

NEST-SITE ATTRIBUTES AND REPRODUCTIVE SUCCESS OF WHITE-HEADED AND HAIRY WOODPECKERS ALONG THE EAST-SLOPE CASCADES OF WASHINGTON STATE

JEFFREY M. KOZMA¹

Yakama Nation, Timber, Fish and Wildlife/Fisheries Resource Management, P.O. Box 151, Toppenish, Washington 98948, USA

Abstract. Primary cavity excavators serve as keystone species because their abandoned cavities are utilized by other species for nesting, denning, and roosting. Understanding the habitat requirements of primary excavators is necessary to conserve their populations. I studied nest-site selection and reproductive success of White-headed (*Picoides albolarvatus*) and Hairy Woodpeckers (*P. villosus*) within managed and fire-salvaged stands in the ponderosa pine (*Pinus ponderosa*) zone along the eastern slope of the Cascade Mountains. These species differed in nesting chronology and their choice of snags for nesting. Hairy Woodpeckers initiated nests earlier, used firmer snags, and located their cavities higher. White-headed Woodpeckers initiated nests later, tended to locate their cavities lower, and selected snags in the most advanced stages of decay. Mayfield nest success estimates were nearly identical, but White-headed Woodpeckers fledged significantly fewer young. Only 55% of eggs laid by White-headed Woodpeckers resulted in fledged young compared to 71% of eggs laid by Hairy Woodpeckers. Managed stands may be lower quality habitat for White-headed Woodpeckers because predation rates and clutch size do not account for the differences in egg success. Abandoned cavities excavated by these two species are used almost exclusively by Western Bluebirds (*Sialia mexicana*). Declines in woodpecker densities could have significant adverse impacts on populations of Western Bluebirds. The major conservation challenges associated with ponderosa pine habitat in this area are increasing the number of snags retained and increasing the old-growth component of ponderosa pine within stands managed for timber production.

Key Words: Hairy Woodpecker, nest success, *Picoides*, ponderosa pine, White-headed Woodpecker.

ATRIBUTOS DE LOS NIDOS Y LOGROS REPRODUCTIVOS EN LOS PÁJAROS CARPINTEROS CABEZA BLANCA (WHITE-HEADED WOODPECKERS) Y PÁJAROS CARPINTEROS CON PENACHO (HAIRY WOODPECKERS), A LO LARGO DE LAS PENDIENTES ORIENTALES DE LAS MONTAÑAS CASCADAS DEL ESTADO DE WASHINGTON

Resumen. Los excavadores de cavidades primarios sirven como especie de clave porque sus cavidades abandonadas son utilizados por otras especies para anidar, crear guarida y posarse para dormir. Comprender los requerimientos del hábitat de excavadores primarios es necesario para la conservación de sus poblaciones. He estudiado la selección de nidos y logros reproductivos de los pájaros carpinteros cabeza blanca (*Picoides albolarvatus*) y los pájaros carpinteros con penacho (*P. villosus*) en los sitios controlados y salvados después de incendios de la zona de pinos ponderosa (*Pinus ponderosa*) a lo largo de las pendientes orientales de las montañas Cascadas del Estado de Washington.

Estas especies difieren en la cronológica de hacer sus nidos, y la selección de árboles muertos para anidar. Los pájaros carpinteros con penacho hicieron sus nidos más temprano, usaron árboles muertos más firmes y hicieron sus agujeros más alto. Los pájaros carpinteros cabeza blanca inician sus nidos un poco más tarde, con tendencia de localizar sus agujeros en las partes bajas de los árboles, seleccionando árboles muertos en estado avanzado de pudrición. El éxito reproductor Mayfield estima que el logro de anidar es casi idéntico, pero los pájaros carpinteros cabeza blanca nacen y empluman mucho menos polluelos.

Solamente el 55% de los huevos incubados por los pájaros carpinteros cabeza blanca tienen éxito en nacer y emplumar comparados al 71% de los huevos incubados por los pájaros carpinteros con penacho. Los sitios controlados podrán ser hábitat de menor calidad para los pájaros carpinteros cabeza blanca debido a que los índices de depredación y el tamaño de la nidada no explican las diferencias del éxito de la incubación. Los agujeros hechos por estas especies son usados casi exclusivamente por los pájaros azules occidentales (*Sialia mexicana*). La disminución en la población de los

¹E-mail: jeffk@yakama.com

pájaros carpinteros podría tener un impacto adverso significativo en las poblaciones de los pájaros azules occidentales (Western Bluebirds). Los mayores retos en la conservación asociados con el hábitat del pino ponderosa en esta área son aumentar el número de árboles muertos para anidar, e incrementar el componente de bosque antiguo del pino ponderosa en los sitios controlados para la producción de madera.

INTRODUCTION

Forests in Washington State have long been impacted by human induced disturbances such as commercial forest management practices (Youngblood 2001, Hessburg and Agee 2003, Ripper et al. 2007). In addition to timber management, the ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) forest types have been altered considerably across the Northwest due to decades of effective fire suppression (Harrod et al. 1999, Everett et al. 2000).

Prior to European settlement, fire maintained ponderosa pine forests were park-like and described as having widely spaced, large diameter trees (Agee 1996, Harrod et al. 1999). Today, ponderosa pine forests have changed dramatically and are characterized as having higher stem densities, smaller diameter and younger trees, and a greater abundance of shade tolerant tree species in the understory (Douglas-fir and grand fir [*Abies grandis*]) (Agee 1996, Fulé et al. 1997, Hessburg and Agee 2003, Keeling et al. 2006). It is important to determine how these changes may be impacting species that inhabit ponderosa pine forests.

The White-headed Woodpecker (*Picoides albolarvatus*) is a primary excavating species that is dependent on ponderosa pine throughout its distribution (Garrett et al. 1996). In the northern portion of its range in Washington, Idaho (Ligon 1973), and British Columbia, White-headed Woodpeckers rely exclusively on ponderosa pine. In the southern part (Oregon and California) of its range, two or more large-seeded pine species are used (Garrett et al. 1996). In Washington, this lack of habitat plasticity may result in adverse impacts to their populations when ponderosa pine forests become altered from timber harvest and/or fire suppression. In order to assess habitat quality, it is important to determine how well dependent species are reproducing (Muller et al. 1997).

In this study, I investigated nest-site selection and reproductive success of the White-headed Woodpecker and the sympatric Hairy Woodpecker (*Picoides villosus*) (Morrison and With 1987) within managed stands of ponderosa pine along the eastern slope of the Cascade Mountains of Washington State. I chose the Hairy Woodpecker for comparison because, unlike the White-headed Woodpecker, the

Hairy Woodpecker is a forest habitat generalist (Mills et al. 2000, Ripper et al. 2007) occurring in many forest types across its wide range. In addition, even though the Hairy Woodpecker is common, there are serious deficiencies in quantitative data for most of its breeding biology (Jackson et al. 2002).

A few studies have investigated how White-headed and Hairy Woodpeckers partition resources, but those have only dealt with differences in foraging (Morrison and With 1987, Morrison et al. 1987). Nest-site characteristics of these two species have been addressed individually (Milne and Hejl 1989, Buchanan et al. 2003) or more commonly as part of a larger community study (Raphael and White 1984, Martin and Li 1992, Steeger and Dulisse 2002, Martin et al. 2004).

However, no studies have investigated if interspecific resource partitioning exists in regards to nest-site selection of White-headed and Hairy Woodpeckers in Washington state. My objectives were to: (1) determine clutch size, nesting success, nest initiation dates, and egg success for each species; (2) compare micro and macrohabitat variables between nest sites of White-headed and Hairy Woodpeckers and; (3) test the hypothesis that Hairy Woodpeckers will have greater nest success, greater egg success, and fledge more young than White-headed Woodpeckers in stands managed for timber production. The latter hypothesis is based on the reasoning that managed stands may represent suboptimal habitat for the White-headed Woodpecker, a ponderosa pine specialist, compared to the Hairy Woodpecker, a forest habitat generalist.

METHODS

STUDY AREA

I conducted this study along the eastern slope of the Cascade Mountains within Yakima, southern Kittitas, and northern Klickitat Counties of Washington State. Fifteen study sites were located in the Okanogan-Wenatchee National Forest and on Washington Department of Natural Resources and Western Pacific Timber Company lands. Study sites were chosen by locating pairs of White-headed Woodpeckers from sightings posted to a local list-server by

birdwatchers in the Yakima valley, locating birds during field reviews of proposed timber harvests, and by reviewing a historical sightings database maintained by the Washington Department of Fish and Wildlife.

The study area is comprised of a broken topography with intermixed aspects and slopes (Everett et al. 2000). Ponderosa pine was the dominant overstory tree of all sites with a smaller 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 snowbrush ceanothus (*Ceanothus velutinus*), antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos alba*), and Douglas spirea (*Spirea douglasii*).

The majority of sites can be classified as "hot dry shrub/herb" (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Agropyron spicatum*]) or "warm dry shrub/herb" (Douglas-fir/bitterbrush/bluebunch wheatgrass) vegetation associations (Harrod et al. 1999). All study sites were in managed stands with a recent history of timber harvest. Nine of these sites were under uneven-aged management, harvested by methods such as thinning from below. The remaining six sites were in burned stands ranging from one to six years post-fire at the time they were sampled and all had some degree of salvage logging. Elevation of sites ranged from 560 to 1280 m.

NEST SEARCHING AND MONITORING

In 2003–2007, I searched for nests beginning the first week of April and continuing into mid-June of each year. Due to time constraints, not all of the 15 sites were searched in each year. Because both sexes of these woodpeckers take part in cavity excavation and incubation, I followed adult birds of either sex during the nesting season to find cavities. If this failed to result in locating a cavity, I relied on adults carrying food, adult distress calls, or sounds of begging chicks to reveal the cavity location.

In 2005–2007, I inspected cavities with a Tree Top Peeper IV elevated nest inspection system (Sandpiper Technologies, Inc.). When checking a nest, I recorded date and time, nesting stage, clutch size, number of young, and an estimate of nest age. I checked each nest at least once a week until nest fate could be determined. I categorized nests as successful if I observed at least one fledgling near the cavity or if I observed young in the cavity within two days of fledging (24–26 days old for White-headed Woodpeckers and 26–28 days old for Hairy Woodpeckers; Ehrlich et al. 1988).

I calculated nest initiation dates (day the first egg was laid) by backdating from the day of hatching, assuming that incubation began on the last egg, and assuming that one egg was laid each day (Keyser et al. 2004). I recorded nests as depredated if all eggs/young were gone before the anticipated time of incubation or nestling stage was complete (Kozma and Matthews 1997). I calculated egg success by dividing the number of young fledged by the number of eggs laid (Murray 2000).

VEGETATION SAMPLING

I sampled vegetation characteristics after cavities were vacated. At each tree/snag that contained an active cavity, I recorded the microhabitat characteristics cavity height, tree/snag height, type (decay class) of snag, diameter at breast height (dbh), tree/snag species, cavity orientation, and canopy cover. I measured nest height and tree height with a meter tape or clinometer. I used a diameter tape to measure dbh, and I determined cavity orientation with a compass. To estimate canopy cover, I used a concave hemispherical densiometer at the base of the nest tree/snag and averaged all four cover estimates taken in each of the cardinal directions for total canopy cover (Farnsworth and Simons 1999).

I modified methods described by James and Shugart (1970) to sample macrohabitat in 2-, 5-, and 11.3-m radius (0.04 ha) circles centered on each nest snag. Within the 2-m radius circle, I estimated the percent cover of bare ground, rock, grass, forbs, litter, and woody debris where total percent cover of all variables equaled 100 percent. Within the 5-m radius circle, I visually estimated the percent cover of each shrub species and recorded average shrub height. Within the 11.3-m radius circle, I tallied trees in three dbh size classes (25.4 to <50.8 cm, 50.8 to <76.2 cm, and ≥76.2 cm) and snags in two dbh size classes (25.4 to <50.8 cm and 50.8–76.2 cm). After sampling vegetation, the nest tree/snag was permanently marked with an aluminum tree tag.

STATISTICAL ANALYSES

Due to small sample sizes in each year, I combined nests across years for nest success, micro, and macrohabitat analyses (Barber et al. 2001). I estimated nest success using the Mayfield Method (Mayfield 1961, 1975) and calculated the standard error of nesting success estimates as described by Johnson (1979). I used a 14-day incubation period and 26-day nestling period for White-headed Woodpeckers and a 13-day incubation period and 27-day nestling period for Hairy Woodpeckers (Ehrlich et al. 1988).

TABLE 1. MICRO AND MACROHABITAT CHARACTERISTICS OF WHITE-HEADED AND HAIRY WOODPECKER NEST SITES ALONG THE EASTERN SLOPE OF THE CASCADE MOUNTAINS IN WASHINGTON, 2003–2007. SIGNIFICANT DIFFERENCES ARE IN BOLD.

	White-headed Woodpecker	Hairy Woodpecker
Dbh (cm)	36.6 (2.1) ^a	36.9 (1.7) ^b
Cavity height (m)	3.81 (0.5)^a	5.54 (0.6)^b
Snag height (m)	10.3 (1.5)^a	12.6 (1.0)^c
Canopy Cover (%)	42.6 (3.6) ^a	43.0 (3.5) ^d
Shrub height (m)	0.47 (0.04) ^e	0.43 (0.04) ^f
Shrub cover (%)	19.3 (3.9) ^g	15.2 (2.8) ^h
Herbaceous vegetation (%)	51.8 (3.5) ⁱ	46.7 (3.2) ^h
Woody Debris (%)	9.6 (1.5) ⁱ	9.9 (1.4) ^h
Litter (%)	26.5 (2.9) ⁱ	22.9 (1.8) ^h
Rock (%)	2.1 (0.6) ⁱ	3.4 (0.7) ^h
Bare ground (%)	8.1 (1.7) ⁱ	13.3 (2.4) ^h
LIVE TREES (>25.4 cm dbh ha ⁻¹)	50.7 (11.0)^j	27.7 (6.9)^h
SNAGS (>25.4 cm dbh ha ⁻¹)	34.3 (8.3) ^j	42.4 (9.3) ^h
ALL STEMS (>25.4 cm dbh ha ⁻¹)	85.0 (12.3) ^j	69.7 (9.7) ^h

^a*n* = 36, ^b*n* = 54, ^c*n* = 53, ^d*n* = 56, ^e*n* = 29, ^f*n* = 41, ^g*n* = 30, ^h*n* = 46, ⁱ*n* = 33, ^j*n* = 35.

Descriptive statistics and statistical analyses were performed using SYSTAT (1998). I combined the density of all three size classes of trees into one category (LIVE TREES; number >25.4 cm dbh ha⁻¹), both size classes of snags into a second category (SNAGS; number >25.4 cm dbh ha⁻¹), and all trees and snags into a third category (ALL STEMS; number >25.4 cm dbh ha⁻¹).

I used the Mann-Whitney *U*-test, due to non-normality of the data, to compare micro and macrohabitat variables between the two species, and I applied Spearman's Coefficient of Rank Correlation to determine if correlations existed between the habitat variables (Steel and Torrie 1980). I pooled nest orientations into eight, 45-degree categories (e.g., N, NE, E, SE) and used the chi-square goodness of fit test to determine if nest orientation differed from a uniform distribution. All statistical tests were conducted at $\alpha = 0.05$. Values reported in the results section are means \pm standard error (SE).

RESULTS

I located 36 White-headed Woodpecker nests and 56 Hairy Woodpecker nests from 2003 to 2007. Micro and macrohabitat features of nest sites differed slightly between the two species (Table 1). Hairy Woodpecker cavities were significantly higher ($U = 1315.5$, $P = 0.002$), and they used snags/trees that were significantly taller ($U = 1190$, $P = 0.024$) than those used by White-headed Woodpeckers.

Cavity height was significantly correlated with tree/snag height, and dbh was significantly correlated with cavity height and tree/snag height for Hairy Woodpecker nests ($r_s = 0.30$, $P = 0.014$, $n = 53$; $r_s = 0.27$, $P = 0.028$, $n = 53$; and $r_s = 0.58$, $P = <0.001$, $n = 53$; respectively).

For White-headed Woodpeckers, dbh of nest trees/snags was significantly correlated with cavity height and cavity height was significantly correlated with tree height ($r_s = 0.39$, $P = 0.009$, $n = 36$ and $r_s = 0.39$, $P = 0.008$, $n = 36$; respectively).

Nest sites of White-headed Woodpeckers had significantly more LIVE TREES than Hairy Woodpecker nest sites ($U = 975.5$, $P = 0.05$). Both woodpeckers excavated cavities most frequently in snags in the most advanced stages of decay (Table 2). However, 54% of Hairy Woodpecker cavities were located in firmer snags (Type 2 and Type 3) and live trees compared to only 39% of White-headed Woodpecker cavities.

Both White-headed and Hairy woodpeckers used ponderosa pine most often for nesting (80.6% and 76.8% of nest sites; respectively). Orientation of Hairy Woodpecker cavities differed from a uniform distribution, favoring an east-southeast-south aspect ($P = 0.03$, $\chi^2 = 15.9$, $df = 7$, $n = 54$) (Fig. 1). Orientation of White-headed Woodpecker cavities did not differ from a uniform distribution ($P = 0.08$, $\chi^2 = 12.9$, $df = 7$, $n = 36$) but showed a tendency for a south-southwest aspect. Peak nest initiation for Hairy Woodpeckers was three to four weeks earlier than for White-headed Woodpeckers (Fig. 2).

Reproductive parameters were similar between the two species (Table 3). However, Hairy Woodpeckers fledged significantly more young than White-headed Woodpeckers ($U = 427.5$, $P = 0.048$). Although the *P*-value is close to α , non-overlapping standard error intervals (Browne 1979) and intervals that do not contain zero (Schenker and Gentleman 2001), indicate a significant difference. A larger percentage of Hairy Woodpecker eggs result in fledged young (Table 3). Mayfield estimates of daily and period survival rates were nearly

TABLE 2. NUMBER OF WHITE-HEADED AND HAIRY WOODPECKER NESTS LOCATED IN EACH SUBSTRATE DECAY TYPE^a ALONG THE EASTERN SLOPE OF THE CASCADE MOUNTAINS IN WASHINGTON, 2003–2007.

	White-headed Woodpecker	Hairy Woodpecker
Type 1	0	4
Type 2	6	13
Type 3	8	13
Type 4	22	26
Total	36	56

^a Type 1 = live tree, Type 2 = recently dead trees with some needles still present, Type 3 = moderate decay with no visible needles and unstable branches, Type 4 = advance stages of decay with unstable upper portions and roots; often contain a broken top and loose bark. Classification corresponds to Washington State Forest Practice Rules (2008, WAC 222-16-010).

TABLE 3. REPRODUCTIVE PARAMETERS OF WHITE-HEADED AND HAIRY WOODPECKERS ALONG THE EASTERN SLOPE OF THE CASCADE MOUNTAINS IN WASHINGTON, 2003–2007. SIGNIFICANT DIFFERENCES ARE IN BOLD.

	White-headed Woodpecker	Hairy Woodpecker
Clutch size	4.0 (0.15) ^a	3.69 (0.10) ^b
Number young fledged ¹	2.54 (0.15)^c	2.93 (0.16)^d
Egg success (%)	54.7 ^a	67.9 ^e
Daily probability of survival incubation	0.997 (0.001) ^f	1.000 ^g
Daily probability of survival nestling	0.995 (0.001) ^f	0.994 (0.001) ^g
Period probability of survival incubation	0.96 (0.04) ^f	1.0 ^g
Period probability of survival nestling	0.87 (0.05) ^f	0.86 (0.04) ^g
Period probability of survival incubation and nestling	0.84 ^f	0.86 ^g

^a*n* = 21, ^b*n* = 35, ^c*n* = 24, ^d*n* = 28, ^e*n* = 30, ^f*n* = 26, ^g*n* = 40.

¹Calculated for successful nests.

identical for both species (Table 3). For White-headed Woodpecker nests with a known outcome, 84.6% (*n* = 22) were successful, 11.5% (*n* = 3) were depredated, and 3.8% (*n* = 1) failed from unknown causes. For Hairy Woodpecker nests with a known outcome, 77.5% (*n* = 31) were successful, 10% (*n* = 4) were depredated, 10% (*n* = 4) were lost through competition with other species (two to Lewis’s Woodpeckers [*Melanerpes lewis*], one to European Starling [*Sturnus vulgaris*], and

one to northern flying squirrel [*Glaucomys sabrinus*]), and 2.5% (*n* = 1) were abandoned.

The cavities of these two woodpeckers are widely used by Western Bluebirds. As a part of this study, I monitored nests of Western Bluebirds and found that 39% of their nests were located in abandoned White-headed and Hairy Woodpecker cavities. Another 44% of additional bluebird nests were found in cavities with similar size openings, but I was unable to determine

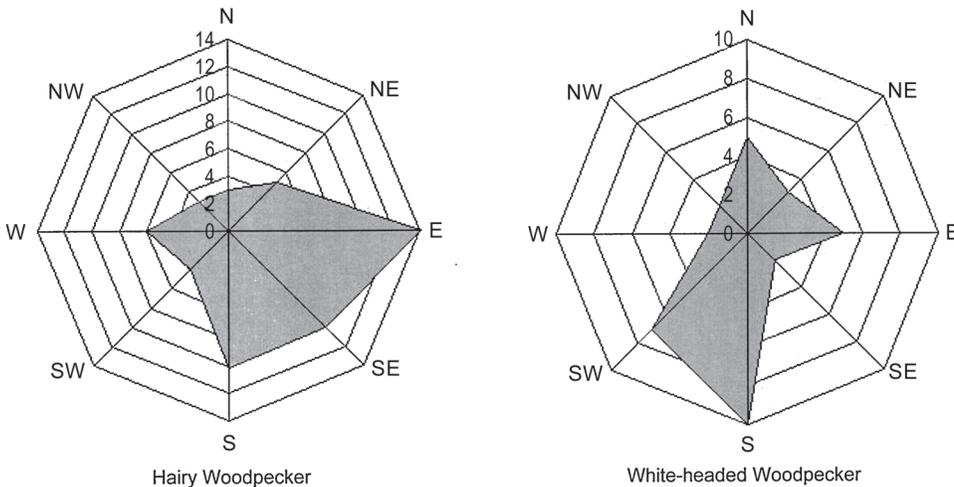


FIGURE 1. Number of Hairy and White-headed Woodpecker nests grouped by 45-degree orientation intervals along the eastern slope of the Cascade Mountains in Washington, 2003–2007.

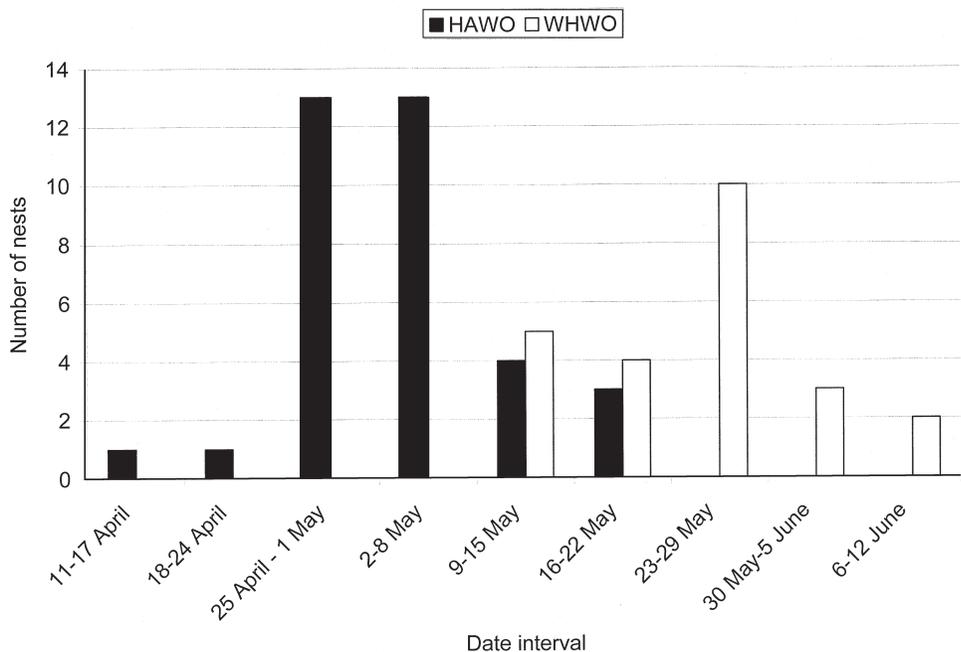


FIGURE 2. Number of Hairy and White-headed Woodpecker nests initiated during seven-day time periods along the eastern slope of the Cascade Mountains in Washington, 2005–2007.

the original excavator. However, other cavity excavators of similar size, such as Red-naped Sapsucker (*Sphyrapicus nuchalis*), Williamson's Sapsuckers (*S. thyroideus*), and Black-backed Woodpeckers (*Picoides arcticus*) were uncommon in my study area. Therefore, approximately 83% of all cavities used by Western Bluebirds are believed to have been excavated by Hairy and White-headed Woodpeckers.

DISCUSSION

The identification of ecological characteristics that allow sympatric woodpeckers to co-exist has been a frequent focus of scientific research (Cody 1969, Crockett and Hadow 1975, Jackson 1976, Morrison and With 1987, Hågvar et al. 1990, Martin et al. 2004). Sympatric, congeneric species will most likely exhibit an overlap in niche utilization, yet should be different enough to prevent competition for resources. This is the pattern I observed for White-headed and Hairy Woodpeckers in regard to location of nest cavities. The nest sites of these two species had very similar micro and macrohabitat characteristics (Table 1). However, they differed in the chronology of the nesting cycle, how high they locate their cavities, height of nest tree/snag, density of live trees surrounding the nest-site, and to a lesser degree, the decay characteristics of the nest tree/snag.

The difference in nest initiation dates between Hairy and White-headed Woodpeckers probably reflects a difference in diet, foraging strategies, and prey availability. The White-headed Woodpecker typically forages by bark gleaning on live trees and rarely drills deep into live, decaying or dead wood to obtain insect prey (Raphael and White 1984, Garrett et al. 1996). This could explain the greater density of live trees surrounding White-headed Woodpecker nest sites compared to Hairy Woodpeckers, which forage more frequently on snags (Morrison and With 1987).

During the breeding season, the diet of White-headed Woodpeckers is comprised mainly of ants, beetles, termites, and scale insects (Garrett et al. 1996). All these insects most likely become more active and abundant in the landscape as ambient temperatures increase (Elchuk and Wiebe 2003, Gaylord et al. 2008). Therefore, White-headed Woodpeckers may nest later than Hairy Woodpeckers because they rely on insects that are mainly found on the bark of trees and which do not become abundant until ambient temperatures are warmer. Although opportunistic in its search for food, the Hairy Woodpecker is capable of excavating deeply into the cambium layer to obtain prey mostly unavailable to White-headed Woodpeckers (Jackson et al. 2002). This prey resource is available regardless of ambient air temperatures,

which may allow Hairy Woodpeckers to initiate nests earlier. In addition, earlier nesting by Hairy Woodpeckers could limit competition with White-headed Woodpeckers for nest sites (Ingold 1989).

Another way for sympatric species to avoid competition for nest sites is to select different parameters associated with cavity location (Ingold 1989, Hågvar et al. 1990). White-headed Woodpeckers are considered weak primary excavators, requiring snags with moderate to advanced stages of decay in order to excavate a nest cavity (Raphael and White 1984, Milne and Hejl 1989, Garret et al. 1996, Buchanan et al. 2003). In contrast, Hairy Woodpeckers are stronger excavators and therefore are capable of creating cavities in firmer snags (Mannan et al. 1980, Schepps et al. 1999, Saab et al. 2004).

In my study area, Hairy Woodpeckers used firmer snags more frequently for cavity excavation than White-headed Woodpeckers. These firmer snags often had intact tops, which accounts for Hairy Woodpecker cavities being higher and in taller snags than White-headed Woodpeckers. Therefore, differences in foraging strategies, nesting chronology, and nest-site parameters allow these two sympatric species to coexist with limited competition.

White-headed Woodpeckers fledged significantly fewer young and had a 13% lower egg success rate than Hairy Woodpeckers. Nest success rates, however, were nearly identical indicating that nest predation, the primary cause of nest failure for both species, does not account for these differences. It is unclear what is causing White-headed Woodpeckers to fledge fewer young than Hairy Woodpeckers. One plausible explanation is that managed stands may not provide White-headed Woodpeckers with the adequate resources to fledge as many young. Stand structure surrounding nest sites of White-headed Woodpeckers was predominately comprised of younger, smaller diameter trees (47.8 trees, 25.4–50.8 cm dbh ha⁻¹; 3.7 trees, ≥50.8 to 76.2 cm dbh ha⁻¹; and 0.7 trees, ≥76.2 cm dbh ha⁻¹).

Previous studies have determined that bark foraging birds tend to choose large diameter trees for foraging and that larger diameter trees have a greater surface area and hence a greater abundance of insect prey (Raphael and White 1984, Weikel and Hayes 1999, Covert-Bratland et al. 2006). Ponderosa pine stands consisting of mostly smaller diameter trees may force White-headed Woodpeckers to forage over a much larger area to acquire enough food to feed themselves and their developing nestlings. This could result in food limitation causing a decrease in nestling feeding rates leading to fewer fledged chicks due to starvation (Fort and

Otter 2004, Granbom and Smith 2006). If trees in these stands had larger diameters, White-headed Woodpeckers might be able to increase their foraging efficiency by flying to fewer trees (Franzreb 1985, Mariani and Manuwal 1990) and thereby increasing nestling feeding rates.

Thinned and post-fire salvage logged stands consisting of small diameter trees most likely represent suboptimal habitat for White-headed Woodpeckers compared to historic ponderosa pine stands. However, in Washington, there is no information regarding nesting success of White-headed Woodpeckers in unmanaged stands for a direct comparison. Previous studies have found that birds breeding in suboptimal habitats, such as those impacted by forest management and fragmentation, have lowered reproductive output (Virkkala 1990, Hinsley et al. 1999).

Virkkala (1990) and Hinsley et al. (1999) attributed lower reproductive output of tits (*Parus spp.*) in England and Finland to diminished food resources in poorer quality habitat. Similar studies have found that the availability of food influences reproductive output and nestling provisioning. Aho et al. (1999) demonstrated that reproductive success for Eurasian Treecreepers (*Certhia familiaris*) decreased with lower prey abundance through competition with red wood ants (*Formica rufa* group) and Strong et al. (2004) found that productivity of female Bicknell's Thrushes (*Catharus bicknelli*) was limited by prey biomass. Schaefer et al. (2004) determined that Red-cockaded Woodpeckers (*Picoides borealis*) with nests located close to trees infested with southern pine beetles (*Dendroctonus frontalis*) delivered a significantly greater biomass of arthropod prey to nestlings, which reduced nestling provisioning rates.

These studies lend support for my hypothesis that managed ponderosa pine stands in Washington may be suboptimal habitat for nesting White-headed Woodpeckers based on their lower reproductive output compared to Hairy Woodpeckers. However, further research is critically needed in regards to assessing prey abundance and nestling feeding rates to test this hypothesis.

MANAGEMENT AND CONSERVATION CHALLENGES

The abandoned cavities of White-headed and Hairy Woodpeckers provide a critical resource for the secondary cavity-nesting Western Bluebird. Western Bluebirds rely almost exclusively on the cavities of these two woodpeckers for nest sites in this area (Kozma, unpublished data). A decrease in their

populations will likely have adverse impacts on populations of Western Bluebirds. Therefore, it is imperative that land managers incorporate and preserve habitat components required by Hairy and White-headed Woodpeckers during timber management activities. Protecting natural snag areas (e.g., where trees have died from root rot [*Armillaria spp.*] or insect outbreaks) will provide foraging and nesting sites for both these species. Retention of larger diameter ponderosa pine trees as legacy trees during timber harvest will help to maintain a late-seral/old growth component important to White-headed Woodpeckers for foraging.

ACKNOWLEDGMENTS

I thank S. Pinkham for her assistance in monitoring nests and measuring habitat variables during the 2007-nesting season. The Washington Department of Natural Resources and Western Pacific Timber Company provided access to their lands. Funding was provided from the Bureau of Indian Affairs. Thanks also to J. Matthews and G. King for helpful comments on earlier versions of this manuscript.

LITERATURE CITED

- AGEE, J. K. 1996. Achieving conservation biology objectives with fire in the Pacific Northwest. *Weed Technology* 10:417–421.
- AHO, T., M. KUITUNEN, J. SUHONEN, A. JÄNTTI, AND T. HAKKARI. 1999. Reproductive success of Eurasian Treecreepers, *Certhia familiaris*, lower in territories with wood ants. *Ecology* 80:998–1007.
- BARBER, D. R., T. E. MARTIN, M. A. MELCHORS, R. E. THILL, AND T. B. WIGLEY. 2001. Nesting success of birds in different silvicultural treatments in southeastern U.S. pine forests. *Conservation Biology* 15:196–207.
- BROWNE, R. H. 1979. On visual assessment of the significance of a mean difference. *Biometrics* 35:657–665.
- BUCHANAN, J. B., R. E. ROGERS, D. J. PIERCE, AND J. E. JACOBSON. 2003. Nest-site habitat use by White-headed Woodpeckers in the eastern Cascade Mountains, Washington. *Northwestern Naturalist* 84:119–128.
- CODY, M. L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. *Condor* 71:222–239.
- COVERT-BRATLAND, K. A., W. M. BLOCK, AND T. C. THEIMER. 2006. Hairy Woodpecker winter ecology in ponderosa pine forests representing different ages since wildfire. *Journal of Wildlife Management* 70:1379–1392.
- CROCKETT, A. B., AND H. H. HADOW. 1975. Nest site selection by Williamson's and Red-naped Sapsuckers. *Condor* 77:365–368.
- EHRlich, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, NY.
- ELCHUK, C. L., AND K. L. WIEBE. 2003. Ephemeral food resources and high conspecific densities as factors explaining lack of feeding territories in Northern Flickers (*Colaptes auratus*). *Auk* 120:187–193.
- EVERETT, R. L., R. SCHELLHAAS, D. KEENUM, D. SPURBECK, AND P. OHLSON. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *Forest Ecology and Management* 129:207–225.
- FARNSWORTH, G. L., AND T. R. SIMONS. 1999. Factors affecting nest success of Wood Thrushes in Great Smoky Mountains National Park. *Auk* 116:1075–1082.
- FORT, K. T., AND K. A. OTTER. 2004. Effects of habitat disturbance on reproduction in Black-capped Chickadees (*Poecile atricapillus*) in northern British Columbia. *Auk* 121:1070–1080.
- FRANZREB, K. E. 1985. Foraging ecology of Brown Creepers in a mixed-coniferous forest. *Journal of Field Ornithology* 56:9–16.
- FULÉ, P. Z., W. W. COVINGTON, AND M. M. MOORE. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7:895–908.
- GARRETT, K. L., M. G. RAPHAEL, AND R. D. DIXON. 1996. White-headed Woodpecker (*Picoides albolarvatus*). In A. Poole [ed.], *The Birds of North America Online*. Cornell Lab of Ornithology. Ithaca, NY. [Online.] <<http://bna.birds.cornell.edu/bna/species/252>> (March 2008).
- GAYLORD, M. L., K. K. WILLIAMS, R. W. HOFSTETTER, J. D. McMILLIN, T. E. DEGOMEZ, AND M. R. WAGNER. 2008. Influence of temperature on spring flight initiation for southwestern ponderosa pine bark beetles (Coleoptera: Curculionidae, Scolytinae). *Environmental Entomology* 37:57–69.
- GRANBOM, M., AND H. G. SMITH. 2006. Food limitation during breeding in a heterogeneous landscape. *Auk* 123:97–107.
- HÄGVAR, S., G. HÄGVAR, AND E. MØNNES. 1990. Nest site selection in Norwegian woodpeckers. *Holarctic Ecology* 13:156–165.
- HARROD, R. J., B. H. McRAE, AND W. E. HARTL. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *Forest Ecology and Management* 114:433–446.

- HESSBURG, P. F., AND J. K. AGEE. 2003. An environmental narrative of inland northwest United States forests, 1800-2000. *Forest Ecology and Management* 178:23-59.
- HINSLEY, S. A., P. ROTHERY, AND P. E. BELLAMY. 1999. Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *Journal of Avian Biology* 30:271-281.
- INGOLD, D. J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings. *Auk* 106:209-217.
- JACKSON, J. A., H. R. OUELLET, AND B. J. JACKSON. 2002. Hairy Woodpecker (*Picoides villosus*). In A. Poole [ed.], *The Birds of North America Online*. Cornell Lab of Ornithology. Ithaca, NY. [Online.] <<http://bna.birds.cornell.edu/bna/species/702>> (February 2008).
- JACKSON, J. A. 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied Woodpeckers in Kansas. *Condor* 78:67-76.
- JAMES, F. C., AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727-736.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651-661.
- KEELING, E. G., A. SALA, AND T. H. DELUCA. 2006. Effects of fire exclusion on forest structure and composition in unlogged ponderosa pine/Douglas-fir forests. *Forest Ecology and Management* 237:418-428.
- KEYSER, A. J., M. T. KEYSER, AND D. E. L. PROMISLOW. 2004. Life-history variation and demography in Western Bluebirds (*Sialia mexicana*). *Auk* 121:118-133.
- KOZMA, J. M., AND N. E. MATHEWS. 1997. Breeding bird communities and nest plant selection in Chihuahuan Desert habitats in south-central New Mexico. *Wilson Bulletin* 109:424-436.
- LIGON, J. D. 1973. Foraging behavior of the White-headed Woodpecker in Idaho. *Auk* 90:862-869.
- MANNAN, R. W., E. C. MESLOW, AND H. M. WIGHT. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:787-797.
- MARIANI, J. M., AND D. A. MANUWAL. 1990. Factors influencing Brown Creeper (*Certhia americana*) abundance patterns in the southern Washington Cascade Range. *Studies in Avian Biology* 13:53-57.
- MARTIN, K., K. E. H. AITKEN, AND K. L. WIEBE. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106:5-19.
- MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- MAYFIELD, H. 1975. Suggestions for calculating nesting success. *Wilson Bulletin* 87:456-466.
- MILLS, T. R., M. A. RUMBLE, AND L. D. FLAKE. 2000. Habitat of birds in ponderosa pine and aspen/birch forest in the Black Hills, South Dakota. *Journal of Field Ornithology* 71:187-384.
- MILNE, K. A., AND S. J. HEJL. 1989. Nest-site characteristics of White-headed Woodpeckers. *Journal of Wildlife Management* 53:50-55.
- MORRISON, M. L., AND K. A. WITH. 1987. Interseasonal and intersexual resource partitioning in Hairy and White-headed Woodpeckers. *Auk* 104:225-233.
- MORRISON, M. L., K. A. WITH, I. C. TIMOSI, W. M. BLOCK, AND K. A. MILNE. 1987. Foraging behavior of bark foraging birds in the Sierra Nevada. *Condor* 89:201-204.
- MULLER, K. L., J. A. STAMPS, V. V. KRISHNAN, AND N. H. WILLITS. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* 150:650-661.
- MURRAY, B. G., JR. 2000. Measuring annual reproductive success in birds. *Condor* 102:470-473.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 86:1-66.
- RIPPER, D., J. C. BEDNARZ, AND D. E. VARLAND. 2007. Landscape use by Hairy Woodpeckers in managed forests of northwestern Washington. *Journal of Wildlife Management* 71:2612-2623.
- SAAB, V. A., J. DUDLEY, AND W. L. THOMPSON. 2004. Factors influencing nest occupancy of nest cavities in recently burned forests. *Condor* 106:20-36.
- SCHAEFER, R. R., R. N. CONNER, D. C. RUDOLPH, AND D. SAENZ. 2004. Red-cockaded Woodpecker nestling provisioning and reproduction in two different pine habitats. *Wilson Bulletin* 116:31-40.
- SCHENKER, N., AND J. F. GENTLEMAN. 2001. On judging the significance of differences by examining the overlap between confidence intervals. *American Statistician* 55:182-186.
- SCHEPPE, J., S. LOHR, AND T. E. MARTIN. 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? *Auk* 116:658-665.
- STEEGER, C., AND J. DULISSE. 2002. Characteristics and dynamics of cavity nest trees in southern British Columbia, pp. 275-289. In W. F. Laudenslayer, Jr., P. J. Shea, B. E. 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. USDA Forest Service General Technical Report PSW-GTR-181. Albany, CA.
- STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and Procedures of Statistics, 2nd ed. McGraw Hill, NY.
- STRONG, A. M., C. C. RIMMER, AND K. P. MCFARLAND. 2004. Effect of prey biomass on reproductive success and mating strategy of Bicknell's Thrush (*Catharus bicknelli*), a polygynandrous songbird. *Auk* 121:446–451.
- SYSTAT. 1998. Systat: The system for statistics. Version 8.0 ed., SPSS Inc. Chicago, IL.
- VIRKKALA, R. 1990. Ecology of the Siberian tit *Parus cinctus* in relation to habitat quality: effects of forest management. *Ornis Scandinavica* 21:139–146.
- WASHINGTON STATE FOREST PRACTICE RULES. 2008. General definitions: wildlife reserve trees. WAC 222-16-010. [Online.] <http://www.dnr.wa.gov/Publications/fp_rules_ch222-16wac.pdf> (January 2009).
- WEIKEL, J. M., AND J. P. HAYES. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern Coast Range of Oregon. *Condor* 101:58–66.
- YOUNGBLOOD, A. 2001. Old-growth forest structure in eastern Oregon and Washington. *Northwest Science* 75:110–118.