the University of Idaho's Interactive Numeric Spatial Information and Data Engine (INSIDE) recorded at the

Table 1. Covariates we used to model daily nest survival rates of cavity-nesting birds in burned forests of western Idaho, 1994–2004.

Category	Variable name	Variable description
Abiotic	Temp. (°C)	Averaged max. daily temp over the interval between nest visits
	Precipitation (mm)	Averaged precipitation over the interval between nest visits
Biotic	Distance to unburned forest (m)	Estimated using the euclidean distance tool in spatial analyst
	Nest ht (m)	Measured with a clinometer
	Logged vs. unlogged	Tree harvest on logged units was approximately 40% removal of snags $\geq$23 cm dbh
Temporal	Year postfire	1–12 yr after fire
	Calendar year	1994–1999 and 2002–2004
	Postfire period	Early postfire period = 1–4 yr after fire
		Late postfire period = 5–12 yr after fire

nearest weather station to both study areas in Idaho City (University of Idaho 2002). We used maximum daily temperature and precipitation over the interval between nest visits to estimate weather conditions (Table 1). Biotic factors included nest height, distance to unburned forest, and habitat condition as unlogged or partially logged (see Table 2 for supporting hypotheses).

We also included three temporal covariates in our models: year postfire (a continuous variable), calendar year (a fixed effect), and postfire period (early and late periods; Tables 1 and 2). We assigned nests monitored within the first 4 years after fire to the early postfire period, whereas we assigned those monitored at or after 5 years postfire to the late postfire period, indicating potentially substantial shifts in insect availability (Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006), snag falling rates (Saab et al. 2004, Russell et al. 2006), nest density (Saab et al. 2007), and habitat use following wildfire (Saab et al. 2009). We did not assess the effects of calendar date or nest age because rarely were we able to accurately determine age of the nest, and Julian date had a strong positive correlation with temperature (Pearson correlation coeff. 0.65, $P < 0.001$).

Modeling Nest Survival

We evaluated 22 models of nest survival for each species based on a priori hypotheses about the influence of abiotic, biotic, and temporal factors (Table 2). We modeled DSR for all species using SAS 2003 (SAS Institute, Cary, NC), as described by Rotella et al. (2004). We employed a generalized linear models approach (McCullagh and Nelder 1989) based on a binomial likelihood, where we modeled daily survival rates as a function of nest-, group-, or time-specific covariates. The model employed a logit link as it is a natural link for the binomial distribution (McCullagh and Nelder 1989) and bounds estimates of survival in the (0, 1) interval. Thus, we modeled daily survival rate of a nest on day i as

$$\frac{\exp\left(\beta_0 + \sum_j \beta_j x_{ji}\right)}{1 + \exp\left(\beta_0 + \sum_j \beta_j x_{ji}\right)}$$

where x_{ji} ($j = 1, 2, \ldots, J$) are values for J covariates on day i and β_j are coefficients estimated from the data. Thus, we modeled the relationship between the logit of S_i, that is, $\ln(S_i/(1 - S_i))$, and the covariates as linear, whereas the

Table 2. Candidate models and supporting hypotheses comparing random, biotic, or abiotic influences on nest survival of cavity-nesting birds in burned forests of western Idaho, 1994–2004.

Models	Alternative hypotheses
Null	Nest survival is random, likely due to random predation events
Intercept-only	
Abiotic and temporal	More variation exists in abiotic factors than habitat characteristics at nest sites; abiotic factors may have a stronger influence on nest survival
Temp	
Precipitation	
Temp, precipitation	
Year postfire	Year postfire will indicate a consistent linear change over time on nest survival
Temp, precipitation, year postfire	
Postfire period	Postfire period will indicate a change in nest survival between 4 and 5 yr after fire, concomitant with variation in other biological factors
Temp, precipitation, postfire period	
Calendar year	Calendar year will account for unmeasured non-linear annual effects on nest survival
Biotic	Habitat and nest-tree characteristics may provide greater protection from predators; biotic factors will have a stronger influence on nest survival
Distance to unburned forest	
Nest ht	
Distance to unburned forest, nest ht	
Logged vs. unlogged	Habitat features in unlogged (vs. partially logged) conditions will provide more nesting and foraging opportunities for higher nest survival of beetle-foraging species; whereas partially logged conditions will provide foraging options for higher nest survival of aerial- and ground-foraging species
Combination (biotic + abiotic)	Biotic and abiotic factors (lower temp, lower precipitation, greater distances to unburned forest, greater nest ht) may increase nest survival because of good environmental conditions and protection from predators
Distance to unburned forest, temp	
Distance to unburned forest, precipitation	
Nest ht, temp	
Nest ht, precipitation	
Combination (biotic + temporal)	A combination of habitat characteristics and time since fire provide the best conditions for protection from predators, and diverse foraging opportunities for high nest survival
Distance to unburned forest, year postfire	
Distance to unburned forest, postfire period	
Nest ht, year postfire	
Nest ht, postfire period	
Global	
Abiotic, biotic, year postfire	

relationship between S_i and the covariates was logistic or S-shaped. We generated estimates of DSR for covariate conditions of interest by solving the regression equation and back transforming the answer. We then estimated nest success as a derived quantity from the estimates of the modeled DSRs using the appropriate number of days and covariate conditions for the species of interest. Additional details on the general approach we used to estimate daily nest survival rate are provided by Dinsmore et al. (2002).

Abiotic factors (maximum daily temperature and daily precipitation amount) addressed weather effects, and biotic factors helped to evaluate predation risk (nest height and distance from the nest to the nearest unburned forest) and availability of foraging and nesting substrates (logging status; Table 2). We also included temporal factors (calendar year, year postfire, and postfire period) to help detect responses to unmeasured factors related to biological and physical changes with time since fire (Table 2). Numerical responses by beetle-foraging bird species usually peak at 4–5 years after fire, then decline as bark and wood-boring beetle (Scolytidae, Cerambycidae, Buprestidae) abundances decline (Bock et al. 1978, Apfelbaum and Haney 1981, Murphy and Lehnhausen 1998, Covert-Bratland et al. 2006, Saab et al. 2007).

We used small-sample corrected Akaike's Information Criterion (AIC_c) to select the most parsimonious model. We evaluated all models within 2 ΔAIC_c units of the top model because such models are considered to provide substantial support for containing the best model (Burnham and Anderson 2002). In addition, we evaluated models of considerably less support, that is, models within 4–7 ΔAIC_c units of the model with the minimum AIC_c value (Burnham and Anderson 2002) only in cases where no models were within 2 ΔAIC_c units of the top model. We also reported 95% confidence intervals for parameter estimates in the top models to identify uninformative parameters (Arnold 2010). Furthermore, we calculated the relative importance of covariates across all candidate models and incorporated those values in the interpretation of our results.

We evaluated goodness-of-fit of the global model (models containing all covariates except calendar year and postfire period) and the best model(s) for each species using methods presented by Sturdivant et al. (2007). To illustrate results for the best models (models within 2 ΔAIC_c points of the model with the minimum AIC_c value), we selected average values for covariates contained in the models and then calculated nesting success (i.e., probability of surviving from initiation to fledging) by raising 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) and calculated 95% confidence limits using the delta method (Powell 2007).

RESULTS

We monitored 1,797 nests over an 11-year period. Variables in top models differed among species (Table 3). Goodness-of-fit tests for all global models and all best models as selected by AIC_c for all species were adequate with $P > 0.10$ in all cases (Table 3).

We found supporting evidence for our hypotheses relating DSR of nests to abiotic factors (temperature and precipitation) for two species (Table 3). Increasing temperatures had negative effects on DSR of Lewis's woodpecker and western bluebird, whereas increasing precipitation had nega-

Table 3. Model selection results based on non-linear models of nest survival for six cavity-nesting bird species in burned forests of western Idaho, 1994–2004. Models are ranked according to corrected Akaike's Information Criterion (AIC_c) differences ($\Delta AIC_{ci} = AIC_{ci} - AIC_{min}$), from most plausible ($\Delta AIC_c = 0$) to least plausible; k = number of parameters; n = number of nests. We list all models within 2 ΔAIC_c units of the top model (or the second best model in cases where no models were within 2 units of the top model) and the null model (model without covariates) for each species. We list goodness-of-fit (GOF) statistics for the global model.

Bird species	Model	k	ΔAIC_c	w[a]
Lewis's woodpecker ($n = 716$)	Abiotic + temporal (postfire period)	4	0.00	0.90
$n = 470$ logged; $n = 246$ unlogged	Global	7	4.41	0.11
Global model GOF $P = 0.254$, min $AIC_c = 1293.42$	Null	1	29.64	0.00
Hairy woodpecker ($n = 183$)	Biotic (logged vs. unlogged)	2	0.00	0.50
$n = 55$ logged, $n = 128$ unlogged	Null	1	3.86	0.07
Global model GOF $P = 0.893$, min $AIC_c = 195.26$	Abiotic	3	3.97	0.07
Black-backed woodpecker ($n = 46$)	Biotic (distance to unburned forest)	2	0.00	0.54
$n = 7$ logged, $n = 39$ unlogged	Abiotic (precipitation)	2	2.90	0.13
Global model GOF $P = 0.243$, min $AIC_c = 37.31$	Null	1	4.47	0.06
Northern flicker ($n = 293$)	Temporal (year postfire)	2	0.00	0.15
$n = 134$ logged, $n = 159$ unlogged	Temporal (postfire period)	2	0.22	0.14
Global model GOF $P = 0.677$, min $AIC_c = 502.92$	Abiotic (precipitation)	2	0.49	0.12
	Null	1	1.02	0.09
	Abiotic (temp)	2	1.18	0.08
	Biotic + temporal (distance to unburned forest, year postfire)	3	1.74	0.06
	Biotic + temporal (nest ht, year postfire)	3	1.96	0.06
Western bluebird ($n = 317$)	Abiotic + biotic (temp, distance to unburned forest)	2	0.00	0.43
$n = 175$ logged, $n = 142$ unlogged	Abiotic (temp)	2	2.66	0.12
Global model GOF $P = 0.713$, min $AIC_c = 620.14$	Null	1	6.00	0.02
Mountain bluebird ($n = 242$)	Biotic + temporal (nest ht, year postfire)	3	0.00	0.25
$n = 60$ logged, $n = 182$ unlogged	Biotic (nest ht)	2	0.96	0.15
Global model GOF $P = 0.154$, min $AIC_c = 546.64$	Temporal (calendar year)	7	1.97	0.09
	Null	1	3.49	0.04

[a] Akaike weight, the relative likelihood of the model as the best model given the set of models.

Table 4. Parameter estimates and 95% confidence limits (LCL = lower 95% CL, UCL = upper 95% CL) for parameters in top models of nest survival for six cavity-nesting bird species in burned forests of western Idaho, 1994–2004.

Bird species	Parameter[a]	Estimate	LCL	UCL
Lewis's woodpecker	Intercept	8.814	6.902	10.726
	Postfire period[b]	−0.797	−1.188	−0.406
	Precipitation	−0.209	−0.308	−0.111
	Temp	−0.038	−0.060	−0.016
Hairy woodpecker	Intercept	5.640	4.980	6.290
	Logged vs. unlogged[c]	−1.070	−1.940	−0.200
Black-backed woodpecker	Intercept	3.706	2.285	5.127
	Distance to unburned forest	0.020	0.000	0.041
Northern flicker	Intercept	4.591	4.355	4.827
Western bluebird	Intercept	6.272	4.173	8.370
	Temp	−0.028	−0.054	−0.003
	Distance to unburned forest	0.002	0.000	0.003
Mountain bluebird	Intercept	3.440	2.910	3.970
	Nest ht	0.510	0.000	0.103
	Year postfire	0.600	−0.010	0.129
	Intercept	3.730	3.320	4.150
	Nest ht	0.540	0.002	0.105
	Intercept (year = 1994)	4.206	3.399	5.013
	1995 vs. 1994	−0.794	−1.743	0.155
	1996 vs. 1994	0.558	−0.483	1.599
	1997 vs. 1994	−0.444	−1.371	0.483
	2002 vs. 1994	−0.247	−1.269	0.776
	2003 vs. 1994	0.248	−0.794	1.29
	2004 vs. 1994	0.278	−0.789	1.345

[a] See Table 1 for parameter definitions.
[b] Reference condition is late postfire period.
[c] Reference condition is logged.

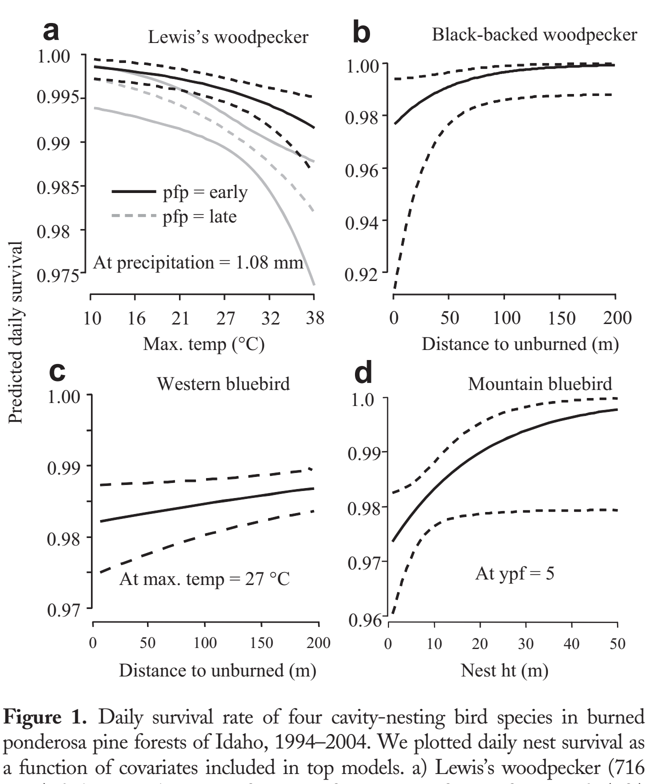

Figure 1. Daily survival rate of four cavity-nesting bird species in burned ponderosa pine forests of Idaho, 1994–2004. We plotted daily nest survival as a function of covariates included in top models. a) Lewis's woodpecker (716 nests) daily survival rate as a function of max. temp, for postfire periods (pfp) early and late at an average daily precipitation of 1.08 mm, b) black-backed woodpecker (46 nests) daily survival rate as a function of distance to unburned forest, c) western bluebird (317 nests) daily survival rate as a function of distance to unburned forest at an average max. daily temp of 27 °C, and d) mountain bluebird (242 nests) daily survival rate as a function of nest ht during year 5 postfire (ypf). Solid lines represent estimates, and dotted lines represent 95% CI.

tive effects on DSR of Lewis's woodpecker nests (Tables 3 and 4 and Fig. 1). Relative importance (RI) of the covariates temperature and precipitation were equally quantified (RI = 1) for Lewis's woodpecker. Postfire period also had a high RI value of 0.90 for Lewis's woodpecker but all other covariates were of little relative importance (range of RI values 0–0.10) to its nest survival. Temperature (RI = 0.65) and distance to unburned forest (RI = 0.62) were of high importance for western bluebird DSR, whereas evidence for other covariates was lacking (range of RI values 0.03–0.13).

Time since fire had no discernable influence on DSR of beetle-foraging or aerial-ground insectivores, except for Lewis's woodpecker (Tables 3 and 4). Daily survival rates of Lewis's woodpecker declined in the later postfire period (Table 4 and Fig. 2), contrary to our a priori hypothesis. When nesting success was estimated for Lewis's woodpecker using average maximum temperature and precipitation values, success was higher in the early (0.822, 95% CL [0.758, 0.871]) than in the late (0.649, 95% CL [0.5817, 0.708]) postfire period (Fig. 2).

We found mixed support for our hypotheses relating DSR of nests to biotic factors. Effects of salvage logging were evident for hairy woodpeckers, supporting our a priori prediction that salvage logging would influence nest survival of beetle-foraging species. Daily survival rate was lower in the partially logged burned forest (0.989, 95% CL [0.982, 0.993]) versus the unlogged burned forest (0.997, 95% CL [0.994, 0.998]) for this species. Nesting success was lower for hairy woodpeckers in logged postfire areas

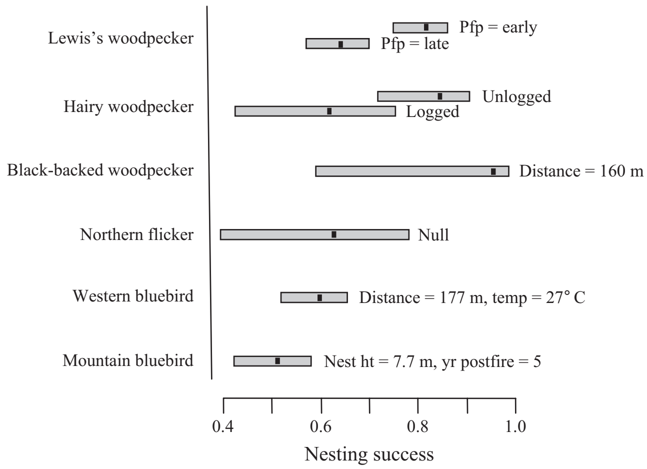

Figure 2. Estimated nesting survival in relation to the most parsimonious models for six cavity-nesting bird species in burned ponderosa pine forests of Idaho, 1994–2004. Estimates are calculated at average values of covariates included in the best models of survival for each species as selected by Akaike's Information Criterion for small sample sizes (AIC_c). Bars represent 95% CI, squares represent the estimate of nest survival. Pfp = postfire period; Pfp = early is 1–4 years after fire, Pfp = late is 5–12 years after fire.

(0.623, 95% CL [0.435, 0.764]) than it was in unlogged postfire areas (0.849, 95% C.L. [0.731, 0.919]; Fig. 2). The importance of unlogged versus logged areas to DSR of hairy woodpecker was evident based on an RI value of 0.58, whereas other covariates had much lower RI values (0–0.18).

We could not effectively test for a logging effect on black-backed woodpecker nest survival due to constraints of covariate conditions for the small sample (seven nests) in the logged area. Consequently, the logged–unlogged covariate was not included in models of nest survival for black-backed woodpecker. Black-backed woodpecker had the highest estimated nesting success of any species (0.958), but precision of the estimate was not high due to the modest sample size for this species (95% CL [0.600, 0.996]). Salvage logging had no measurable effect on daily nest survival rates of aerial-ground insectivores, in corroboration with our prediction.

Nest height appeared in two of the three top-ranking models of DSR for mountain bluebird. Year postfire and calendar year appeared in the top models as well, although model uncertainty was evident for mountain bluebird. Daily survival rate of nests for this species increased as nest height increased (Table 4 and Fig. 2), support for our nest height hypothesis. Nest height and year postfire were of nearly equal importance (RI values of 0.43 and 0.42, respectively) among models. Although postfire period did not appear in the top models, its RI value of 0.19 provided some support for the influence of this covariate on mountain bluebird DSR. Other covariates in the mountain bluebird models had low RI values (0.06–0.12).

Results for two species supported our prediction regarding distance to unburned forest. Nest survival probability for black-backed woodpecker and western bluebird nests increased as a function of distance to unburned forest (Table 4 and Figs. 1 and 2). Distance to unburned forest had the highest importance (RI = 0.58) to DSR of black-backed woodpecker, whereas supportive evidence for other covariates was deficient (range in RI values 0.02–0.15).

Northern flicker was the only species that did not support any prediction and for which the null model (no covariates) appeared in top models of DSR. Model selection uncertainty for this species was high; seven models had AIC_c values within two points of the top model (Table 3). Relative importance values for the covariates in the flicker models also reflected uncertainty, with nearly equal importance for four covariates (year postfire [RI = 0.28], postfire period [RI = 0.24], precipitation [RI = 0.22], and temperature [RI = 0.19]).

DISCUSSION

Multiple abiotic and biotic factors, other than direct effects of salvage logging, affected daily nest survival rates of breeding cavity-nesting birds. The salvage logging in our study area was designed to maintain a portion of large diameter snags, those >23 cm diameter at breast height with an average density of 45.0 ± 5.1 snags/ha, that appeared to provide adequate nesting substrate without apparent effects on survival of most cavity-nesting birds. Hairy woodpecker was the only species whose daily survival rates were significantly lower in salvaged forests. This beetle-foraging woodpecker had higher survival in unlogged forests, where snags were more abundant and likely provided greater foraging opportunities (cf. Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Saab et al. 2007). In contrast, partially salvage logged areas had no measurable impact on nest survival of aerial-ground insectivores (Lewis's woodpecker, and western and mountain bluebirds), a pattern consistent with trends reported for nest density and nesting success of these species in similarly managed burned forests (Haggard and Gaines 2001, Saab et al. 2007). The top-ranked models for hairy and Lewis's woodpeckers were composed of covariates that corroborated with categorical comparisons of nest success reported earlier by Saab et al. (2007; logged vs. unlogged and early vs. late postfire period), compelling evidence for the strong influence of these covariates on their nest survival.

Abiotic factors of precipitation and temperature had significant associations with nest survival in the context of postfire salvage logging, a key finding previously unreported that may have implications for nest survival with anticipated climate change. Daily nest survival rates decreased with increasing temperatures in our burned forest study areas for two species. After wildfire, forests lack canopy closure and snags lack insulation created by limbs and foliage. Such conditions likely cause extremely warm temperatures that may exceed heat tolerance levels of eggs or nestlings (cf. Conway and Martin 2000, Wiebe 2001, Jehle et al. 2004). Lewis's woodpecker and western bluebird were the species whose nest survival declined with increasing temperatures, and these two species had the latest average fledge dates (18 Jul and 28 Jun, respectively) among the six species in our study area (range 15 Jun–18 Jul). Consequently these two species attempted nesting during the hottest period of the breeding season.

We also expected increased precipitation to decrease nest survival of aerial-ground insectivores through reduced insect activity (Rodenhouse 1992, Neal et al. 1993, Dinsmore et al. 2002, Jehle et al. 2004). Only Lewis's woodpecker experienced reduced nest survival with increasing precipitation. This species relies on flying arthropods as its primary food source during the breeding season, particularly as compared to other cavity nesters in our study area. Increased precipitation in temperate environments can reduce arthropod activity and subsequently decrease food availability for insectivorous birds, potentially having negative consequences on their nest survival and productivity (cf. Rodenhouse 1992, Neal et al. 1993, Dinsmore et al. 2002, Jehle et al. 2004).

Contrary to our expectations, we found no evidence that nest survival of aerial-ground insectivores would increase with time since fire, or that nest survival of black-backed or hairy woodpeckers would decrease. Despite increasing nest densities of Lewis's woodpeckers in the late postfire period (Saab et al. 2007), daily nest survival rates declined for this species. Food availability for this species is expected to increase in later postfire periods (Hobson and Schieck 1999, Hannon and Drapeau 2005), and the exact mechanism responsible for declining nest survival rates is unknown. Lewis's woodpeckers may have to spend more time defending their nests against increasing numbers of predators as time since fire increases, resulting in declining nest success (cf. Saab and Vierling 2001). Western bluebird nest densities increased in later postfire years along with increasing nest numbers of Lewis's woodpecker (Saab et al. 2007). However, nest survival for this bluebird species did not decline in later years.

We found evidence of an effect of distance to unburned forest on western bluebird and black-backed woodpeckers. Nests farther from unburned areas were more successful, suggesting that nest survival of cavity nesters could be improved if unlogged reserves are located centrally within postfire forests and distant from unburned habitats. Unburned forests may act as a source of nest predators (Saab et al. 2004), such as red squirrels, which are conifer seed specialists associated with live trees and dense canopy cover (Carey 1989, Fisher and Wilkinson 2005, Holloway and Malcolm 2006, Russell et al. 2010). Unburned forested areas near a nest may also indicate a lower quality territory where foraging adults must travel farther to obtain food. However, Nappi and Drapeau (2009) found that black-backed woodpeckers produced more nestlings near unburned edges in recently burned boreal forests of Quebec. Food availability and nest predator assemblages likely differ between Idaho dry coniferous forests dominated by ponderosa pine and the Quebec boreal forests dominated by black spruce (*Picea mariana*). Regardless, in our study area, nest survival for black-backed woodpecker and western bluebird improved in areas more centrally located within the burn, suggesting that these two species may need larger burned forests for successful nesting in dry coniferous forests.

Mountain bluebird was the only species for which nest survival had a positive relationship with nest height, providing support for our hypothesis regarding nest height. Bluebirds are secondary cavity nesters and rely on other species for cavity excavation, although available cavities did not appear limiting in our study area (Saab et al. 2009). Nest cavity heights were similarly selected by individuals within a species (Appendix), thus we were unable to detect an association between height and nest survival for most species. Evidence varies for a nest height effect on survival of cavity-nesting birds (Rendell and Robertson 1989, Li and Martin 1991, Albano 1992, Christman and Dhondt 1997, Wiebe 2001). The lack of a nest height relationship with survival for most species in our study area could be related to a reduced risk of predation due to lower densities of squirrels and other small mammals in forests recently burned by wildfire (Fisher and Wilkinson 2005). Additionally, a swamping effect (cf. Ims 1990) could occur for nest predators searching for occupied cavities in recent burns, where snags and nest cavities are very abundant relative to unburned forests.

Nest survival in relation to salvage logging practices and time since fire was largely consistent with trends reported for nest density of the species we studied (Saab et al. 2007), with the exception of Lewis's woodpecker. For black-backed woodpecker, northern flicker, and mountain bluebirds on our study sites, nest densities were significantly higher but nest survival rates did not differ in unlogged compared to logged areas (Saab et al. 2007), suggesting that densities could be reliable indices of overall productivity. For these three species, unlogged forests with high nest densities will produce more fledglings than logged forests with fewer nests and equivalent survival rates. Additionally, hairy woodpecker had not only higher nest densities but also significantly higher nest survival rates in unlogged forests. In contrast, Lewis's woodpecker daily nest survival rates decreased although their nest densities increased during the later postfire years. Results for hairy and Lewis's woodpeckers suggest that logged forests and older burned forests on our study sites may represent sink habitat for these two species, respectively (Pulliam 1988, Runge et al. 2006). Conversely, Gentry and Vierling (2007) reported that older burned forests (14–17 yr after wildfire) in South Dakota functioned as source habitat for Lewis's Woodpecker. Differences in predator assemblages in the two study areas may account for the disparity in our conclusions. American black bears and red squirrels were extirpated or conspicuously absent in the South Dakota study area (Gentry and Vierling 2007), whereas these two species were commonly observed and documented nest predators in our Idaho study area and were well known nest predators of woodpeckers (Walters and Miller 2001, Tozer et al. 2009).

Although our study was observational with few spatial replicates, we had large samples of years (11 yr) and nests (1,797 nests) from which to draw conclusions. Application of our results is likely limited to dry coniferous forests of the interior northwestern United States, where other studies of habitat use and nesting success corroborate much of our results (Haggard and Gaines 2001, Hutto and Gallo 2006, Gentry and Vierling 2007).

Partially salvage logged areas, designed to maintain large snags, provided nesting habitat for Lewis's woodpeckers, northern flickers, and western and mountain bluebirds without discernable impacts on nest survival. Unlogged forests, however, would produce more fledglings (nest densities × nest survival), and consequently support a higher carrying capacity of cavity nesters due to the higher densities of northern flicker, mountain bluebird, and hairy and black-backed woodpeckers. Later years (>5 yr postfire) after wildfire may represent sink habitat for Lewis's woodpeckers with lower nest survival despite high densities.

MANAGEMENT IMPLICATIONS

Increased wildfires and tree mortality, followed by more opportunities for salvage logging, are expected with climate change (Lindenmayer and Noss 2006). Managers implementing carefully planned salvage logging prescriptions that include both unlogged reserves and partially logged areas can expect to maintain habitat for successfully breeding cavity-nesting birds in the interior northwestern United States. Our results indicate that reserving unlogged postfire forests will provide habitat for successful nesting of beetle-foraging woodpeckers. Management of partially logged areas that retain moderate diameters (>23 cm dbh) and densities (>45 snags/ha) of snags will likely result in successful breeding of cavity-nesting birds whose diet does not rely on bark and wood-boring beetles. Additionally, our results suggest that nest survival for some species of cavity-nesting birds could be improved if unlogged reserves are located centrally in postfire forests, distant from unburned habitats that potentially serve as sources of nest predators.

ACKNOWLEDGMENTS

Our primary source of funding was United States Department Agriculture, Forest Service, Rocky Mountain Research Station. Other funding was provided by the Intermountain and Pacific Northwest Region of the Forest Service, the Boise National Forest, principally the Mountain Home District, the National Fire Plan, and the Joint Fire Science Program. L. Donohoo provided logistical support and assistance with study design. J. Evans quantified burn severity on our wildfire locations. We thank all the many field assistants that collected data during the study. We appreciate the thoughtful comments by K. Mellen-Mclean, C. Groves, C. Vojta, J. Hollenbeck, and two anonymous reviewers.

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Associate Editor: Leonard Brennan.

Appendix: Mean, minimum, and maximum value for variables measured at nests of six cavity-nesting bird species in burned forests of western Idaho, 1994–2004.

	Nest ht (cm)			Distance to unburned (m)			Precipitation (mm)			Max. daily temp. (°C)		
Bird species	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum	$\bar{x}$	Minimum	Maximum
Lewis's woodpecker (n = 716)	11.3	1.8	6.7	194.1	0	588.1	0.9	0	12.5	28.3	11.9	39.7
Hairy woodpecker (n = 183)	9.5	1.8	36.5	189.3	0	544.5	1.4	0	8.8	23.6	12.4	38.9
Black-backed woodpecker (n = 46)	8.9	2.0	23.2	158.7	0	447.6	1.7	0	14.8	22.4	7.8	33.9
Northern flicker (n = 293)	7.0	0.4	30.0	190.8	0	624.9	1.2	0	10.5	25.1	11.9	39.7
Western bluebird (n = 317)	6.8	0.9	29.3	224.7	0	571.9	1.0	0	10.5	26.5	11.9	38.9
Mountain bluebird (n = 242)	7.6	0.2	26.5	176.9	0	571.7	1.0	0	10.5	25.6	12.0	38.9

See Table 1 for variable descriptions.