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Woodpecker nest cavity orientation in dry conifer forests of the Pacific Northwest, USA

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Abstract. Birds are under selective pressure to orient their nests in a direction that reduces the impact of climatic extremes and the risk of the nest being detected by predators. Woodpeckers (Picidae), despite raising young in tree cavities that are safer from predators, should orient the entrances of their nest cavities in a direction that results in a favorable cavity microclimate. Because Picid nest cavity orientation is not well-studied in the Pacific Northwest of North America, we measured nest cavity orientation of White-headed *Dryobates albolarvatus*, Hairy *D. villosus*, and Black-backed *Picoides arcticus* Woodpeckers, Northern Flicker *Colaptes auratus*, and Williamson's Sapsucker *Sphyrapicus thyroideus* within burned and unburned, dry conifer forests of the eastern Cascade Range in Washington, USA (N = 684). Each woodpecker species had a mean angle of nest cavity orientation in a northerly or easterly direction and ranged from 12.3° for the Northern Flicker to 117.6° for the Black-backed Woodpecker. Hairy Woodpeckers, Northern Flickers, and White-headed Woodpeckers showed strong evidence for nonrandom nest cavity orientation, and Northern Flickers showed particularly high dispersion with a multimodal distribution of cavity orientations. Although the mean and variance of cavity orientations did not differ substantially between woodpeckers, cavity orientation differed based on nest tree species. Woodpeckers may orient their nest cavities in an easterly direction so that cavities warm quicker in the morning, to avoid hot afternoon temperatures and prevailing west and north westerly winds, and because the majority of cavities were located in burned forest where shading from canopy cover is reduced.

Key words: woodpeckers, nest orientation, snags, *Dryobates*, *Picoides*, *Sphyrapicus*, Ponderosa Pine, Douglas-fir

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INTRODUCTION

Selection of a nest site is critical for successful avian reproduction because it determines the exposure of the adults, eggs, and young to the environment and predators (Walsberg 1981, Lloyd & Martin 2004). Therefore, birds are likely under selective pressure to orient their nests in a direction that reduces the impact of climatic extremes (e.g., heavy rain, high or low temperatures) and the risk of the nest being detected by predators. It is for this reason that some bird species orient nest structures and openings in nonrandom directions. For example, Western Kingbirds *Tyrannus verticalis* avoid placing nests on the west side of trees to avoid excessive diurnal heat gain, heat loss at night, and high winds (Bergin 1991), and Cactus Wrens *Campylorhynchus brunneicapillus* were found to orient their nest openings in a northerly direction to minimize heat input from direct solar radiation (Facemire et al. 1990). In addition, some species, like the Rufous Hornero *Furnarius rufus* and Great Kiskadee *Pitangus sulfuratus*, change the orientation of their nests from year to year based on changes in ambient temperature (Schaaf & de la Peńa 2020).

Woodpeckers (Picidae) lay their eggs most frequently in tree cavities that they excavate in living or dead wood (Short 1982, Jackson & Jackson 2004), a process that can take days to years. Despite their nests being located in cavities, which offer greater protection from predators and provide more stable temperatures (Li & Martin 1991, Wiebe 2001), woodpeckers may exhibit nonrandom orientation of their nest cavities because orientation directly influences the microclimate inside the nest cavity (Inouye et al. 1981, Rico & Sandoval 2014). However, in order to excavate a cavity into wood, woodpeckers are faced with a variety of factors that limit where they can create a nest cavity. These factors include wood hardness (Schepps et al. 1999, Losin et al. 2006, Lorenz et al. 2015), the presence of wood-decaying fungi (Jusino et al. 2016, Kozma et al. 2022), angle of lean of the nest substrate (Conner 1975), a woodpecker's excavating ability (Kirby 1980, Lorenz et al. 2015), and branch configuration of the nest substrate (Zwartjes & Nordell 1998). Despite these factors restricting where woodpeckers can excavate a cavity, woodpeckers do show a tendency to orient entrances to their nest cavities in nonrandom patterns (Landler et al. 2014). In the southwestern deserts of North America, woodpeckers tend to orient cavity entrances in a northerly direction, presumably to reduce thermal heating of the nest cavity (Inouye et al. 1981, Zwartjes & Nordell 1998), while in cooler, more northerly (i.e., higher) latitudes, woodpeckers tend to orient cavity entrances to the south because these cavities tend to be warmer (Inouye 1976, Wiebe 2001, Butcher et al. 2002). These findings are also supported by Landler et al. (2014) who demonstrated that in the Northern Hemisphere, woodpecker populations at higher latitudes preferred a more southerly nest cavity orientation. However, even in the Northern Hemisphere regional differences exist that do not follow the trend for a southerly cavity orientation. For example, Lander et al. (2022) found that the Red-cockaded Woodpecker *Dryobates borealis* excavates cavities with a strong westerly orientation and cavity orientation became more northerly with increasing latitude, while Hooge et al. (1999) showed that Acorn Woodpecker *Melanerpes formicivorus* nest cavity entrances were biased in an easterly direction and that east facing cavities were warmer. Therefore, although orientation of woodpecker nest cavity entrances generally become more southerly as latitude increases in the Northern Hemisphere, regional differences in orientation are likely influenced by local factors such as wind direction, temperature, and fungal decay (Losin et al. 2006, Landler et al. 2014).

Despite the relationship between nest cavity orientation and nest site selection for primary excavators, cavity orientation has not received the scientific attention compared to other factors associated with cavity construction (Landler et al. 2014). Cavity orientation can have cascading effects on nest survival, yet it is frequently overlooked as a consequential trait in ecological and phylogenetic studies. Cavity orientation may also show phenotypic plasticity throughout a species range, where birds modify nest orientation in response to various factors (e.g., predation pressure, temperature). In the Pacific Northwest, USA, information on nest cavity orientation is particularly sparse (but see Buchanan et al. 2003) despite the relatively high diversity and abundance of woodpeckers in the region. To address this information gap, we measured the entrance orientation of Black-backed Woodpecker *Picoides arcticus*, Hairy Woodpecker *D. villosus*, Northern Flicker *Colaptes auratus*, White-headed Woodpecker *D. albolarvatus*, and Williamson's Sapsucker *Sphyrapicus thyroideus* nest cavities in Washington State, USA. Our objectives were to provide information on the distribution of nest cavity orientations for each species, test whether woodpeckers selected cavity locations with a nonrandom orientation, and compare distributions among woodpecker species and primary tree species used for cavity excavation. Because our study site is located at a relatively high latitude in the Northern Hemisphere, we predicted that woodpeckers would orient their nest cavity entrances favoring a southerly direction to help regulate the internal nest temperature.

METHODS

Study area

We conducted this study from 2003–2023 in 4, nonrandomly selected study sites along the eastern slope of the Cascade Range in Yakima, Kittitas, and Chelan Counties, central Washington State, USA (~46°28′N, ~121°10′W and 47°51′N, ~120°23′W; Fig. 1), although a few nest cavities (< 10) occurred outside the study area, but within the same forest type and elevational limit. Two of the study sites were on lands owned by the U.S. Department of Agriculture Forest Service (USFS), while the other two were a combination of lands owned by the Washington Department of Fish and Wildlife, Washington Department of Natural Resources (WDNR), and 4 private landowners. We estimated that the study sites were harvested for timber at least once after 1950 based on USFS timber harvest activity reports and WDNR forest practice applications. Most of these harvests were described as either a complete or partial removal of the mature overstory. A portion of all the study sites burned due to mixed-severity prescribed fire or wildfire either during the study or within 10–15 yr of the start of this study, and are actively grazed by domestic sheep and cattle in summer and fall. Elevation of trees containing nest cavities were located between 380–1780 m. The year round prevailing winds from the nearest weather stations are from the west in Yakima, Washington and from the northwest in Ellensburg, Washington (Western Regional Climate Center 2023).

The composition of woody vegetation in the study sites varied based on aspect, slope, and elevation. Ponderosa Pine *Pinus ponderosa* was dominant or co-dominant with Douglas-fir *Pseudotsuga menziesii* over most of the study area and below 1500 m. Above 1500 m, dominant trees were Lodgepole Pine *Pinus contorta*, Subalpine Fir *Abies lasiocarpa*, and Englemann Spruce *Picea englemannii*. Other tree species in order of decreasing abundance included Grand Fir *Abies grandis* and Western Larch *Larix occidentalis* in upland forest, and Black Cottonwood *Populus trichocarpa* and Quaking Aspen *P. tremuloides* along riparian areas. Understory shrubs were dominated by Antelope Bitterbrush *Purshia tridentata*, Wax

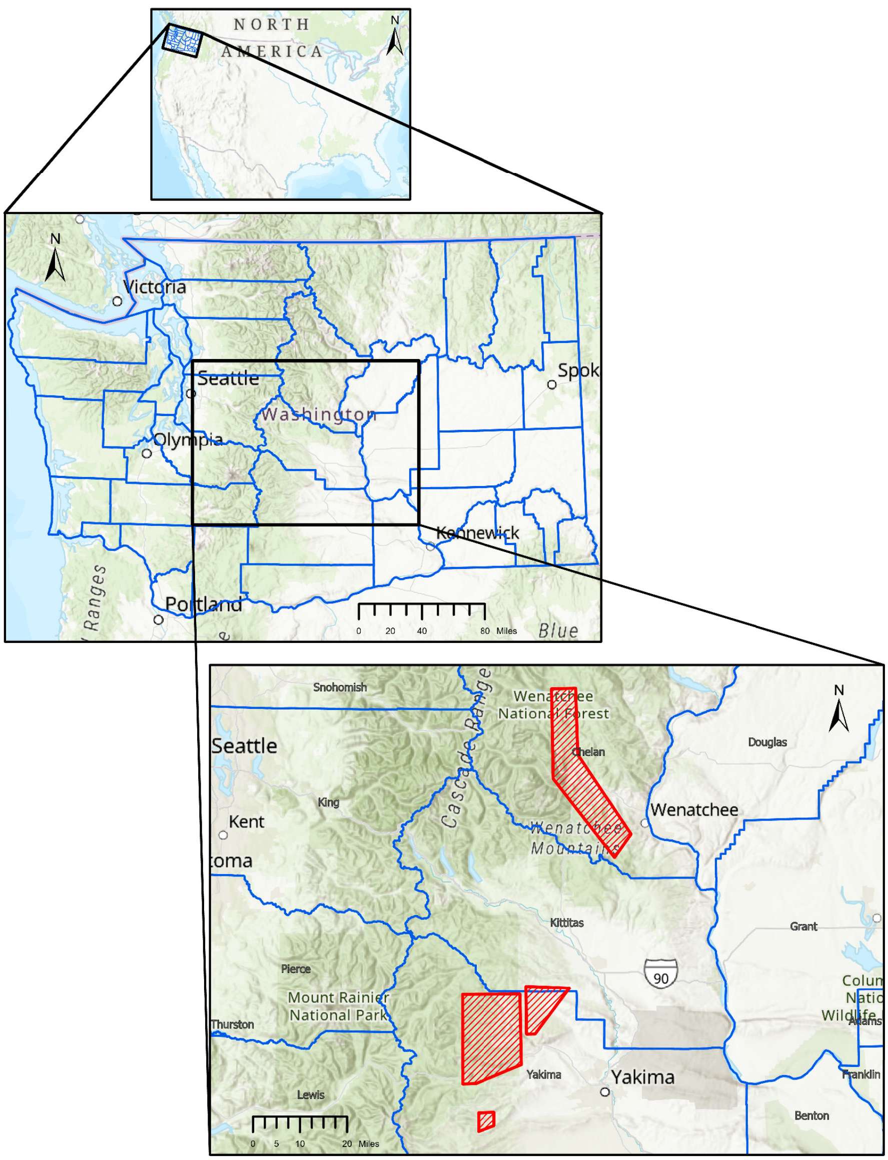


Fig. 1. Location of study sites (red hashed polygons) where woodpecker nest cavities were monitored in Yakima, Kittitas and Chelan Counties, Washington, USA, 2003–2023.

Currant *Ribes cereum*, Common Snowberry *Symphoricarpus alba* and Snowbrush *Ceanothus velutinus*. The climate of the study area is characterized by hot (mean = 29.5 °C in August), dry summers and cold (mean = -6.5 °C in December), wet winters with over 80% of annual precipitation occurring during the winter (Wright & Agee 2004).

Data collection

We searched for nest cavities from April to July in each year of the study, but because this is a long-term study area where nest cavity data was collected during different research projects, the study sites and the 5 woodpecker species did not receive the same search effort in every year. We used playbacks of calls and drumming to locate adult White-headed, Hairy, and Black-backed Woodpeckers (Nappi & Drapeau 2009, Kozma 2012) and then used behaviors such as adults carrying food, adults' distress calls, or sounds of begging chicks to reveal the cavity location. We used the same procedure for locating Northern Flicker and Williamson's Sapsucker nest cavities, but we did not use call playbacks. We verified that a breeding attempt occurred for each cavity by inspecting cavities with a TreeTop Peeper IV (Sandpiper Technologies, Inc., Manteca, CA; Kozma & Kroll 2010), if we heard or saw nestlings, or if adult behavior indicated incubation or nestling feeding was underway (Jackson 1977). After each nesting attempt was completed, we measured the cavity orientation with a compass and recorded the tree species containing the nest cavity. We corrected all cavity orientations for magnetic north prior to analysis.

Statistical analysis

We calculated a directional mean cavity orientation for each species and calculated a measure of angular dispersion ($1 - r$; Zar 1984), where $1 - r = 1.0$ represents maximum dispersion (i.e., equally distributed across the 360 compass directions). Next, we tested the hypothesis that cavity orientations are nonrandom using a Rayleigh's test and Rao's spacing test for each species (Batschalet 1981). Rayleigh's test measures the amount of dispersion around the mean vector and uses the relative index (r) to test whether orientations are uniformly distributed. An r value of 1.0 indicates that all orientations are the same, and a value of 0 indicates that they are uniformly distributed. Although the test performs well when data are expected to be unimodal, Rayleigh's test has low power to detect deviations from uniform in multimodal datasets (e.g., several "peak" cavity orientations) (Bergin 1991, Landler et al. 2018). Rao's spacing test is a common alternative for multimodal distributions, and we calculated the Rao's U test statistic for each woodpecker species to compare results between alternative tests. We tested for differences in cavity orientation among woodpecker species using a Watson-Wheeler test for homogeneity of means. Last, we tested whether average cavity orientations were different for Ponderosa Pine and Douglas-fir, the two most common tree species in the dataset, using a Watson's two-sample test of homogeneity. We assessed test results against the null hypothesis (uniform distribution) at significance level $\alpha = 0.05$ for all statistical tests. P-values reported as a range are estimated by simulation based on the fraction of samples drawn from a uniform distribution that have a test statistic higher than the observed test statistic. All analyses were completed in R version 4.2.2 using the package "circular" (R Core Team 2022, Agostinelli & Lund 2023). When performing these calculations, we only included nest cavities that were used once. For example, cavity reuse by the Northern Flicker is common (Gentry & Vierling 2008, Kozma 2012). Therefore, if a Northern Flicker reused a nest cavity in multiple years, we included it only once in our analyses.

RESULTS

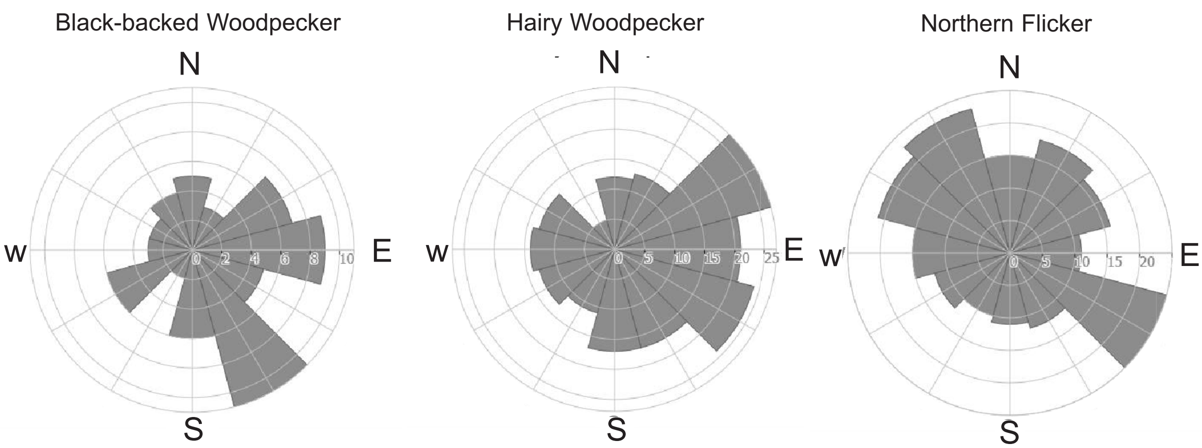
We found a total of 684 active nest cavities of the 5 woodpecker species, which included 213 White-headed Woodpecker, 189 Northern Flicker, 187 Hairy Woodpecker, 64 Black-backed Woodpecker, and 31 Williamson's Sapsucker cavities. Over 90% of all cavities were located in completely dead substrates (i.e., snags), with 70% (N = 479) located in Ponderosa Pine, 19% (N = 129) in Douglas-fir, 4% (N = 30) in Quaking Aspen, 4% (N = 26) in Grand Fir, 2% (N = 13) in other conifer species (e.g., Lodgepole Pine, Engelmann Spruce), and 1% (N = 7) in unidentified conifer species. More White-headed Woodpecker nest cavities (68%) were found in unburned forest, while more Black-backed Woodpecker (100%), Hairy Woodpecker (72%), Northern Flicker (65%), and Williamson's Sapsucker (64%) nest cavities were found in burned forest.

The distribution of Hairy Woodpecker and White-headed Woodpecker nest cavity orientations

Table 1. Nest cavity orientation statistics for five woodpecker species in the eastern Cascade Range, Washington, USA, 2003–2023.

Species	N	Mean Angle (degrees)	Rayleigh's test r (p-value)	Rao's test U (p-value range)	Dispersion (1-r)
Black-backed Woodpecker	64	117.6	0.22 (p = 0.046)	122.88 (p > 0.10)	0.78
Hairy Woodpecker	187	110.7	0.20 (p < 0.001)	150.59 (p < 0.01)	0.81
Northern Flicker	189	12.3	0.11 (p = 0.10)	159.90 (p < 0.001)	0.89
White-headed Woodpecker	213	72.7	0.15 (p = 0.008)	145.45 (p < 0.05)	0.85
Williamson's Sapsucker	31	65.3	0.14 (p = 0.567)	148.65 (p > 0.10)	0.86

showed a relatively unimodal pattern (Fig. 2), and both the Rayleigh's and Rao's tests indicated that cavity orientation was nonrandom for these species (Table 1). Black-backed Woodpeckers and Northern Flickers showed relatively multimodal distributions of nest cavity orientations, evidenced by the qualitative difference between Rayleigh's and Rao's test results (Table 1). Northern Flicker cavity orientation showed a nonrandom multimodal distribution (Rao's $U = 159.90$, $p < 0.001$) and Black-backed Woodpecker cavity orientation did not show a strong difference from a uniform distribution (Rao's $U = 122.88$, $p > 0.10$). Nest cavity orientation for Williamson's Sapsuckers did not show evidence for nonrandom patterns (Rayleigh's $r = 0.14$, $p = 0.567$). All woodpecker species except for the Northern Flicker had a mean angle of orientation in an easterly direction ranging from 65.3° for the Williamson's Sapsucker to 117.6° for the Black-backed Woodpecker (Table 1, Fig. 2). Overall, 33% (N = 226) of all nest cavities were oriented to the east (45° to 135°). The



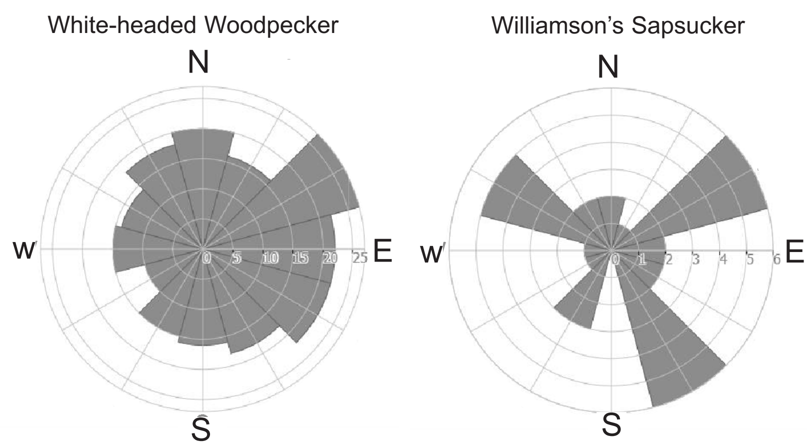


Fig. 2. Distribution of nest cavity entrance orientations for the Black-backed Woodpecker, Hairy Woodpecker, Northern Flicker, White-headed Woodpecker, and Williamson's Sapsucker. Axis divisions represent a range of 30° (e.g., North = 345°–14°) and each wedge represents the number of nest cavities with orientations within that 30° range.

Fig. 3. Distribution of nest cavity entrance orientations in Ponderosa Pine and Douglas-fir. Axis divisions represent a range of 30° (e.g., North = 345°–14°) and each wedge represents the number of nest cavities with orientations within that 30° range.

cavity orientation of all five woodpecker species had a large amount of dispersion, with highest dispersion in the Northern Flicker (Table 1). We did not detect a significant difference between the mean and variance of cavity orientations between woodpecker species (Watson-Wheeler test W = 13.1, p = 0.108). However, nest cavity orientation did differ between the two most commonly-used tree species (Watson's two-sample test U^2 = 0.23, simulated p = 0.01–0.05). Cavities excavated in Ponderosa Pine had a mean angle of orientation of 96°, while cavities excavated in Douglas-fir had a mean angle of orientation of 27° (Fig. 3).

DISCUSSION

We found that White-headed and Hairy Woodpeckers, and the Northern Flicker oriented their nest cavity entrances in a nonrandom pattern. This finding supports those of other studies that report woodpeckers orient nest cavities nonrandomly (Landler et al. 2014, Schaaf 2019, Stillman et al. 2019). In contrast, the Black-backed Woodpecker and Williamson's Sapsucker oriented their cavities randomly. Both of these species had the smallest sample sizes of the species we sampled, which may have affected our ability to detect a nonrandom pattern because large sample sizes increase the power of the Rayleigh's and Rao's tests to detect nonrandom patterns (Landler et al. 2018). It's possible that the Black-backed Woodpecker and Williamson's Sapsucker do in fact orient cavities randomly in our study area, but our sample size may have precluded us from detecting statistically nonrandom patterns.

Each of the woodpecker species had nest cavity entrance orientations with a high degree of dispersion, meaning that orientation of cavities was well distributed across all directions. High dispersion values associated with cavity nest orientation is common in woodpeckers; having been observed in woodpeckers that nest in columnar cacti in deserts (Korol & Hutto 1984, Kerpez & Smith 1990) to those nesting in cooler, montane forests (Butcher et al. 2002, Losin et al. 2006). Compared to birds that build open cup nests, woodpeckers face a variety of factors that limit where they can excavate a nest cavity; the most important being hardness of the wood. Many woodpeckers rely on wood-decaying fungi to soften the interior wood of live and dead trees prior to excavating a cavity (Jackson & Jackson 2004, Losin et al. 2006, Jusino et al. 2016). For instance, wood surrounding woodpecker cavities contained higher levels of decay-causing fungal enzymes compared to controls (Kozma et al. 2022). In a similar study of wood hardness, Lorenz et al. (2015) determined that only 4–14% of dead trees in their study area contained soft enough wood for cavity excavation by White-headed and Black-backed Woodpeckers. Therefore, the high amount of dispersion in cavity orientation we observed may be due to the limited availability of suitable excavation sites that face an optimal or preferred angle of orientation (Ojeda et al. 2021).

Contrary to our prediction, none of the woodpecker species had a mean angle of nest cavity orientation in a southerly direction. Instead, woodpeckers in our study had a mean angel of cavity orientation ranging from 12.3° (north) for the Northern Flicker to 117.6° (southeast) for the Black-backed Woodpecker. The mean northerly orientation of flicker cavities in our study contrasts with a population of flickers north of our study area in British Columbia where the mean cavity orientation was almost due south; though flickers there nested almost entirely in Quaking Aspen (Wiebe 2001). It is possible that adequate rot patterns for flickers to excavate a cavity differ in the wood of Quaking Aspen, a deciduous tree, compared to the rot patterns of wood in the evergreen trees in our study area. The White-headed Woodpecker had a mean cavity orientation of 72.7°, which is similar to the 80° mean orientation reported for this species by Buchanan et al. (2003) in eastern Washington. Black-backed Woodpecker nest cavities in our study had a slightly more southerly orientation than the 80° mean orientation exhibited by this species in California (Stillman et al. 2019).

Previous studies have shown that east and south facing cavities are warmer than those facing other directions (Hooge et al. 1999, Wiebe 2001, Jarolimek & Vierling 2019). In the montane habitats of our study area, mean night temperatures from July to August are cool (~14.0 °C; Vierling et al. 2018) and orienting cavities in an easterly direction may allow them to warm more quickly in the morning. This would be advantageous because it would allow adult woodpeckers to stop brooding nestlings earlier in the day, enabling both adults to partake in a greater number of foraging bouts to feed nestlings. In addition to east facing cavities warming more quickly in the morning, facing east also avoids exposure of the cavity entrance to the warmer, westerly afternoon sun. Furthermore, most of our nests were located in burned forest where live tree canopy cover is reduced. Because canopy cover can moderate nest cavity temperature (Jarolimek & Vierling 2019), woodpeckers may avoid orienting their nest cavities to the west because the reduced canopy cover results in less shade that would help keep west facing cavities cooler. Finally, prevailing winds in our study area are from the west or northwest and increase in speed throughout the day. Avoiding the prevailing winds by orienting cavities in an easterly direction would prevent the warmer, drier, afternoon air from entering the cavity and increasing the cavity temperature (Bergin 1991, Charter et al. 2010).

Orienting cavities toward the east may be particularly important when they are excavated in Ponderosa Pine, in which 70% of our woodpecker nests were located. Indeed, we found that nest cavities in Ponderosa Pine had a mean angle of 96° and differed significantly from those in Douglas-fir where the mean angle was 27°. Compared to the other evergreen trees used for nesting in this study, Ponderosa Pine has the thickest volume of sapwood compared to heartwood, comprising 50–75% of the tree's volume (Farris et al. 2004). The sapwood decays much quicker than the heartwood (Bull et al. 1997) and it is primarily in the sapwood of Ponderosa Pine that woodpeckers excavate a nest cavity. Nest cavities in the sapwood are closer to the external bark, which may cause cavities facing west to overheat more frequently. For example, Vierling et al. (2018) found that the internal temperature of ~18% of 84 tree cavities in Ponderosa Pine in eastern Washington reached ≥ 40 °C, which is lethal to avian embryos. When excavating cavities in Douglas-fir, more cavities may be excavated to the north due to differences in wood decay, where the cooler, north side of Douglas-fir may retain bark and wood moisture longer, thereby encouraging a greater abundance of wood-decaying fungi capable of breaking down the extensive heartwood.

In summary, the rarity of west facing cavities excavated by woodpeckers in our study may be explained by several factors, including hot temperatures during nesting season, prevailing west to northwest winds, cavities being located most frequently in sapwood, and most nests located in burned forest where shading from the tree canopy is more limited. Although Landler et al. (2014) demonstrated that woodpeckers in more northerly latitudes orient nest cavities to the south, our results suggest that cavity orientation is more nuanced and can be influenced by regional climate and the tree species in which the cavity is excavated.

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STRESZCZENIE

[Ekspozycja otworów wejściowych dziupli dzięciołów w suchych lasach iglastych w stanie Waszyngton (zach. USA)]

Do czynników wpływających na wybór miejsca na gniazdo może należeć m.in. ekspozycja względem stron świata. Dobór miejsca pod tym względem może mieć na celu zmniejszenie negatywnego wpływu warunków pogodowych (silne deszcze, niskie lub wysokie temperatury) lub ryzyka wykrycia gniazda przez drapieżniki. W związku z powyższym można oczekiwać nielosowej ekspozycji gniazd ptaków względem stron świata. Dziuple w drzewach, w których dzięcioły wychowują swoje pisklęta, stanowią bezpieczne miejsce lęgowe. Dlatego prawdopodobnym czynnikiem wpływającym na kierunek ekspozycji otworu wejściowego dziupli jest zapewnienie odpowiedniego mikroklimatu w jej wnętrzu. Analizy wskazują, że na półkuli północnej, szczególnie w wyższych szerokościach geograficznych, dzięcioły preferują ekspozycję otworów wejściowych dziupli w kierunku południowym. Jednak wiele innych czynników może wpływać na wybór miejsca wykucia dziupli przez dzięcioły. Ponadto, na wynik analiz pod kątem stwierdzenia, czy rozkład ekspozycji gniazd ma charakter losowy, czy też nielosowy, może mieć wpływ wielkość próby. Konieczne są więc dalsze badania, szczególnie prowadzone na gatunkach występujących sympatrycznie, które mogą pozwolić na określenie zarówno ogólnych trendów, jak i trendów występujących u poszczególnych gatunków.

Badania prowadzono w suchych lasach iglastych na wschodnich stokach Gór Kaskadowych w stanie Waszyngton (USA) (Fig. 1). Badaniami objęto pięć gatunków: dzięcioła białogłowego, włochatego, północnego, różowoszyjego oraz oskomika ciemnogłowego. Dla każdej dziupli określano jej ekspozycję oraz gatunek drzewa, w którym była wykuta. Do analiz wykorzystano statystyki kołowe, aby uwzględnić fakt, że różne wartości (np. 358° i 2°) wskazują ten sam kierunek ekspozycji otworu wejściowego. Każda dziupla została użyta w analizach tylko raz, pomimo, że niektóre z gatunków objętych badaniami (szczególnie dzięcioł różowoszyi) wykorzystują te same dziuple w kolejnych latach.

Łącznie w latach 2003–2023 znaleziono 684 dziuple dzięciołów objętych badaniami. Większość z nich (70%) wykuta była w sośnie żółtej. Rozkład ekspozycji dziupli dzięcioła włochatego i białogłowego był zasadniczo jednomodalny i nielosowy (Tab. 1, Fig. 2). W przypadku dzięcioła różowoszyjego i północnego rozkład był zasadniczo wielomodalny, a dodatkowo u dzięcioła północnego — nielosowy. Losowy rozkład ekspozycji dziupli stwierdzono u oskomika, chociaż na ten wynik może mieć wpływ niewielka liczba badanych gniazd (Fig. 2). Dla wszystkich gatunków dzięciołów prócz różowoszyjego średnia wartość ekspozycji otworów wejściowych dziupli wskazywała na kierunek wschodni (Tab. 1, Fig. 2). Na wschód (wartości w zakresie 45–135°) skierowanych było 33% znalezionych dziupli. Nie stwierdzono różnic w ekspozycji otworów wejściowych dziupli pomiędzy gatunkami dzięciołów, natomiast różnice takie stwierdzono dla dwóch gatunków drzew, w których dzięcioły najczęściej wykuwały swoje dziuple. Dziuple w sośnie żółtej skierowane były częściej na wschód, zaś w daglezji zielonej przeważały dziuple skierowane na północ (Fig. 3). Jako potencjalną przyczynę tych różnic pomiędzy tymi gatunkami drzew autorzy wskazują m.in. udział bieli i twardzieli u każdego z gatunków.

Autorzy wskazują, że dzięcioły preferują wschodnią ekspozycję dziupli, dzięki czemu rano dziuple szybciej się nagrzewają, a jednocześnie unikają wysokich temperatur w godzinach popołudniowych. Dodatkowo, dzięki takiemu kierunkowi ekspozycji ptaki unikają zachodnich i północno-zachodnich wiatrów, które przeważają na terenie badań. Na wyniki może mieć wpływ fakt, że znaczna część drzew z dziuplami znajdowała się na terenach, na których w poprzednich latach występowały pożary, w związku z czym zacienienie dziupli przez korony drzew było ograniczone. Podsumowując, autorzy nie potwierdzili przewidywań, że w związku z położeniem geograficznym terenu badań, w ekspozycji dziupli dzięciołów powinien dominować kierunek południowy. Wyniki te wskazują, że czynniki wpływające na orientację dziupli są bardziej złożone i zależą zarówno od lokalnego klimatu, jak i składu gatunkowego drzewostanu.