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Annual survival of adult White-headed Woodpeckers (*Dryobates albolarvatus*) in ponderosa pine forest with a history of forest management

Jeffrey M. Kozma,^{1*} Andrew J. Kroll,² and Kevin S. Lucas³

ABSTRACT—Vital rates can provide important insights into management effects on wildlife populations. However, for many North American birds, especially woodpeckers (Picidae), vital rates are not well documented. Here, we estimated adult annual survival of the White-headed Woodpecker (*Dryobates albolarvatus*) across a 10 year period (2011–2021) in managed ponderosa pine (*Pinus ponderosa*) forests along the eastern slope of the Cascade Range in Washington, USA. We banded male and female woodpeckers with unique color band combinations and resighted them on breeding territories from March to July in each year. We banded 116 woodpeckers, most of which we aged as hatch-year ($n = 49$) or second-year ($n = 32$) when banded, and all were past the critical dependence period when mortality is highest. We estimated recapture and annual survival probabilities for 33 breeding males and 24 breeding females using open-population Cormack-Jolly-Seber models that included 2 covariates: age at first capture (AGE) and sex (SEX). We combined birds into 3 AGE classes: class 1 (hatch-year), class 2 (second-year and after hatch-year), and class 3 (\geq after second-year). Female recapture probabilities were higher than males, although both were >0.85 . AGE class 1 birds had the lowest recapture probabilities, but the estimates were imprecise. Survival probabilities were >0.80 for all birds, regardless of which model we evaluated. These survival estimates could be inflated because some adults that are nonbreeders and dispersed from the study area may have lower rates of survival. We did not find any evidence of differences in survival probabilities by SEX or AGE. Our results suggested that, despite managed ponderosa pine stands having trees smaller in diameter and greater in density than historical stands, White-headed Woodpeckers had a high probability of surviving year to year in this forest type. Received 6 February 2022. Accepted 27 April 2022.

Key words: color bands, mark-recapture, pine stands, survival estimates, Washington.

Sobrevivencia anual de los adultos del carpintero *Dryobates albolarvatus* en bosques de pino ponderosa con historial de manejo forestal

RESUMEN (Spanish)—Las tasas vitales pueden proveer una visión de los efectos del manejo en poblaciones de fauna silvestre. Sin embargo, para muchas aves de Norteamérica, especialmente para carpinteros (Picidae), dichas tasas vitales no están bien documentadas. Aquí estimamos la sobrevivencia anual del carpintero *Dryobates albolarvatus* a lo largo de un periodo de 10 años (2011–2021) en bosques manejados de pino ponderosa (*Pinus ponderosa*) en la vertiente este de la cordillera Cascade en Washington, EUA. Anillamos machos y hembras de carpintero con combinaciones únicas de anillos de colores y los re-observamos en sus territorios reproductivos de marzo–julio de cada año. Anillamos 116 carpinteros, la mayoría de los cuales determinamos como del primer año ($n = 49$) o del segundo año ($n = 32$) al momento de ser anillados y todos habían pasado el periodo de dependencia crítica cuando la mortandad es más alta. Estimamos probabilidades de recaptura y sobrevivencia anual de 33 machos y 24 hembras reproductivos usando modelos Cormack-Jolly-Seber para poblaciones abiertas que incluyeron 2 covariables: edad de primera captura (AGE) y sexo (SEX). Combinamos estas aves en 3 clases de AGE: clase 1 (del primer año), clase 2 (del segundo año y después del segundo año) y clase 3 (\geq después del segundo año). Las probabilidades de recaptura de hembras fueron más altas que las de los machos, aunque ambas fueron >0.85 . Las aves de la clase 1 de AGE tuvieron la más baja probabilidad de recaptura, aunque estas estimaciones fueron imprecisas. Las probabilidades de sobrevivencia fueron >0.80 para todas las aves, independientemente del modelo evaluado. Estas estimaciones de sobrevivencia podrían estar infladas porque algunos adultos que son no-reproductivos y se dispersaron del área de estudio podrían tener tasas de sobrevivencia más bajas. No encontramos evidencia de diferencias en la probabilidad de sobrevivencia por SEX o AGE. Nuestros resultados sugieren que, si bien las parcelas con plantaciones de pino ponderosa bajo manejo tienen árboles de diámetros menores y mayores densidades que las parcelas históricas, estos carpinteros tienen una alta probabilidad de sobrevivencia año con año en este tipo de bosque.

Palabras clave: anillos de colores, captura-recaptura, estimaciones de sobrevivencia, parcelas de pino, Washington.

Woodpeckers are keystone species in forest ecosystems because they create cavities and excavations while nesting and foraging that other species use (Blendinger 1999, Aitken and Martin 2007), help to disperse the spores of wood-decaying fungi (Farris et al. 2004, Jusino et al.

2016), and aid in controlling insects harmful to forests (Koplin and Baldwin 1970, Fayt et al. 2005, Lindell et al. 2008). These activities suggest that woodpeckers are disproportionately important to their ecosystems (Virkkala 2006) and motivate their use as surrogates for forest bird diversity and richness (Mikusiński et al. 2001, Drever et al. 2008). Due to their importance to forested environments, land management agencies use woodpeckers as indicator species (Saab et al. 2007) and, consequently, are concerned with their

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population size (Martin and Eadie 1999). Therefore, increased understanding of vital rates and population dynamics can contribute to progressive conservation and management actions.

In the last 20 years, the role of woodpeckers as keystone species has encouraged research focused on their nesting ecology and habitat selection. However, despite the increased research focus, few survival estimates exist for picid species (Pasinelli 2006, Wiebe 2006, Cava et al. 2014). In part, this lack of information is due to the difficulty in capturing large numbers of woodpeckers to estimate survival (Bull 2001), short battery life (often ≤ 6 months) of transmitters used on woodpeckers during telemetry studies (Robles et al. 2007, Cox and Kesler 2012a, Lorenz et al. 2015), and the length of time (often > 5 years) needed to conduct capture–recapture studies (e.g., Sandercock and Jaramillo 2002, Brown and Roth 2009). However, species-specific survival rates are important measures of habitat quality (Johnson et al. 2006) and can provide population-level effects of management decisions (Mounce et al. 2014).

In Washington, the White-headed Woodpecker (*Dryobates albolarvatus*) is listed as a species of concern because of its association with old-growth ponderosa pine (*Pinus ponderosa*) forests (Dixon 1995, Buchanan et al. 2003, Krannitz and Duralia 2004). Over the last decade, research has shown that White-headed Woodpeckers also occupy forests with a history of timber management (Lindstrand and Humes 2009, Kozma 2011, Linden and Roloff 2015) as well as recently burned forests (Wightman et al. 2010, Tarbill et al. 2015). Within these forest types, research has focused on nest success (Wightman et al. 2010, Kozma and Kroll 2012), home range size (Lorenz et al. 2015), foraging (Kozma 2010, Kozma and Kroll 2013, Lorenz et al. 2016), and habitat suitability (Campos et al. 2020, Latif et al. 2020). These studies have greatly expanded our understanding of how White-headed Woodpeckers use managed and disturbed landscapes. However, no studies to date have investigated adult annual survival of White-headed Woodpeckers (Kozma et al. 2020), a key life history parameter that can be used to create demographic models for conservation and management (Bayne and Hobson 2002). To address this information gap, we conducted a 10 year mark–recapture study of a population of White-headed Woodpeckers along the eastern

slope of the Cascade Range to estimate the annual survival rate of adults. Our objective was to determine if age- and/or sex-specific differences influenced annual adult White-headed Woodpecker survival in managed ponderosa pine forests.

Methods

Study area

We conducted our study along the eastern slope of the Cascade Range, 38 km northwest of Yakima, Washington (46°53'N, –120°48'W) from 2011 to 2021. The study area encompasses 1,267 ha of forest interspersed with lithosol areas consisting of thin soiled basalt formations containing primarily forbs and grasses (Kozma et al. 2019). Fifty-one percent (651 ha) of the study area is forested with an overstory tree component dominated by ponderosa pine with a few scattered Douglas-fir (*Pseudotsuga menziesii*) in the uplands, and black cottonwood (*Populus trichocarpa*), quaking aspen (*P. tremuloides*), and black hawthorn (*Crataegus douglasii*) along narrow riparian corridors. Antelope bitterbrush (*Purshia tridentata*) and wax currant (*Ribes cereum*) dominated the upland understory. Overall, the area is characterized by hot, dry summers with over 80% of annual precipitation occurring during winter (Wright and Agee 2004) and falls within the “hot dry shrub/herb” (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Pseudoroegneria spicata*]) vegetation type (Harrod et al. 1999). Elevation of the area ranged from 713 to 950 m.

Almost the entire study area is currently owned and managed by the Washington Department of Natural Resources (WDNR), with only a few small, private land holdings. Prior to being owned by WDNR, some sections of the study area were owned by private timber companies. Thus, 90% of the study area has been managed, predominantly by the thinning of overstory trees, within the last 50 years. These activities have resulted in upland conifer trees being small, with a mean diameter at breast height (dbh) of 31.7 cm \pm 0.6 SE ($n = 1,138$, trees > 25 cm dbh; extracted from Kozma [2011]), and stands having a mean density 157.3 trees/ha \pm 12.7 SE (trees > 25 cm dbh; extracted from Kozma [2011]). Thus, our study area has a higher density of smaller diameter trees compared to historical ponderosa pine stands that contained a

mean of 50 trees/ha and a mean dbh of 60–70 cm (Agee 1996, Gaines et al. 2007).

Woodpecker capture and data collection

We captured White-headed Woodpeckers (hereafter woodpeckers) during the nesting and post-nesting period. During the nesting period, we captured adults at nest cavities when the nestlings were >10 d old and brooding by adults had ceased. For details regarding our nest searching protocol see Kozma and Kroll (2012). We only attempted to capture adults at nest cavities if both adults were present and feeding the nestlings. We used 2.5×6 m long, 38 mm mesh polyester mist nets placed in front of the nest cavities and captured the adults when they returned to the cavity with food. This technique only allowed us to capture adults at nest cavities <5.0 m in height. We were not able to catch all adults at cavities because some cavities were too high, some adults avoided the nets, some nest cavities we were unable to find, and some nests failed before we could attempt to capture the adults. In these instances, we resorted to capturing woodpeckers at water stations starting in mid-July to September in areas known to be heavily used by woodpeckers. Hatch-year birds captured during this time were past the period when they are dependent on adults—a time when juvenile mortality is highest (Robles et al. 2007, Cox and Kesler 2012a). Each water station consisted of a 22.7 L rubber tub filled with water and placed on the ground (Fig. 1). We placed 1–3 large rocks in the tub on one end of a dead branch with the other end of the branch protruding out of the tub, which allowed for small mammals such as chipmunks (*Tamias* sp.) to escape the water if they fell in and also provided a perch for woodpeckers to easily access the water. Each water tub was located near 2–3 ponderosa pine trees and was placed inside a 91×91×66 cm cage made of 15×15 cm livestock fencing to prevent large ungulates and free ranging cattle from drinking the water. We filled water stations at least once a week and after the stations had been set up for >1 week, we observed them to make sure woodpeckers were using the water. Once woodpeckers were visiting a water station, we placed 3 mist nets (same dimensions as those used at nest cavities) in a triangle pattern surrounding



Figure 1. Water stations used to capture White-headed Woodpeckers consisted of a rubber tub filled with water containing rocks in the bottom and a branch wedged in the rocks, all placed within a cage made of livestock fencing. Dead tree branches were fastened to the wire cage to make it easier for woodpeckers to land and access the water.

the water station to capture the woodpeckers as they attempted to access the water.

Upon capture, we gave each woodpecker a unique combination of 3 plastic (Darvic) colored leg bands and a numbered aluminum United States Geological Survey leg band. We affixed 2 colored bands on 1 leg and a colored band and numbered aluminum band on the other leg. We gave the same color combination to male and female woodpeckers second-year (SY) or older that we captured on the same breeding territory to identify them as a breeding pair. We used 9 different colors of plastic bands, excluding black, which easily blends with the woodpeckers' body plumage making it difficult to see at a distance (Milligan et al. 2003). We aged each woodpecker using general plumage coloration for hatch-year (HY) birds and primary covert molt patterns for older birds (Pyle 1997).

We searched territories for banded woodpeckers using playbacks of calls and drumming (Johnson et al. 1981) from March to July in each year. Because we have been studying this population of woodpeckers since 2003, we knew the general boundaries of most territories in the study area. We used 10×42 binoculars to read the color band combinations and we searched each territory containing banded woodpeckers until we determined banded woodpeckers were present or were replaced. A woodpecker was considered to have been replaced if a non-banded or different banded woodpecker took its place as a breeder. Upon

sighting banded and non-banded woodpeckers, we followed them or returned on subsequent visits to determine if they were a breeding pair by listening for pair-contact vocalizations (*kweek* and *chuf* calls; Kozma et al. 2020), observing copulation, or finding an active nest cavity. This was important because we occasionally detected nonbreeding banded woodpeckers (i.e., floaters) on territories, especially in early spring. Once a banded woodpecker was resighted in a given year, we did not search for that bird again in that year. Thus, the majority of woodpeckers had only a single observation per year unless they were resighted during other field work, such as trapping at a nest cavity or water station.

Mark–recapture modeling

We estimated annual survival using open-population Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992, Amstrup et al. 2005). One problem with mark–recapture methods is that survival estimates may be biased low if a large number of marked individuals are never resighted again (DeSante et al. 1995). Because most of the HY woodpeckers we banded were never observed in the study area after we banded them, we included only adult woodpeckers in our analyses that were seen breeding in the year they were banded or at least 1 year following the year they were initially banded if not banded at a nest cavity. This methodology may result in inflated estimates of adult annual survival because some adults (\geq SY) who are nonbreeders and choose to leave the study area may have lower rates of survival. Because this species is nonmigratory, pairs remain on the same territory throughout the year with no evidence of seasonal movements, and only 3 woodpeckers (all males) were observed to have switched breeding territories, we assumed that replaced woodpeckers had perished rather than emigrated from the study area. We only sighted a few individuals more than once in each calendar year, so we compiled multiple observations to create a single capture record for each individual for that year (Sandercock and Jaramillo 2002, Mounce et al. 2014). The CJS models consist of 2 sub-models estimating recapture and survival probabilities, which are linear functions of explanatory covariates fit with a logistic link function (Lebreton et al. 1992). We collected 2 covariates

for woodpeckers: age at first capture (AGE) and sex (SEX). To incorporate these covariates easily, we utilized the regression parameterization of CJS models (McDonald and Amstrup 2001, Amstrup et al. 2005). This parameterization uses maximum likelihood to estimate parameters of the logistic functions. Survival and recapture probabilities were estimated from the parameters of the logistic functions (McDonald and Amstrup 2001).

Given the 2 covariates, and the relatively modest number of individuals tagged and recaptured in our study, our approach was to fit all models and to compare the recapture and survival probability estimates. We had a general idea that both probabilities were high across all individuals, and the main objective of the analysis was to estimate the probabilities and confidence intervals. We placed woodpeckers into 6 different age classes based on plumage criteria: HY, after hatch-year (AHY), SY, after second-year (ASY), third-year (TY), and after third-year (ATY). Because we had small sample sizes in some age classes, we combined data into 3 categories: AGE class 1 (HY), AGE class 2 (SY and AHY; birds that were at least 1 year old), and AGE class 3 (ASY, TY, and ATY; birds that were >1 year old). We did not assess temporal trends in either recapture or survival probabilities because we collapsed year categories due to low sample sizes. We used R 4.1.0 (R Development Core Team 2017) for data manipulation and version 2.16.11 of the R package *mra* to estimate model parameters (function *F.cjs.estim*). For each model, we assessed goodness-of-fit using tests implemented in package *mra* (function *F.cjs.gof*) based on common procedures in logistic regression (Hosmer and Lemeshow 2000, Sakar and Midi 2010).

Results

Data summaries

We banded a total of 116 woodpeckers from 2011 to 2020; 59 were females and 57 were males. We captured 72% at water stations and 28% at nest cavities. The majority of females and males were HY and SY when banded (Table 1). Of the 116 banded, 24 females and 33 males were confirmed as breeding individuals and were used in the survival analyses. The majority of these 57 birds were also HY and SY when banded (Table 1). When we combined age classes there were 11

Table 1. Number of White-headed Woodpeckers banded by sex and age along the eastern slope of the Cascade Range, Washington, 2011–2020.

Age	Total banded		Total used in survival analysis	
	Male	Female	Male	Female
Hatch-year	23	26	11	3
After hatch-year	2	3	1	1
Second-year	15	17	13	11
After second-year	3	2	2	1
Third-year	7	5	3	2
After third-year	7	6	3	6
Total	57	59	33	24

males in Age Class 1, 14 in Age Class 2, and 8 in Age Class 3, and 3 females in Age Class 1, 12 in Age Class 2, and 9 in Age Class 3. The number of woodpeckers captured annually ranged from 1 to 21 individuals (Table 2). The number of woodpeckers that were banded increased during the initial years and stabilized approximately midway through our investigation (Table 2). Yearly variability in the number of woodpeckers banded was due to new breeding territories being discovered, the rate of replacement of banded woodpeckers by those that were not banded, and woodpeckers becoming easier to capture as we modified our trapping techniques.

On breeding territories males were detected for a mean of 3.58 ± 0.32 years ($n = 33$) and females for a mean of 3.55 ± 0.29 years ($n = 24$). Males that disappeared after holding a territory lived to a mean age of 3.58 ± 0.50 years ($n = 19$) while females that disappeared after holding a territory lived to a mean age of 3.86 ± 0.50 years ($n = 14$). One male banded as an ASY lived to at least 9 years 7 months and another banded as a HY was still alive at 9 years 11 months when he was resighted in 2021 at a nest cavity. Both are the oldest known ages for a White-headed Woodpecker (M. Rogosky, pers. comm). One female banded as an ASY was still alive at 8 years 8 months and another banded as an ATY was still alive at 8 years 9 months when they were resighted in 2021. Because the exact ages of these females were not known at capture, their longevity estimates should be considered conservative. Of the 57 woodpeckers we followed from year to year, only 1 male lost a color band and we were sure of his identity because his remaining color band combination was

Table 2. Number of White-headed Woodpeckers banded and the total number in the study population that were followed annually (i.e., confirmed breeding in the study area) along the eastern slope of the Cascade Range, Washington, 2011–2020.

Year	Hatch-year	Adult (\geq Second-year)	Total banded	Number in study population
2011	2	9	11	6
2012	2	4	6	9
2013	4	6	10	12
2014	1	0	1	10
2015	9	10	19	13
2016	9	10	19	16
2017	8	6	14	22
2018	12	9	21	28
2019	0	7	7	30
2020	2	8	10	33

unique to him. In addition, the lead author of this study performed $>90\%$ of the woodpecker resightings, which eliminated resight errors associated with multiple observers (Tucker et al. 2019). Thus, we are confident in the accuracy of our identification of the woodpeckers in our study population.

Recapture and survival probabilities

Female recapture probabilities were higher than males, although both were >0.85 (Table 3). We estimated lower recapture probabilities for AGE class 1 birds, but the estimates were imprecise. Survival probabilities were >0.80 for all birds, regardless of which model we evaluated (Table 3). We did not find any evidence of differences in survival probabilities by sex or age at first capture. The results of goodness-of-fit tests did not raise concerns regarding inadequate model fit for any of the models. The Hosmer-Lemeshow test was not significant ($P > 0.40$ for all models), and the Receiver Operating Characteristic curve displayed acceptable discrimination (>0.75 for all models).

Discussion

Our study is the first to estimate annual survival rates of adult White-headed Woodpeckers. The majority of woodpeckers we banded were HY and SY birds. We expected this result as we captured HY woodpeckers frequently at water stations in late summer when they typically start to disperse

Table 3. Recapture and survival probabilities and 90% confidence intervals for adult White-headed Woodpeckers along the eastern slope of the Cascade Range, Washington, 2011–2021. We estimated annual survival with open-population Cormack-Jolly-Seber (CJS) models.

Model	Recapture estimates (90% confidence interval)	Survival estimates (90% confidence interval)
p(.)survival(.)	0.87 (0.79–0.95)	0.85 (0.78–0.93)
p(.)survival(sex)	0.88 (0.80–0.96)	Female: 0.83 (0.70–0.96) Male: 0.87 (0.79–0.95)
p(sex)survival(.)	Female: 0.92 (0.79–1.00) Male: 0.86 (0.76–0.96)	0.85 (0.78–0.93)
p(sex)survival(sex)	Female: 0.93 (0.80–1.00) Male: 0.86 (0.76–0.96)	Female: 0.81 (0.68–0.94) Male: 0.87 (0.79–0.95)
p(.)survival(age)	0.88 (0.80–0.96)	AGE class 1: 0.86 (0.74–0.98) AGE class 2: 0.86 (0.76–0.96) AGE class 3: 0.85 (0.70–1.00)
p(age)survival(.)	AGE class 1: 0.74 (0.58–0.90) AGE class 2: 0.97 (0.90–1.00) AGE class 3: 0.92 (0.79–1.00)	0.85 (0.78–0.92)
p(age)survival(age)	AGE class 1: 0.73 (0.55–0.91) AGE class 2: 0.97 (0.90–1.00) AGE class 3: 0.92 (0.79–1.00)	AGE class 1: 0.88 (0.70–1.00) AGE class 2: 0.83 (0.76–0.90) AGE class 3: 0.84 (0.71–0.97)

across the landscape as they leave their natal home ranges. Likewise, we expected to capture SY birds at nest cavities, as these birds are seeking their first breeding opportunity and are most likely to replace established breeders on territories when a vacancy occurs. Because we did not band HY woodpeckers at nest cavities, we cannot be certain that HY woodpeckers we banded fledged in the study area. It is still unclear why more HY females were not detected as breeders in the study area as we banded more HY females than males. In general, very little information about natal dispersal by sex is available for other woodpecker species. Cox and Kesler (2012b) and Kesler et al. (2010) did not find differences in natal dispersal distances of male and female juvenile Red-bellied Woodpeckers (*Melanerpes carolinus*) and Red-cockaded Woodpeckers (*D. borealis*), respectively. In contrast, juvenile female Acorn Woodpeckers (*M. formicivorus*) dispersed farther than males (Koenig et al. 2000). However, juvenile females are known to disperse greater distances than juvenile males in other avian groups such as thrushes, swallows, and tits (Nilsson 1989, Plissner and Gowaty 1996, Winkler et al. 2005). Therefore, HY females we banded either dispersed outside their natal area to breed or, if they did not fledge in the study area, were dispersing through and out of the study area.

Our results showed that adult breeding woodpeckers have strong site fidelity to their breeding

territories because only 3 males dispersed (each ≤ 1.5 km) to a new breeding site. Lorenz (2016) also reported strong breeding site fidelity by adult White-headed Woodpeckers in her study area in Washington, with only 2 females reported dispersing ≥ 4.6 km to new breeding sites. Because breeding dispersal distances for male woodpeckers appeared to be shorter than for females, some breeding females may have emigrated from our study area. Greater breeding female dispersal distances have also been observed in the Northern Flicker (*Colaptes auratus*; Fisher and Wiebe 2006) and the Red-cockaded Woodpecker (Walters et al. 1988). We encourage further study into breeding dispersal strategies for the White-headed Woodpecker.

It is unclear why some woodpeckers chose to switch breeding territories. Research on other permanent resident birds has found that dispersal to a new breeding site is uncommon and that the loss of a mate is most frequently associated with breeding dispersal (Daniels and Walters 2000, Andreu and Barba 2006, Furst et al. 2021). However, for the 3 males that dispersed to different breeding sites, we do not know if they dispersed due to the loss of their mates. For 2 males, their original mate was not banded so we were unsure if either female was replaced; for the third male, both he and his banded mate nested in 2015, we could not locate either of them in 2016, and from 2017 to 2020 the male was breeding on a

territory 1.6 km from his original territory with a non-banded female. Given the ability of adult woodpeckers to live for an extended time (>8 years), a high density of occupied territories in our study area, and the presence of floaters waiting to take over a territorial vacancy, the risks to switching territories may be greater than maintaining fidelity to a single site.

Woodpeckers in our study experienced higher annual survival than published annual survival rates for almost all other woodpeckers summarized by Wiebe (2006). Compared to other resident, nonmigratory woodpeckers, annual survival for woodpeckers in our study (0.85 for both sexes combined) was 1.1–3.2× greater (Pasinelli 2006, Wiebe 2006, Robles et al. 2007, Cava et al. 2014, Rota et al. 2014), with the only exception being Red-cockaded Woodpeckers in central Florida (0.90 for males and 0.93 for females; DeLotelle and Epting 1992) and White-backed Woodpeckers (*Dendrocopos leucotus*) in Norway (0.86 for both sexes combined; Stenberg and Carlson 1998). We did not find age- or sex-related differences in survival. The fledgling period is often a time of low survivability for many birds and survival immediately after fledging is often lowest (King et al. 2006, Berkeley et al. 2007). The HY woodpeckers we banded were past the vulnerable fledgling stage and independent of adult care, which could explain why we did not see significant differences in annual survival between AGE class 1 and older birds. In addition, the lack of differences we observed in adult survival among age classes could be due to the fact that only hatch-year woodpeckers that survived and stayed to breed in the local study area were considered in our analyses. Adult woodpeckers have few predators, the most important in our study area being *Accipiter* hawks (e.g., Cooper's Hawk [*Accipiter cooperii*]) and owls (e.g., Northern Pygmy Owl [*Glaucidium californicum*]) year-round, and nest predators such as the long-tailed weasel (*Mustela frenata*) and black bear (*Ursus americanus*) during the breeding season (Kozma et al. 2020). In addition, male woodpeckers incubate the eggs and brood the nestlings at night and during the day, while females only perform these duties during the day (Kozma et al. 2020). However, predation on adult woodpeckers inside cavities is rare in our study area, with only 1 adult documented being killed inside a nest cavity

(Kozma et al. 2020). Thus, it appears that adult woodpeckers experience similar predation pressures throughout the year, which could explain the similar survival estimates we observed between the sexes. Previous studies have also documented similar survival rates between male and female woodpeckers (Delotelle and Epting 1992, Robles et al. 2007, Rota et al. 2014).

Kozma and Kroll (2012) reported that managed ponderosa pine forests may be acting as a sink for this woodpecker because mean annual productivity (0.92; calculated by dividing the number of fledglings per successful nest by 2 [Saab and Vierling 2001] and then multiplying by the period survival rate [Tozer et al. 2011]) was lower than the number of female fledglings per female per year (FFFY) needed to offset mortality (1.13; calculated as $1 - \text{adult survivorship}/\text{juvenile survivorship}$ [Donovan et al. 1995]). However, an annual survival estimate for this species was not available at the time of that publication, so the authors used a mean survival rate of 0.64 for *Dryobates* woodpeckers for that calculation and halved that rate to estimate juvenile survival (Nappi and Drapeau 2009). If we use the 0.85 adult survival probability from this study and a juvenile survival rate to 150 days post-fledging of 0.59 (Kozma et al. 2020), the FFFY needed to offset mortality is 0.25. Thus, because annual productivity is greater than FFFY, our findings suggest that these managed forests may be acting as a demographic source in some years and the role of these forests in the conservation of White-headed Woodpeckers in Washington should be reconsidered.

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