

WOODPECKER NEST SURVIVAL IN BURNED AND UNBURNED MANAGED PONDEROSA PINE FORESTS OF THE NORTHWESTERN UNITED STATES

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Abstract. Woodpeckers are particularly susceptible to habitat changes resulting from forest management because of their reliance on trees and snags for nesting and foraging. However, the influence of habitat variables on the reproductive success of woodpeckers has received less attention than it has in other avian taxonomic groups. We estimated nest-survival rates for the White-headed Woodpecker (*Picoides albolarvatus*), Hairy Woodpecker (*P. villosus*), and Northern Flicker (*Colaptes auratus*) in managed ponderosa pine (*Pinus ponderosa*) forests along the eastern slope of the Cascade Range in Washington, 2005–2010. Using a model-selection framework, we found that the most supported models included terms for a quadratic effect of date and habitat type for the Hairy Woodpecker, a negative effect of percent shrub cover for the White-headed Woodpecker, and a negative linear effect of date and habitat type, a negative linear effect of snag density, and a positive linear effect of tree density for the flicker. Survival rates over the entire cycle (laying + incubation + nestling stages) were 0.51 in unburned stands and 0.41 in burned stands for the Hairy Woodpecker, 0.70 for the White-headed Woodpecker, and 0.41 in unburned stands and 0.80 in burned stands for the flicker. In both habitats of our study survival rates of Hairy Woodpecker nests are lower than those reported in other studies, while those of White-headed Woodpecker nests are comparable to those reported in other areas of that species' range.

Key words: forest management, Hairy Woodpecker, nest survival, Northern Flicker, *Pinus ponderosa*, Washington, White-headed Woodpecker.

Supervivencia del Nido de Carpinteros en Bosques Manejados Quemados y No Quemados de Pino Ponderosa del Noroeste de Estados Unidos

Resumen. Los carpinteros son particularmente susceptibles a los cambios de hábitat que resultan del manejo de los bosques debido a su dependencia de árboles y tocones para anidar y forrajear. Sin embargo, la influencia de las variables del hábitat sobre el éxito reproductivo de los carpinteros ha recibido menos atención que en otros grupos taxonómicos de aves. Estimamos las tasas de supervivencia de los nidos para *Picoides albolarvatus*, *P. villosus* y *Colaptes auratus* en bosques manejados de pino ponderosa (*Pinus ponderosa*) a lo largo de la vertiente este del Cascade Range en Washington, entre 2005 y 2010. Usando un marco de trabajo de selección de modelos, encontramos que los modelos con mayor soporte incluyeron los términos de un efecto cuadrático de la fecha y del tipo de hábitat para *P. villosus*, un efecto negativo del porcentaje de cobertura de arbustos para *P. albolarvatus*, y un efecto lineal negativo de la fecha y del tipo de hábitat, un efecto lineal negativo de la densidad de tocones y un efecto lineal positivo de la densidad de árboles para *C. auratus*. Las tasas de supervivencia a lo largo del ciclo completo (estadios de puesta + incubación + pichones) fueron 0.51 en los rodales no quemados y 0.41 en los rodales quemados para *P. villosus*, 0.70 para *P. albolarvatus* y 0.41 en rodales no quemados y 0.80 en rodales quemados para *C. auratus*. En ambos hábitats de nuestro estudio las tasas de supervivencia de los nidos de *P. villosus* son menores que las reportadas en otros estudios, mientras que aquellas de los nidos de *P. albolarvatus* son comparables con las tasas reportadas para otras áreas del rango de la especie.

INTRODUCTION

The structure of contemporary ponderosa pine (*Pinus ponderosa*) forests of the inland northwest of the United States differs dramatically from historic conditions (Hessburg et al. 2005, Harrod et al. 2007). Historic forest conditions included average densities of 50 trees ha⁻¹, average diameters at breast height (dbh) of 60–70 cm, and fire-return intervals

of 5–15 years (Agee 1996, Gaines et al. 2007). As a result of selective logging (e.g., removal of trees with the largest diameters) prior to 1930 (Hessburg and Agee 2003), continued harvesting, and increased frequency of stand-replacing fires accompanied by a commensurate decline in low-intensity fires, many ponderosa pine forests are now stocked at 3–10 times their historic density, dominated by smaller trees that average 20–30 cm dbh (Harrod et al. 1999), and are prone

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to colonization of an understory of shade-tolerant trees such as Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*); Hessburg and Agee 2003, Keeling et al. 2006). To conserve wildlife populations that use ponderosa pine forests, managers require information about wildlife responses to these drastic changes from historical conditions and actions that can improve habitat quality.

Woodpeckers are considered keystone species because of their broad effects on other species. In nesting and foraging, woodpeckers create cavities and excavations that other species use (Blendinger 1999, Aitken and Martin 2007), they aid in controlling forest insects (Fayt et al. 2005), and they may help in dispersing spores of fungi that are agents of decay (Farris et al. 2004). These activities suggest that woodpeckers are disproportionately important to their ecosystems (Virkkala 2006) and account for their frequent use as indicator species by land-management agencies (Saab et al. 2007a, USDA Forest Service 2008) as well as indicators of forest birds' diversity and richness (Mikusiński et al. 2001, Drever et al. 2008).

Despite the importance of woodpeckers to forested ecosystems, few studies have examined metrics of woodpecker demography such as reproductive success or nest survival (for review see Paclík et al. 2009) or have investigated the associations of habitat characteristics with these or related metrics. While relating metrics such as nest survival to habitat is intuitively appealing (because managers can manipulate habitat features), the available information is mixed about how habitat features influence avian nest survival. For example, studies have shown that nest survival is associated with nest height (Li and Martin 1991, Fisher and Wiebe 2006a), nest concealment (Martin and Roper 1988, Rangen et al. 1999), and vegetation density (Easton and Martin 2002, Hollenbeck et al. 2011). However, other studies have demonstrated that temporal factors, such as date and nest age, account for variation in nest-survival patterns (Rossmann et al. 2007, Bonnot et al. 2008, Kozma and Kroll 2010).

In Washington, the White-headed Woodpecker (*Picoides albolarvatus*) is listed as a species of concern because of its association with old-growth ponderosa pine forests (Dixon 1995, Buchanan et al. 2003, Krannitz and Duralia 2004). Although the White-headed Woodpecker has recently been documented inhabiting early- to mid-seral managed forests (Lindstrand and Humes 2009, Kozma 2011), information is limited regarding its reproductive success in these forests or in other areas of its range (notable exceptions include Wightman et al. 2010, Hollenbeck et al. 2011). To address this information gap, we evaluated temporal factors and habitat features associated with nest survival of the White-headed Woodpecker and two sympatric woodpeckers, the Hairy Woodpecker (*P. villosus*) and Northern Flicker (*Colaptes auratus*), breeding within managed ponderosa pine forests in the eastern Cascade Range. The Hairy Woodpecker is a common generalist (Ripper et al. 2007), occurring in a wide variety of forest types across North America.

While this species has a wide geographic distribution, few quantitative data exist on its breeding biology (Jackson et al. 2002), with most recent research on reproductive success focused within burned forests (Saab and Dudley 1998, Saab et al. 2007b, Vierling et al. 2008). Similarly, the Northern Flicker is also a forest generalist, but detailed information on its breeding biology is restricted to aspen-dominated habitats (Wiebe and Moore 2008).

Our objectives were to (1) evaluate nest survival of each species in burned and unburned ponderosa pine forests with a recent history of management, (2) examine temporal and spatial factors that influence nest survival and compare these factors by species, and (3) document clutch size, egg success, fledging rates, and nest-initiation dates for each species. We predicted that daily survival rates should decrease through the nesting period and be lowest during the nestling phase because woodpecker nestlings beg with loud calls (Briskie et al. 1999, Tozer et al. 2009), which may attract predators. We also predicted that cavity height should be positively associated with nest survival (Fisher and Wiebe 2006a, Mahon and Martin 2006) and that nests in burned habitats should have higher survival (Saab and Vierling 2001, Saab et al. 2007b, Kozma and Kroll 2010).

METHODS

STUDY AREA

We conducted our study within five areas along the eastern slope of the Cascade Range in southern Kittitas, Yakima, and northern Klickitat counties, Washington, from 2005 to 2010 (Fig. 1). The eastern slope of the Cascades is characterized by complex topography (Everett et al. 2000) and hot, dry summers, with over 80% of the annual precipitation falling during winter (Wright and Agee 2004). Our study areas were located on lands managed by the Okanogan–Wenatchee National Forest, the Washington Department of Natural Resources, and three private landowners. We monitored 30 sites in the five study areas, with each site containing one pair of breeding White-headed Woodpeckers. We selected these sites opportunistically on the basis of reviews of proposed timber harvests where we encountered White-headed Woodpeckers and by reviewing a database of historical sightings maintained by the Washington Department of Fish and Wildlife (Buchanan et al. 2003). The sites' elevation ranged from 560 to 1270 m.

The overstory of the study sites was dominated by ponderosa pine with a small component of Douglas-fir, western larch (*Larix occidentalis*), grand fir, and quaking aspen (*Populus tremuloides*), depending upon elevation and topography. The understory was dominated by antelope bitterbrush (*Purshia tridentata*), snowbrush ceanothus (*Ceanothus velutinus*), wax currant (*Ribes cereum*), snowberry (*Symphoricarpos alba*), and birch-leaved spiraea (*Spiraea betulifolia* var. *lucida*). Overall, sites were characteristic of the "hot dry shrub/herb" (ponderosa

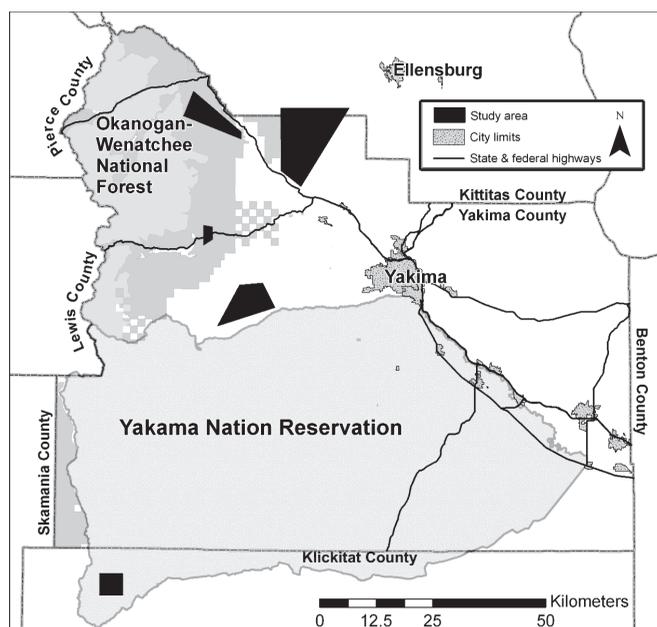


FIGURE 1. Location of study areas searched for Hairy Woodpecker, Northern Flicker, and White-headed Woodpecker nests in Kittitas, Yakima, and Klickitat counties, Washington, 2005–2010.

pine/bitterbrush/bluebunch wheatgrass [*Agropyron spicatum*] and “warm dry shrub/herb” (Douglas-fir/bitterbrush/bluebunch wheatgrass) vegetation types described by Harrod et al. (1999). Twenty sites were in unburned managed stands where timber had been harvested within the past 16 years, and 10 sites were in burned and salvaged stands representing 1–10 years post-fire. Twelve unburned sites were managed by pre-commercial thinning, where small-diameter understory trees were removed leaving more large-diameter trees: average of 157.8 trees ha⁻¹ >10.16 and ≤40.6 cm dbh (95% CI: 128.9, 186.8) and 68.0 trees ha⁻¹ >40.6 cm dbh (95% CI: 41.7, 94.4); $n = 7$ sites; data summarized from Kozma (2011). Eight unburned sites were managed by thinning from below, dominant and co-dominant trees being removed, resulting in evenly spaced trees with a similar dbh and fewer large-diameter trees: average of 136.4 trees ha⁻¹ >10.16 and ≤40.6 cm dbh, (95% CI: 106.5, 166.2) and 27.2 trees ha⁻¹ >40.6 cm dbh (95% CI: 14.4, 40.1); $n = 7$ sites; data summarized from Kozma (2011). Salvage logging occurred in burned stands, and the majority of merchantable dead trees were removed, leaving larger overstory trees that survived the fire mixed with fire-killed trees of smaller diameter.

NEST SEARCHING AND MONITORING

We searched for nests from early April to early July at a subset of the 30 sites each year because of time constraints. We searched sites at least once every 7–10 days, resulting in approximately equal search effort at each site. To make finding nests easier, we used playbacks of calls and drumming to locate White-headed and Hairy Woodpeckers on breeding territories (Johnson et al. 1981, Nappi and Drapeau 2009). We

followed either sex during the nesting season to find cavities (because both sexes excavate cavities and incubate eggs) or we relied on adults carrying food, adults’ distress calls, or sounds of begging chicks to reveal the cavity’s location. We followed the same procedure for locating Northern Flicker cavities, with the exception of call playbacks, and we also checked cavities nesting flickers used in previous years because of their propensity to reuse cavities (Gentry and Vierling 2008).

We viewed contents of cavities up to 11 m above ground with a Tree Top Peeper IV nest-inspection system (Sandpiper Technologies, Inc., Manteca, CA; Kozma and Kroll 2010). When checking a nest, we recorded the date and time, stage of nesting, clutch size, number of young, and an estimate of nest age (determined by incubation start date or hatch date if known, or feather development of young). We attempted to check each nest at least once a week until we determined its fate. We considered a nest successful if we observed ≥1 fledgling near the cavity or if the cavity was occupied by ≥1 young of known age that were within 2 days of fledging. We recorded nests as depredated if all eggs or young were gone before the anticipated time of fledging. If we found a nest during incubation, we calculated nest-initiation dates (day the first egg was laid) by backdating from the day of hatching or fledging, or from the age of young as estimated from feather development, assuming that incubation began on the day the last egg was laid and that one egg was laid each day (Pechacek 2006). We calculated egg success by dividing the number of young fledged by the number of eggs laid (Murray 2000).

VEGETATION SAMPLING

We sampled the vegetation surrounding each nest (cavities containing ≥1 egg) after cavities were vacated. At each nest tree or snag, we recorded cavity height, tree or snag height, dbh, tree or snag species, and canopy cover. We measured cavity height and tree or snag height with a meter tape or clinometer. Using a spherical crown densiometer at the base of the nest tree or snag, we measured canopy cover in the four cardinal directions then averaged the four estimates (Farnsworth and Simons 1999).

We sampled vegetation in 5- and 11.3-m-radius circles centered on each nest tree or snag (modified from James and Shugart 1970). Within the 5-m circle, we visually estimated the percent cover of each shrub species. Within the 11.3-m circle (0.04 ha) we tallied trees and snags in three dbh categories (25.4–<50.8 cm, 50.8–<76.2 cm, and ≥76.2 cm). We measured local-scale habitat features because they are frequently used to investigate the influence of vegetation variables on woodpeckers’ nest-site selection and nest survival (Li and Martin 1991, Fisher and Wiebe 2006a, Bonnot et al. 2008, Tozer et al. 2009). Although landscape-level components may be important at influencing woodpeckers’ reproductive biology (Mazgajski and Rejt 2006, Robles et al. 2008, Wightman et al. 2010), we focus on local-scale habitat features because they are most likely to influence nest predation, the

largest source of nest failure in our study. After vegetation sampling was completed, we marked each nest tree or snag with a numbered aluminum tag.

STATISTICAL ANALYSIS

We used an information-theoretic framework (Burnham and Anderson 2002) to evaluate support for 13 candidate models of survival of woodpecker nests. We fit models in a two-stage process. First, we fit four models to account for temporal variation in survival, including date, a quadratic effect of date (date^2), nest stage (i.e., laying, incubation, or nestling; Grant et al. 2005), and an interaction between date and nest stage, as well as constant (intercept only) and global models. We used the best model from this first stage as a base model to examine seven additional models that included spatial factors such as differences in habitat characteristics, differences among trees and snags used for nesting, and habitat type (burned or unburned). We considered the following habitat characteristics: cavity height (m), dbh of the nest tree or snag (cm), total number of snags (sum of all snags ≥ 25.4 cm dbh 0.04 ha^{-1}), total number of live trees (sum of all trees ≥ 25.4 cm dbh 0.04 ha^{-1}), percent shrub cover, and canopy cover. We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation.

We used the logistic-exposure method (Shaffer 2004) to model daily nest survival. This method 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, we treated each interval between visits to a nest as one observation. We calculated period-survival rates (PSR, laying + incubation + nestling stages; Shaffer and Thompson 2007) and defined period lengths as follows: for egg laying, 4 days for White-headed and Hairy Woodpeckers and 7 days for the Northern Flicker (on the basis of mean clutch sizes; Table 1); for incubation, 12 days for each species (Table 1); for the nestling period, 25, 26, and 27 days for the Northern Flicker (Wiebe and Moore 2008), White-headed Woodpecker (Garrett et al. 1996), and Hairy Woodpecker (Jackson et al. 2002), respectively. This resulted in a 42-, 43-, and 44-day nesting period for the White-headed Woodpecker, Hairy Woodpecker, and Northern Flicker, respectively. Using a logit-link function, we fit nest-survival models with PROC GENMOD (SAS/STAT version 9.1, SAS Institute, Cary, NC).

We examined the fit of the global model (the model with all covariates included in the analysis) by the goodness-of-fit test of Hosmer and Lemeshow (2000). We identified models with the most support by using Akaike's information criterion adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). We computed Akaike weights (w_i) for each model, where w_i represents the weight of evidence for a specific model being the best approximating model of those in the candidate

set (Burnham and Anderson 2002). We calculated effective sample size (n) as the number of days that nests were known to survive plus the number of intervals in which a failure occurred (Rotella et al. 2004). We examined confidence intervals for parameter estimates and graphed fitted values as a function of the independent covariates (Hosmer and Lemeshow 2000).

As suggested by an anonymous reviewer, we calculated the source/sink status of the three species in the habitats that we sampled. This calculation required an estimate of the mean number of female fledglings per female per year (FFFY) needed to offset mortality. We used estimates of adults' and juveniles' survival to determine mortality (Tozer et al. 2011). We obtained survival of adult Northern Flickers (0.43) by averaging rates of survival of male and female flickers (Fisher and Wiebe 2006b) and that of adult Hairy Woodpeckers in the Northwest (0.61) from the Monitoring Avian Productivity and Survivorship program (Michel et al. 2006). We could find no published rates of survival of adults or juveniles of the White-headed Woodpecker. Instead, we used the lowest (0.26), the highest (0.93), and then the average rates of survival of *Picoides* woodpeckers (0.64) (Wiebe 2006) to estimate the lowest, highest, and average FFFY needed to offset mortality. We assumed that juvenilesurvivorship is 50% of adult survivorship and so divided adult survival rates in half to obtain juvenile survival rates for each species (e.g., Nappi and Drapeau 2009). We then calculated FFFY as $(1 - \text{adult survivorship}) / \text{juvenile survivorship}$ (Donovan et al. 1995). We calculated annual productivity (the number of female fledglings per adult female) by dividing the number of fledglings per successful nest by two (assuming an equal sex ratio of nestlings; Saab and Vierling 2001) and then multiplying by the period-survival rate (Tozer et al. 2011). We considered the population to be a potential demographic source if annual productivity was greater than FFFY and a potential sink if annual productivity was less than FFFY (Saab and Vierling 2001).

Because of small sample sizes in some years, we combined nests across years to summarize demographic data (Barber et al. 2001). We used SYSTAT version 8.0 (SPSS, Chicago) to calculate descriptive statistics including mean and 95% CI. Results in the text are presented as mean \pm SE unless otherwise noted.

RESULTS

We monitored 67 White-headed Woodpecker, 69 Hairy Woodpecker, and 100 Northern Flicker nest attempts. We had data sufficient to analyze the survival of 55 White-headed Woodpecker (35 in unburned and 20 in burned), 54 Hairy Woodpecker (17 in unburned and 37 in burned), and 88 Northern Flicker (43 in unburned and 45 in burned) nests (effective sample size = 1577, 1342, and 2680, respectively). Of these 197 nests, 52%, 23%, and 25% were found during the egg-laying, incubation, and nestling stages, respectively. The mean interval between nest visits was 5.9 ± 0.1 days ($n = 1003$). The

TABLE 1. Mean incubation period, clutch size, number of young fledged per successful nest, number of unhatched eggs, number of young that died prior to fledging, and nest-initiation (Julian) date for the White-headed Woodpecker, Hairy Woodpecker and Northern Flicker in managed ponderosa pine forests, eastern Cascade Range, Washington, 2005–2010.

	White-headed Woodpecker				Hairy Woodpecker				Northern Flicker			
	<i>n</i> ^a	Mean	Range	CI ^b	<i>n</i>	Mean	Range	CI	<i>n</i>	Mean	Range	CI
Incubation period	17	12.3	11–14	11.9, 12.7	9	12.4	11–13	11.9, 13.0	14	12.2	11–13	11.9, 12.5
Clutch size	51	3.9	2–5	3.64, 4.08	55	3.8	3–5	3.64, 3.96	82	7.0	4–12	6.76, 7.31
No. young fledged	47	2.6	1–4	2.41, 2.86	40	2.9	1–4	2.65, 3.20	58	6.1	2–9	5.75, 6.39
No. unhatched eggs	41	0.6	0–2	0.40, 0.82	50	0.4	0–2	0.26, 0.61	48	0.5	0–3	0.25, 0.67
No. young died ^c	42	0.6	0–2	0.35, 0.75	33	0.2	0–2	0.06, 0.42	41	0.5	0–5	0.20, 0.82
Nest-initiation date ^d	63	148	132–175	145, 150	61	125	105–153	122, 127	95	137	121–164	135, 139

^aNumber of nests.

^b±95% confidence interval.

^cNumber of young assumed to have died from starvation or partial nest predation prior to fledging.

^dDate the first egg was laid.

global model of nest survival provided an adequate fit for the Hairy Woodpecker ($\chi^2 = 8.78$, $df = 8$, $P = 0.36$), White-headed Woodpecker ($\chi^2 = 6.0$, $df = 8$, $P = 0.64$), and Northern Flicker ($\chi^2 = 6.87$, $df = 8$, $P = 0.65$).

The best models from the first stage of the logistic-exposure analysis included quadratic effects of date ($w_i = 0.70$), a constant time trend ($w_i = 0.45$), and a linear effect of date ($w_i = 0.57$) for the Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker, respectively. The most supported

model for the Hairy in the second stage of the analysis included an effect of habitat type (Table 2). Daily survival rates were higher in unburned stands than in burned stands (Fig. 2). For the White-headed, the most supported model included a negative association with shrub cover (Tables 2 and 3, Fig. 3). The most supported model for the flicker included an effect of habitat type, a negative linear association with the number of snags, and a positive linear association with the number of live trees (Tables 2 and 3). Daily survival rates were lower in unburned

TABLE 2. Best-ranked nest-survival models (cumulative weight ≥ 0.90) for the Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker in managed ponderosa pine forests, eastern Cascade Range, Washington, 2005–2010.

Species	Model	Log(<i>L</i>)	<i>K</i>	ΔAIC_c	w_i
Hairy Woodpecker ^a	Habitat type	107.6	4	0.00	0.21
	Base	109.9	3	0.29	0.19
	Dbh	108.2	4	0.60	0.16
	Snags	109.2	4	1.57	0.10
	Shrub cover	109.2	4	1.63	0.09
	Canopy cover	109.4	4	1.74	0.09
White-headed Woodpecker ^b	Shrub cover	113.7	2	0.00	0.27
	Base	116.5	1	0.75	0.18
	Snags	114.7	2	0.97	0.17
	Number of live trees	116.0	2	2.23	0.09
	Cavity height	116.1	2	2.38	0.08
	Habitat type	116.4	2	2.68	0.07
	Dbh	116.5	2	2.73	0.07
Northern Flicker ^c	Snags + Number of live trees	176.7	5	0.00	0.58
	Number of live trees	180.8	4	2.09	0.21
	Global	170.9	9	2.27	0.19
	Snags	186.8	4	8.11	0.01

^aThe base model includes only a quadratic effect of date. All other models include the base model in addition to habitat covariates. Lowest $AIC_c = 115.6$.

^bThe base model includes a constant effect (intercept only). Lowest $AIC_c = 117.7$.

^cAll models include a linear effect of date in addition to the habitat-type covariate. Lowest $AIC_c = 186.7$.

TABLE 3. Parameter estimates for the best models of daily nest survival for the Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker in managed ponderosa pine forests, eastern Cascade Range, Washington, 2005–2010.

Species	Parameter	Estimate	95% confidence interval
Hairy Woodpecker	Unburned ^a	-44.62	-85.30, -3.93
	Burned	-45.47	-86.42, -4.52
	Date	0.70	0.15, 1.24
	Date ²	-0.002	-0.0042, -0.0006
White-headed Woodpecker	Intercept	4.77	4.22, 5.31
	Shrub cover	-0.44	-0.94, 0.05
Northern Flicker	Unburned ^a	10.67	5.77, 15.56
	Burned	12.04	7.01, 17.06
	Number of snags	-0.47	-0.87, -0.08
	Number of live trees	1.025	0.23, 1.82

^aSeparate intercepts were fit for unburned and burned stands.

stands than in burned stands (Fig. 4). The PSRs for White-headed Woodpecker nests were 0.79 (95% CI: 0.59, 0.90), 0.66 (95% CI: 0.50, 0.78), and 0.48 (95% CI: 0.18, 0.73) for 0%, 25%, and 50% shrub cover, respectively. The overall PSR (constant + shrub cover) for the White-headed Woodpecker was 0.70 (95% CI: 0.55, 0.82). Hairy Woodpecker and Northern Flicker nests initiated earlier in the season had survival rates higher than nests initiated later in the season, regardless of habitat type. The PSRs of early- (initiated on 29 April) and late-season (initiated on 14 May) Hairy Woodpecker nests in unburned stands were 0.62 (95% CI: 0.30, 0.85) and 0.44 (95% CI: 0.19, 0.68); in

burned stands, PSRs were 0.56 (95% CI: 0.20, 0.79) and 0.34 (95% CI: 0.09, 0.63). The overall PSR (date² + habitat type) for the Hairy Woodpecker (nests initiated on 12 May, the average starting date) was 0.51 (95% CI: 0.26, 0.71) in unburned stands and 0.41 (95% CI: 0.15, 0.66) in burned stands. We estimated PSRs for the Northern Flicker by holding the number of snags and live trees at their average values of 0.80 and 1.6, respectively. The PSRs for early- (initiated on 29 April) and late-season (initiated on 29 May) Northern Flicker nests in unburned stands were 0.71 (95% CI: 0.47, 0.86) and 0.34 (95% CI: 0.10, 0.60); in burned stands, PSRs were 0.92 (95% CI: 0.79,

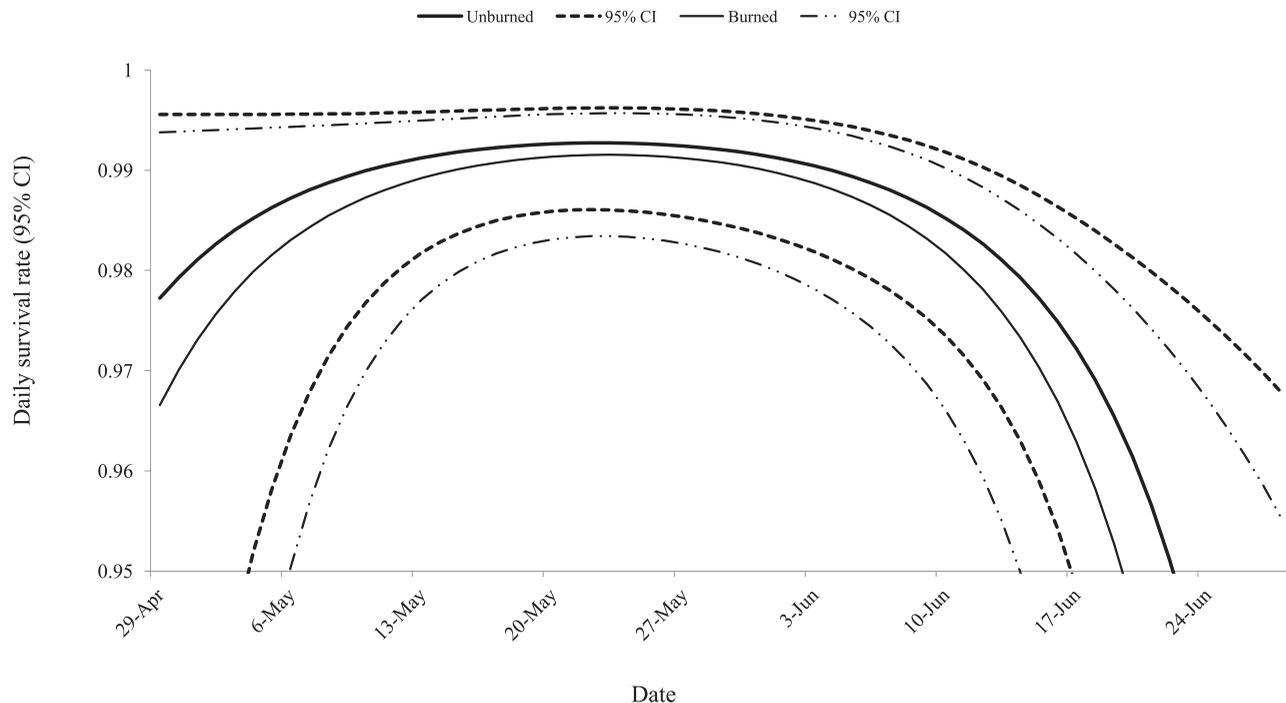


FIGURE 2. Daily survival rates and 95% CI for Hairy Woodpecker nests, estimated from a model with quadratic date and habitat-type effects, eastern Cascade Range, Washington, 2005–2010.

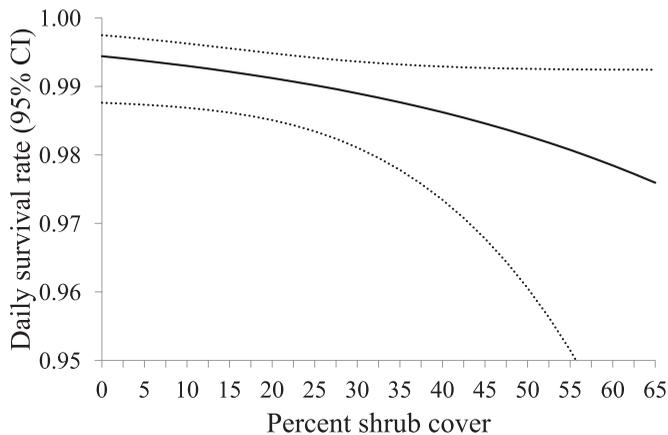


FIGURE 3. Daily survival rates and 95% CI for White-headed Woodpecker nests, estimated from a model with shrub-cover effect, eastern Cascade Range, Washington, 2005–2010.

0.97) and 0.76 (95% CI: 0.50, 0.89). The overall PSR (date + habitat type) for the Northern Flicker (nests initiated on 24 May, the average starting date) was 0.41 (95% CI: 0.17, 0.64) in unburned stands and 0.80 (95% CI: 0.58, 0.91) in burned stands. Based on the approximations that we used for mortality (Fig. 5), the Hairy Woodpecker's annual productivity was not high enough to compensate for adult and juvenile mortality. The White-headed Woodpecker's annual productivity was high enough to compensate for adult and juvenile mortality only if adults' survival rate was 0.93 (i.e., lowest FFFY). The Northern Flicker's annual productivity was sufficient to compensate for mortality, but only in burned stands (Fig. 5).

Estimates of demographic variables were most similar for the Hairy and White-headed Woodpeckers (Table 1). None of the demographic variables differed by habitat type for either of these species, which is why we pooled these variables and do not present them separately. Northern Flickers laid larger clutches (Table 1) than either Hairy or White-headed Woodpeckers and so fledged more young per successful nest (Table 1). Clutch sizes of the Hairy and White-headed Woodpeckers were nearly identical (Table 1). The number of unhatched eggs and the number of young dying prior to fledging were similar for all three species (Table 1). The three species' mean nest-initiation date differed (Table 1), with Hairy Woodpeckers nesting earliest (mean nest-initiation date 5 May) and White-headed Woodpeckers nesting the latest (mean nest-initiation date 28 May). Predation accounted for 68% ($n = 52$) of all nest failures with nest usurpation by other cavity-nesting birds being responsible for 12% ($n = 9$) of failures (Table 4). Egg success was 58% for the Northern Flicker, 57% for the Hairy Woodpecker, and 50% for the White-headed Woodpecker.

DISCUSSION

In order to conserve populations of cavity-nesting birds, particularly keystone species such as woodpeckers, managers

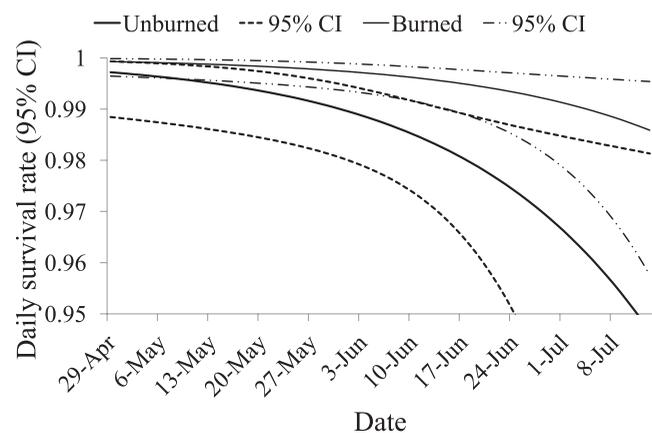


FIGURE 4. Daily survival rates and 95% CI for Northern Flicker nests estimated from a model containing a linear effect of date, number of snags, and number of live trees and habitat type, eastern Cascade Range, Washington, 2005–2010. Number of snags and live trees were held at their average values (0.80 snags 0.04 ha^{-1} and 1.6 trees 0.04 ha^{-1}).

require information about factors associated with nest survival. With few exceptions, we found little support for an association between woodpeckers' nest survival and the habitat variables that we measured. Instead, temporal covariates and habitat type explained most of the variation we found. Our ability to estimate the populations' status as a source or sink was limited because we were unable to measure adults' and juveniles' survivorship. Therefore, our estimates of source–sink status have a substantial degree of uncertainty associated with them. We suggest that further studies investigate mortality of adults and juveniles of these three species within burned and unburned managed ponderosa pine forests so these populations' status as sources or sinks can be estimated more accurately.

WHITE-HEADED WOODPECKER

The White-headed Woodpecker's nest survival was negatively associated with shrub cover. We attributed 83% of its nest failures to predation. We observed the yellow pine chipmunk (*Tamias amoenus*), Douglas's squirrel (*Tamiasciurus douglasii*), and golden-mantled ground squirrel (*Spermophilus lateralis*) in or near nest cavities and think that these species accounted for most cases of predation. These species or genera are known to feed on eggs and small nestlings (Reitsma et al. 1990, Craig 1998) and, with the exception of the Douglas squirrel, are primarily terrestrial. As shrub cover around nest sites increases, populations of some small mammals such as the yellow pine chipmunk increase (Smith and Maguire 2004), and the ability of adult woodpeckers to detect ground-traveling predators as they approach the nest snag may decrease, resulting in higher nest-predation rates. White-headed Woodpeckers excavate cavities close to the ground ($3.9 \pm 0.3 \text{ m}$, $n = 76$; JMK unpubl.

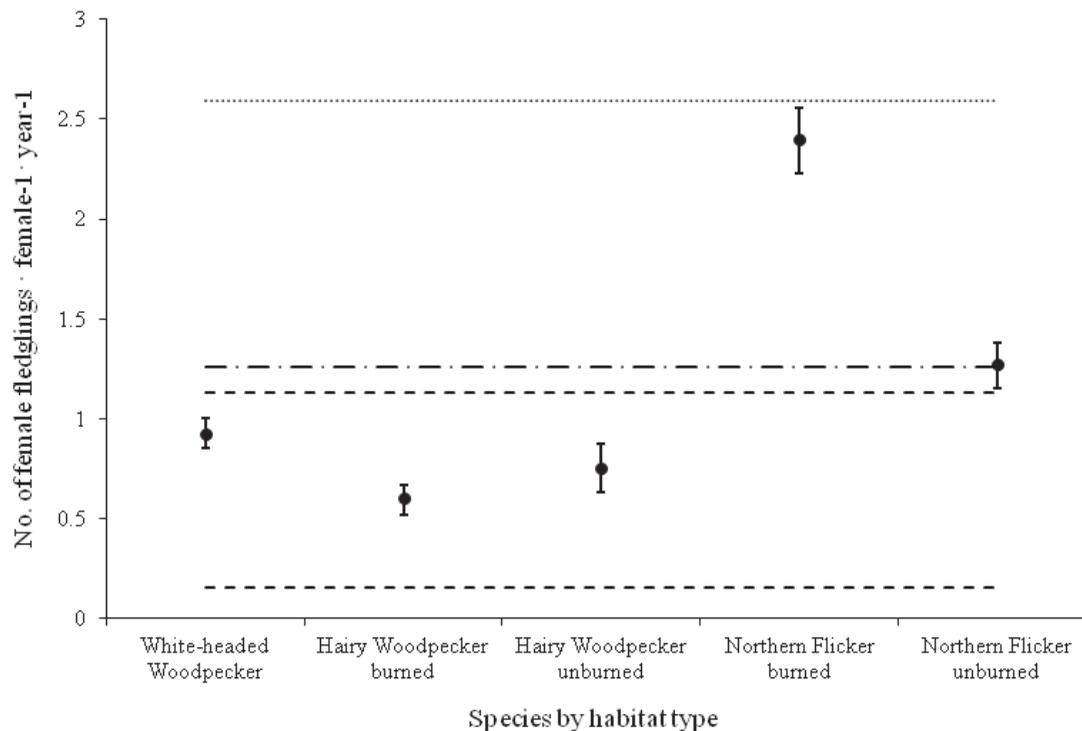


FIGURE 5. Number of female fledglings per female per year (FFFY) for the White-headed Woodpecker, Hairy Woodpecker, and Northern Flicker, eastern Cascade Range, Washington, 2005–2010. The upper and lower vertical lines represent the 95% confidence interval. The solid dot represents the mean FFFY. Horizontal dashed lines (---) show the lowest and mean estimates of the number of female White-headed Woodpecker nestlings required to offset mortality. We did not plot the highest estimate of FFFY. Horizontal line of alternating dots and dashes (-·-·-) is the number of female Hairy Woodpecker nestlings required to offset mortality. Horizontal dotted line (.....) is the number of female Northern Flicker nestlings required to offset mortality.

data), so the early detection of predators may be critical to nest defense, particularly if predators are more visible at nest sites surrounded by less understory vegetation (Belles-Isles and Picman 1986, Finch 1989).

Our estimated PSR for the White-headed Woodpecker (0.70) is within the range reported for this species in Oregon and Idaho, suggesting that these managed ponderosa pine stands can provide breeding habitat for this species. For example, Wightman et al. (2010) reported a PSR of 0.76 for the White-headed Woodpecker in burned ponderosa pine forests in Oregon. In burned forests of Idaho, Saab and Dudley (1998) reported a PSR of 1.00 for the White-headed Woodpecker, but this was based on a sample of only six nests. In contrast, Hollenbeck et al. (2011) found that White-headed Woodpeckers in unburned forests of central Oregon had a nest success of 0.39. Despite the nest survival we observed being comparable to or higher than that reported in other areas, the results of our source–sink analysis suggest that these managed stands may be functioning as sinks.

The mean nest-initiation dates of the White-headed and Hairy Woodpeckers were the most dissimilar. Hairy Woodpeckers can excavate into the cambium layer to prey on insects and their larvae (Jackson et al. 2002) and may nest earlier than

White-headed Woodpeckers, which primarily glean the surface of bark and foliage for insects (Raphael and White 1984, Garrett et al. 1996), because they are able to exploit insect prey that is less affected by cooler temperatures of an early nesting season. Indeed, 39% of prey brought back to nestlings by adult Hairy Woodpeckers was wood-boring larvae of the Cerambycidae and Buprestidae, in contrast to only 25% of prey brought to nestlings by adult White-headed Woodpeckers (JMK, unpubl. data). Insects consumed by White-headed Woodpeckers, such as ants, beetles, and lepidopteran larvae, likely become more active and abundant as ambient temperatures increase (Elchuk and Wiebe 2003, Rossmanith et al. 2007, Gaylord et al. 2008).

HAIRY WOODPECKER

The Hairy Woodpecker's nest survival was associated with a quadratic effect of date and habitat type. Nests initiated earlier in the nesting season were more successful than those initiated later in the season, a common trend among cavity-nesting birds (Verhulst et al. 1995, Pechacek 2006, Bonnot et al. 2008). Hairy Woodpeckers that initiated nests later in the nesting season may have been young birds experiencing delays in nest initiation because of their inexperience with

TABLE 4. Causes of failure of Hairy Woodpecker, White-headed Woodpecker, and Northern Flicker nests in managed ponderosa pine forests, eastern Cascade Range, Washington, 2005–2010.

	Hairy Woodpecker		White-headed Woodpecker		Northern Flicker		Total
	Burned	Unburned	Burned	Unburned	Burned	Unburned	
Predation ^a	6	1	6	6	7	7	33
Small mammal	1	0	0	2	5	2	10
Usurpation ^b	6	0	0	1	2	0	9
Unknown cause	1	3	1	0	1	3	9
Black bear	0	0	0	0	1	4	5
Corvid	0	1	0	0	0	2	3
Eggs not hatch	0	0	0	1	2	0	3
Weather	1	1	0	0	0	0	2
Ants (Formicidae)	0	0	0	0	0	1	1
Total	15	6	7	10	18	19	75

^aPredator unknown.

^bUsurped by Lewis's Woodpecker (*Melanerpes lewis*; $n = 4$), European Starling (*Sturnus vulgaris*; $n = 3$), and Western Bluebird (*Sialia mexicana*; $n = 1$).

cavity-site selection and excavation. For example, Wiktander et al. (2001) found that the breeding performance of Lesser Spotted Woodpeckers (*Dendrocopos minor*) improved with age and that younger birds initiated egg laying later than older birds, and Pechacek (2006) observed that older Three-toed Woodpeckers (*P. tridactylus*) nested earlier and were more successful.

Hairy Woodpeckers experienced higher nest survival in unburned stands than in burned stands. We predicted that nest survival should be higher in burned stands because populations of nest predators can be lower after forest fires, resulting in higher nest success in burned forests (Saab and Vierling 2001, Saab et al. 2004). For example, the daily survival rates of Western Bluebirds nesting in our study area were higher in burned stands (Kozma and Kroll 2010). However, salvage logging occurred in the burned stands we studied, which may have contributed to the Hairy Woodpecker's lower nest survival. We found that European Starlings and Lewis's Woodpeckers usurped Hairy Woodpecker nests only in burned areas, with seven nest losses attributed to these two species. Lewis's Woodpeckers occur at higher densities and nest more frequently in burned forests that have been logged (Saab and Dudley 1998, Saab et al. 2009). Starlings may be attracted to logged burns because of the presence of snags with cavities for nesting and increased opportunities for foraging offered by the openness of logged areas. Similarly, Saab et al. (2007b) found the Hairy Woodpecker's nest survival significantly higher in unlogged burned stands than in burned areas that were partially logged. While the Hairy Woodpecker's nest survival is higher in unburned stands, its nest-survival rates in both habitats we studied are lower than those reported for the Hairy Woodpecker and 20 other

woodpecker species (Paclík et al. 2009). In addition, annual productivity was lower than FFFY in both habitats, suggesting that these habitats may be sinks and that these managed ponderosa pine stands may not provide adequate breeding habitat for Hairy Woodpeckers.

NORTHERN FLICKER

The Northern Flicker's nest survival was associated with a linear effect of date, an effect of habitat type, a negative linear association with the number of snags, and a positive linear association with the number of live trees. As with the Hairy Woodpecker, earlier nests initiated by Northern Flickers had higher survival than nests initiated later in the season. Fisher and Wiebe (2006a) also found that Northern Flicker nests initiated earlier in the season had a greater probability of success than did nests initiated later. They suggested that nestlings that hatched later in the breeding season may have had lower reproductive value, thus resulting in higher rates of nest abandonment or reduced parental care. Alternatively, Northern Flickers that initiate the earliest nests could be females that are older (i.e., more experienced) and in better body condition (Wiebe and Gerstmar 2010). Older females may select the best nest sites and be more effective at warding off nest predators, resulting in higher nest survival.

Northern Flickers experienced higher nest survival in burned stands than in stands that were unburned. We think that the difference between these two habitat types is accounted for by the proportion of nests that failed and a difference in nest predators. In unburned stands, 37% of nests were depredated, compared to 30% in burned stands. Black bears (*Ursus americanus*) accounted for failures of four Northern Flicker nests in unburned stands but of

only one in burned stands. In addition, Common Ravens (*Corvus corax*) depredated two flicker nests in unburned habitats and none in burned stands. It is unclear why nest survival was negatively associated with the number of snags and positively associated with the number of live trees. The large opening of flicker cavities may be more visible to predators in open areas of high snag density than in areas containing more live trees.

Survival of Northern Flicker nests in the burned stands we studied was comparable to that reported by other studies. In burned forests of southwestern Idaho, Saab and Dudley (1998), using the Mayfield method, recorded an overall nesting success for flickers of 70%. Vierling et al. (2008) recorded nest success ranging from 50% in a low-severity burn to 100% in a high-severity burn. In addition to high nest survival in the burned forests we studied, annual productivity was sufficient to compensate for FFFY, suggesting that this habitat may be functioning as a demographic source. Although we could find no studies that investigated the flicker's nest survival in unburned conifer forests of the western U.S., our observed nest survival of 41% is lower than the 100% Li and Martin (1991) reported for the flicker in aspen stands of central Arizona and is lower than that reported for most woodpecker species (Paclík et al. 2009). Annual productivity was also lower than FFFY, suggesting that unburned forests in our study are acting as sinks.

CONSERVATION IMPLICATIONS

The managed ponderosa pine forests we studied retained conditions that supported high nest-survival rates for the White-headed Woodpecker. Managed ponderosa pine stands are not considered important habitat for this species because they often do not contain a significant "old-growth" component (our stands were also missing this component; Kozma 2011). Our results demonstrated that shrub cover affects White-headed Woodpecker nest survival negatively, and we recommend that land managers incorporate prescribed fire, to reduce shrub cover, into management scenarios that are designed to improve or create breeding habitat for this species. Estimates of home-range size, fledgling survival, and overwinter survival of adults are needed to further evaluate the importance of these managed stands to White-headed Woodpecker ecology.

Hairy Woodpeckers experienced low nest survival in burned and unburned managed ponderosa pine stands, and Northern Flickers experienced low nest survival in unburned managed stands, suggesting that these areas are not optimal as breeding habitat. Unfortunately, published studies from other areas of the eastern Cascade Range are not available for comparison. Future research in the Northwest should investigate nest survival of the Hairy Woodpecker and Northern Flicker in managed and unmanaged landscapes dominated by ponderosa pine to determine if our findings reflect a local or more widespread pattern.

The early portion of the Hairy Woodpecker's and Northern Flicker's nesting seasons, when most nests were

initiated, was more favorable than the latter portion. Forest-management disturbances that cause a delay in nest initiation or loss of early-season nests could reduce nest survival and reproductive output and negatively affect local populations of these two species. We recommend that future research on the effects of logging disturbance on nesting woodpeckers be designed with investigation before and after the disturbance with reference to undisturbed control areas.

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