Forest Ecology and Management 363 (2016) 110–119

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Foraging plasticity by a keystone excavator, the white-headed woodpecker, in managed forests: Are there consequences for productivity?

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ARTICLE INFO

Article history:
Received 8 September 2015
Received in revised form 15 December 2015
Accepted 17 December 2015

Keywords:
Forage site selection
Nest productivity
Picoides albolarvatus
Pinus ponderosa
Ponderosa pine

ABSTRACT

Information on the foraging ecology of animals is important for conservation and management, particularly for keystone species whose presence affects ecosystem health. We examined foraging by an at-risk cavity excavator, the white-headed woodpecker (*Picoides albolarvatus*). The foraging needs of this species are used to inform management of ponderosa pine (*Pinus ponderosa*) forests in some areas of western North America. Past observational studies indicated that white-headed woodpeckers forage predominately on cones and trunks of large-diameter (>68 cm) pines in old-growth stands, although habitat selection while foraging has not been formally examined. We used radio telemetry to track forage substrate use among 37 adult, breeding woodpeckers for 176 h (10,576 min) in forest stands that had been recently thinned and/or burned with prescribed fire. We used discrete choice models to examine forage site selection and multinomial regression to examine consequences of foraging on nest productivity. Woodpeckers foraged on more than ten individual substrates and switched substrates seasonally, presumably to take advantage of prey availability. Dead wood and fir foliage were used commonly in the nesting period (86% and 68% of foraging, respectively), whereas pine foliage and trunk foraging dominated in the fledgling (66% of foraging) and post-fledgling periods (73% of foraging). Average size of used trees was 49 cm (±20 cm) and pine cones were rarely used (4% of foraging). During the nesting period, substrate use ($\chi^2 = 1.49$, df = 4, $P = 0.83$) and distances traveled from nests for foraging did not affect productivity ($F_{(3,16)} = 0.61$, $P = 0.62$), which was high even for birds with the longest (2.1 km) and shortest (0.39 km) maximum forage distances. Habitats selected for foraging matched substrate use, and woodpeckers selected areas with low basal areas of live trees in the nesting period, but high basal areas in the post-nesting period. The variable foraging that we observed suggests that white-headed woodpeckers are plastic in their foraging in managed forests, and this plasticity has no negative consequences for productivity.

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1. Introduction

White-headed woodpeckers (*Picoides albolarvatus*) are important ecosystem engineers that act as keystone species in dry pine forests of western North American. They are one of the closest living relatives of the more widespread Hairy Woodpecker (*Picoides villosus*) (Fuchs and Pons, 2015; Weibel and Moore, 2002a, 2002b) and excavate nest cavities that are important nest and shelter sites for a wide variety of small-bodied animals (Tarbill et al., 2015). Throughout their range they are considered a sensitive or endangered species that has declined in the last century owing to intensive forest management practices (Garrett et al., 1996; Mellen-McLean et al., 2013). Old pine forests were thought to be important for providing snags for nesting and reliable cone crops for foraging (Dixon, 1995a; Mellen-McLean et al., 2013; Raphael and White, 1984). Because of white-headed woodpecker's association with old-growth ponderosa pine, they have also been considered management indicator species for ponderosa pine (*Pinus ponderosa*) restoration in the northwestern U.S.A. (Altman, 2000; Gaines et al., 2007, 2010). Their presence is thought to reflect ecosystem health and habitat quality for other pine-associated species and the management of ponderosa pine in some areas is

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http://dx.doi.org/10.1016/j.foreco.2015.12.021
0378-1127/Published by Elsevier B.V.

based at least partially on the nesting and foraging needs of the white-headed woodpecker.

While their nesting ecology has been well-studied range-wide (Hollenbeck et al., 2011; Milne and Hejl, 1989; Raphael and White, 1984; Wightman et al., 2010), studies of white-headed woodpecker foraging have mostly focused on southern populations (Hanson and North, 2008; Morrison et al., 1987; Morrison and With, 1987; Raphael and White, 1984). Four foraging studies have been conducted in the northwestern states of Oregon, Washington, and Idaho. These studies have helped advance our understanding of white-headed woodpecker foraging in this region, but were limited to relatively small sample sizes (three observations; Ligon, 1973) or single events within the breeding cycle (e.g., nestling period, Kozma and Kroll, 2013; or post-nesting autumn, Dixon, 1995a, 1995b). Management for the white-headed woodpecker in northern parts of their range is therefore guided by a combination of southern studies, and northern studies of limited scope and duration. This is potentially problematic because others have noted spatial and temporal variation in white-headed woodpecker foraging. For example, Morrison and With (1987) observed significant seasonal differences in populations in California. They also noted that populations in the central Sierra Nevada foraged on different tree species than southern populations, and both these sites differed from observations of foraging in Idaho (Ligon, 1973). In fact, in much of their southern range, white-headed woodpeckers forage on trees that do not even occur in the northern parts of their range, such as sugar pine (*P. lambertiana*), Coulter pine (*P. coulteri*), and incense cedar (*Calocedrus decurrens*; Hilkevitch, 1974; Morrison et al., 1987). Thus, although accurate information on foraging is important for management, there is a lack of regionally appropriate data on white-headed woodpecker foraging with which to guide management plans in the northwestern U.S.A. In addition to this region-specific need, no past studies have examined habitat selection by foraging white-headed woodpeckers; past studies have only measured use or selection relative to tree-level characteristics (e.g., Raphael and White, 1984). Information on use alone can lead to biased conclusions on resources that are important for animals (Johnson, 1980). We also could find no past studies that examined demographic consequences of foraging decisions. Thus it is not known whether observed differences in foraging by white-headed woodpeckers may contribute to local population declines, which have been suspected in some areas (Garrett et al., 1996).

Given these information gaps, we designed a study to examine white-headed woodpecker foraging ecology in the northwestern U.S.A. We studied foraging behavior in areas used for concurrent research on woodpecker nest site selection and space use. These areas were subject to both historic timber harvest (~10–80 years) and recent (<10 year) thinning and prescribed fire and contained little or no old growth forest. We had three objectives. First, we measured substrate use by white-headed woodpeckers in these managed forests during a six-month period that encompassed the incubation, nestling, fledgling, and post-fledgling periods in their annual cycle. Our goal was to characterize both substrate use and size of trees used for foraging in areas that had been harvested and/or burned, and which generally lacked the large trees (e.g., 68 cm diameter; Dixon, 1995a) considered important for foraging in other studies. Second, we modeled habitat selection by foraging white-headed woodpeckers during two time periods, the nesting period (combining the incubation and nestling periods) and post-nesting period (combining the fledgling and post-breeding autumn periods). Third, we examined whether differences in foraging behavior affected one important measure of population growth, number of young fledged from nests.

2. Materials and methods

2.1. Study area

We conducted this study from 2011 to 2013 in six study sites on the east slopes of the Cascade Range in central Washington State (approximately 46°45′N, 120°58′W and 47°30′N, 120°33′W). We selected sites in which white-headed woodpeckers were known to occur from past research, or in which reconnaissance surveys revealed breeding woodpeckers. Five of these sites were on U.S. Department of Agriculture, Forest Service land, and one site encompassed both state (Washington Department of Natural Resources, and Washington Department of Fish and Wildlife) and private lands.

Within each of our 6 study sites, forest composition varied based on aspect, slope, elevation, and longitudinal distance from the Cascade Crest. On most sites ponderosa pine was dominant or co-dominant with Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*). Other tree species included western larch (*Larix occidentalis*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). We estimated that ⩾92% of the area within study sites had been harvested for timber at least once since 1950 based on United States Forest Service Timber Harvest activity reports and Washington State Department of Natural Resources forest practice applications (FPAs). Most harvests were described as overstory removal cuts (removal of entire mature overstory) or partial removal cuts (removal of part of the overstory). Age of the dominant forest layer in each sites was estimated at <100 years (Lorenz et al., 2015a). Approximately 10% of the area within each study site had been burned with mixed severity prescribed fire and/or thinned by harvest within 10 years of the start of this study. Two sites each were actively grazed by domestic cattle or sheep during summer.

2.2. Field methods

We used radio telemetry to collect foraging observations on white-headed woodpeckers. From March through May we searched for territorial, adult white-headed woodpeckers in our study sites by broadcasting playback calls and drumming. We randomly selected, without replacement, a subsample of woodpecker nest territories for radio tracking from those within the study sites used in each year. At these territories we captured male white-headed woodpeckers with playbacks using noose traps on taxidermy mounts, and captured male and female woodpeckers at nest sites using mist-nests, noose traps, and hoop nets. We fit one adult from each territory with a 1.2 g VHF transmitter (~2% of body weight; Advanced Telemetry Systems, Islanti, MN) using an elastic leg-loop harness (Rappole and Tipton, 1991) or by gluing transmitters to a central tail feather. We alternated the sex that was radio tagged between territories to ensure equal representation by both sexes in our sample, and we radio tagged only one individual from each territory for independence among individuals. All activities were performed under University of Idaho Animal Use and Care protocol #2011-30.

We began tracking white-headed woodpeckers either with the onset of nest incubation or capture of an adult, whichever came first. We ended tracking either when adults shed their transmitters or with the first frost. During this period we monitored breeding status every 1–5 days by observing behavior of the adults and young (Jackson, 1977), inspecting nests with video inspection probes, and opening nests with a hole-saw (Ibarzabal and Tremblay, 2006). To estimate productivity, we checked nest contents using a hole saw or video inspection probe within 5 days of fledging and counted the number of nestlings. At a subsample of

half of all nests (50%), we also color-banded all nestlings with unique combinations of colors for individual recognition. We then confirmed fledging of individual nestlings by radio tracking adults during the post-fledging period and counting the number of young that were being tended (for failed nests, productivity = 0). For family groups with color-banded nestlings, we searched for and identified nestlings based on their color-bands. For family groups that without color-banded nestlings, we visually followed movements of adults and counted the number of juveniles being tended. Juveniles become vocal and audible from considerable distances within ~1 week of fledging and they follow adults about the territory as a group begging (T. Lorenz, pers. obs.), enabling relatively easy counts of dependent young while radio-tracking adults.

We took several precautions to avoid affecting productivity and nest success of radio-tagged adults (detailed in Lorenz et al., 2015a) and with these precautions in place, it is unlikely that we adversely affected productivity. We observed no cases of nest abandonment following radiotagging or banding nestlings, and across all years productivity of radio-tagged woodpeckers (mean fledglings = 2.17) did not differ from that of non radio-tagged woodpeckers (mean fledglings = 1.85) monitored in the same study areas ($t_{62} = 1.99$, $P = 0.370$). Additional details on measuring nest productivity, and capturing and tracking woodpeckers can be found in Lorenz et al. (2015a).

2.3. Foraging observations

We obtained foraging information on white-headed woodpeckers by homing to radio-tagged individuals, and observing their pecking, probing, gleaning, or flycatching behavior. We alternated the order in which birds were tracked each day, for approximately equal representation of morning (sunrise to noon) and afternoon (noon to sunset) observations for each individual. We marked the locations of all foraging observations on portable GPS units. We then noted the plant species on which the birds were foraging, as well as the foraging substrate (seed cone, live stem, dead stem, foliage), and recorded the length of time that woodpeckers foraging on each substrate. We collected foraging data on woodpeckers for no more than 1 continuous hour at a time, and revisited each individual every 1–5 days. Whenever possible we measured the diameter at breast height for forage trees, or the diameter across the cut surface for stumps. However, woodpeckers sometimes moved too quickly between forage locations for us to measure diameter while remaining within sight of the bird, and in those cases we did not measure diameter. Because our sample may have been biased by missing some trees, we therefore report tree sizes used for foraging, but do not use tree size in any analysis.

We treated individual woodpeckers as independent sample units because they were captured on different territories, were not mated, and we observed no interactions among tagged birds during the course of the study. For examining use of different substrates by white-headed woodpeckers, we divided each individual's tracking period into four periods, corresponding to changes in the breeding cycle between May and October: incubation, nestling, fledgling, and post-fledgling autumn period. Because the length of each period varied following the biology of the species and the number of days each individual was tracked, the lengths of each period varied by individual. On average, we tracked individuals for 7 days during the incubation period (range 1–21 days), 19 days during the nestling period (range 5–25 days), 19 days during the fledgling season (1–44 days), and 36 days during the post-fledgling autumn season (1–94 days).

2.4. Forage site selection model covariates

We restricted our analysis of forage site selection to woodpeckers for which we had an adequate sample of point locations to estimate home ranges and for which we observed foraging, which included 19 woodpeckers during the nesting (incubation and nestling periods; generally May to mid-July) and 23 woodpeckers during the post-nesting period (fledging and post-breeding autumn period; generally mid-July to October). We used an information theoretic approach (Burnham and Anderson, 2002) to investigate whether white-headed woodpeckers selected different habitats while foraging within home ranges. We combined observations from the incubation and nestling periods into a single period, which we called the nesting period, and we combined observations from the fledgling and post-fledgling autumn period into a second period, called the post-nesting period. We examined forage site selection for these two time periods separately.

Territory-scale studies of forage site selection by white-headed woodpecker were not available in the literature so we developed models based on hypotheses from some observational foraging studies and nest-site selection studies. Based on observations of nest sites, Hollenbeck et al. (2011) suggested that white-headed woodpeckers selected areas of high canopy cover for foraging, whereas Dixon (1995a) hypothesized that woodpeckers selected for the largest trees available. Multiple studies have suggested that woodpeckers prefer foraging in ponderosa pines, although Dixon (1995a) and Raphael and White (1984) recorded foraging in firs. During the nesting period, it is also possible that woodpeckers prefer to forage close to nests irrespective of habitat type. Therefore we considered the effects of canopy cover, quadratic mean diameter (QMD), and basal area of ponderosa pine, Douglas-fir, and grand fir on the selection of locations for foraging (Table 1). In the nesting period we also included a covariate for distance to nest.

To estimate these habitat features at locations used for foraging, we used gradient nearest neighbor (GNN) models (Ohmann et al., 2011) derived from a combination of field plots, mapped environmental data, and Landsat Thematic Mapper (TM) satellite imagery from 2012. This dataset provided spatially explicit information on vegetation features at a 30-m resolution for all study sites. From all of the foraging observations that we collected, we randomly selected a subsample of 20 from each individual and season; we did not include every observed forage point to avoid potential autocorrelation in our dataset associated with tracking woodpeckers continuously for 1 h time blocks. We defined availability using the boundary of the 99% kernel home range for each individual. We computed 99% fixed kernel home ranges for the nesting and

Table 1
Description of model parameters used to examine forage-site selection by white-headed woodpeckers in central Washington, U.S.A., 2011–2013.

Parameter	Description	Considered for nesting period selection?	Considered for post-nesting period selection?
Canopy	Mean percent canopy coverage	x	x
Pineba	Mean basal area (m^2/ha) of ponderosa pine	x	x
Firba	Mean basal area (m^2/ha) of Douglas-fir	x	x
QMD	Quadratic mean diameter (cm) of trees	x	x
Nestdistance	Straight-line distance from nest site (m)	x	

post-nesting period using Geospatial Modeling Environment [Beyer, 2012; for additional details on the development of home ranges see Lorenz et al. (2015a)]. Within each of these home ranges, we used the ArcGIS random sample tool to select 20 random locations for comparison with used forage locations. We then extracted Gradient Nearest Neighbor (GNN) data on canopy cover, QMD, and tree basal area for each used and available point. Because of the relatively low spatial resolution of raster data layers (30-m) compared to telemetry data (6-m), we also considered using buffers around telemetry locations to characterize habitats, in which we averaged habitat characteristics within different sized circular buffers centered on each used and available location. We compared habitat composition using point data (e.g., 0-m radius buffer), 15-m radius buffers, 30-m radius buffers, and 45-m radius buffers, and observed high correlations among each of those four datasets for habitat factors that we compared ($r > 0.85$). For simplicity, we therefore used habitats characteristics estimated from point data in our analysis.

2.5. Statistical analysis

We computed straight-line distances between foraging locations and nest sites for the incubation and nestling periods in ArcGIS. We then used two-way repeated-measures ANOVA to compare mean distance traveled for incubation and nestling periods by sex, where period was treated as repeated, or within-subjects factor, and sex was treated as a between-subjects factor. We also used two-way repeated-measures ANOVA to compare proportion of time each substrate was used by male versus female woodpeckers, where substrate was treated as the within subjects factor and sex as a between-subjects factor. We then used repeated measures ANOVA with two repeated factors (substrate and time) to determine whether woodpeckers spent different proportions of time on different substrates by morning versus afternoon. We used one-way repeated-measures ANOVA to compare distance traveled to the two most commonly used substrates, and only for birds that we observed foraging on both. Data were assessed for normality and homogeny of variances, and when overall *F*-statistics indicated a significant difference among means, we used post hoc multiple comparison Tukey–Kramer tests.

We used multinomial logistic regression to determine whether distances traveled for foraging or substrate influenced productivity (# of fledglings/nest). We did not treat the response variable as continuous (as may be expected with linear regression) because among >100 nests monitored over 8 years in our study area (e.g., Kozma and Kroll, 2012; Lorenz et al., 2015a), the only observed numerical options for nest productivity were 0, 1, 2, 3, or rarely, 4 fledglings. Variables considered as possible predictors were maximum forage distance, mean forage distance, and proportion of time spent on different substrates. We tested for correlations among explanatory variables beforehand and found that dead wood and fir foliage foraging were correlated. Consequently, we omitted fir foliage from our regression analysis.

We used discrete choice models to examine forage site selection using the COXME package in R version 3.1.1 (R Core Team, 2013), where each used forage point was paired with one available point in a choice set. Prior to building our models we tested for correlations between all pairwise combinations of covariates and found Douglas-fir was correlated with grand fir basal area for both the breeding and non-breeding periods ($r > 0.70$). We therefore omitted grand fir and used Douglas-fir basal area to represent basal area by both species for foraging woodpeckers. We compared a set of 7–8 *a priori* models for the nesting and post-nesting period using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (Burnham and Anderson, 2002), where models with lower AIC_c and higher weights are better supported than other models. For the top model, we presented parameter estimates, their standard errors, *p*-values, and confidence intervals.

We validated our top model using a modified *k*-fold approach following the methods of Bonnot et al. (2011). We randomly removed 20 percent of cases as "test data", fit the model with the remaining cases ("training data"), and tested the ability of the model to identify used points within choice sets of the test data. We completed five iterations of this method, each time removing another 20% of cases. Based on random chance alone we expected 50% (1 in 2) of used sites to be correctly identified and values >50% suggested that our model predicted use better than random (Bonnot et al., 2011).

We used SAS version 9.3 statistical software (SAS Institute, 2011) and R version 3.1.1 (R Core Team, 2013) for statistical analyses. We report means ± standard deviation unless otherwise noted, and we considered statistical results significant at $\alpha = 0.05$.

3. Results

3.1. Substrates used for foraging

We recorded 10,576 min (176 h) of foraging by 37 breeding white-headed woodpeckers from May through October. Woodpeckers foraged on 11 different substrates and six plant species during this period. For our analyses we grouped foraging observations into six substrate/species categories: dead stems (stumps, trunks, and branches of all tree species), live stems (trunk and branches of all tree species), fir foliage (Douglas-fir and grand fir needles), pine foliage (ponderosa pine needles), seed cones (Douglas-fir and ponderosa pine cones), and other.

We observed foraging by 18 females and 19 males. Combining data from all periods, we observed no overall differences in foraging substrate by sex ($F_{(1,32)} = 0.060$, $P = 0.812$) and combined sexes in subsequent analyses. We also observed no differences in foraging substrate use between morning and afternoon tracking sessions ($F_{(1,32)} = 0.023$, $P = 0.880$), and therefore combined morning and afternoon observations in our analyses.

Dead stems and foliage were the most commonly used substrates for foraging across all periods and individuals, and accounted for 62% of all foraging observations. Most (92%) dead stem foraging was on cut stumps from past timber harvests (Fig. 1). Compared with all visible stumps within forested stands, the stumps used for foraging appeared little decayed, with sound, firm wood and thus we assumed that they had been created by the most recent timber harvest at each site. If this is the case, than stumps used for foraging were typically <10–20 years old. When woodpeckers obtaining wood boring beetle larvae from these stumps they would peck with vigor for minutes at a time, confirming our suppositions that these stumps contained wood with little decay or softening. Additionally, while we did not conduct telemetry studies with sympatric black-backed woodpeckers (*Picoides arcticus*) and hairy woodpeckers that occupied these same stands, we observed that they foraged commonly on the same cut stumps, and these are characteristically considered species with strong excavator morphology (Kirby, 1980). Thus, it is likely that these stumps were recently created (<20 years old) and contained wood with little decay. However, because the age of stumps could not be verified, it is possible the stumps had been created in earlier timber harvests.

Foliage foraging was divided between grand fir (12%), Douglas-fir (32%), and ponderosa pine (57%). Most live stem foraging occurred on the trunks of ponderosa pine trees (99%). Cone foraging was uncommon (7% of all foraging observations) and white-headed woodpeckers foraged nearly equally on ponderosa pine (4% of foraging) and Douglas-fir cones (3% of foraging). The 'other'

Fig. 1. Examples of the two most common foraging behaviors by white-headed woodpeckers breeding in central Washington, 2011–2013. Deadwood foraging (top) and foliage foraging (bottom) accounted for 82% of foraging observations by breeding woodpeckers. Deadwood-foraging occurred mostly on cut stumps left from past timber harvest and foliage-foraging occurred in grand fir, Douglas-fir, and ponderosa pine trees.

category accounted for 8% of foraging and included four uncommon foraging substrates: air (i.e., flycatching), ground, common mullein (*Verbascum thapsus*) flower heads, and ponderosa pine pollen cones.

Woodpeckers switched their use of different foraging substrates across periods (Fig. 2). Deadwood foraging dominated during the incubation and nestling periods (58% and 34% of foraging, respectively), and abruptly stopped with the onset of the fledgling period. Conversely, live stems were commonly used during the post-fledgling autumn period (57% of foraging), and yet were rarely used in the incubation and nestling periods (7% of foraging; Fig. 2). Pine foliage was important during the fledgling period (42% of foraging), was never used in the incubation period, and was used moderately during the nestling and autumn periods. Overlapping confidence intervals suggested that use of fir foliage and cones did not differ substantially among periods (Fig. 2)

Overall average size of used trees was 48.68 cm (±20.27 cm; range 2.54–127.80 cm), and again, overlapping confidence intervals indicated that mean tree size generally did not differ among periods or substrates (Fig. 2). One exception was that smaller trees were used during the nestling period for live-stem and foliage foraging.

3.2. Foraging behavior and productivity

Mean distance traveled from nests for foraging did not differ by period ($F_{(1,19)} = 3.00$, $P = 0.099$), sex ($F_{(2,19)} = 1.05$, $P = 0.368$), or substrate ($F_{(1,12)} = 1.03$, $P = 0.331$). Distance traveled averaged 0.44 km (±0.32 km; range 0.02–2.08 km) for females and 0.46 km (±0.35 km; range 0.02–1.46 km) for males. Grouping both sexes, white-headed woodpeckers traveled 0.47 km (±0.32 km) while foraging on deadwood and 0.45 km (±0.36) while foraging on fir foliage.

We found that productivity was not influenced by foraging behavior. The number of young fledged from nests was poorly correlated with mean ($r = -0.189$) and maximum ($r = -0.162$) foraging distance. Additionally, type 3 effects indicated that mean forage distance ($\chi^2 = 2.980$, df = 4, $P = 0.561$), maximum forage distance ($\chi^2 = 1.786$, df = 4, $P = 0.775$), and proportion of time spent foraging on dead wood ($\chi^2 = 1.486$, df = 4, $P = 0.829$) during the nesting periods did not affect productivity. Productivity was generally high, despite the variation we observed in foraging. For woodpeckers tracked during the nesting period, only one nest failed outright and 75% of individuals fledged at least three young, including the individuals with the longest (2.08 km) and shortest maximum forage distances (0.394 km). Across all radio-tracked adults, average number of fledglings per nest was 2.3, and average number of fledglings per successful nest was 2.6.

3.3. Forage site selection

White-headed woodpeckers selected different habitats for foraging in the nesting versus post nesting periods. While the top-ranked model in both periods was the global model ($w_i = 0.99$ for both periods) (Table 2), parameter estimates indicated that during the nesting period, white-headed woodpeckers selected locations with low pine and fir basal area (Fig. 3) but which were close to nest sites (Table 3). Average distance traveled from nests was 467 m (±356 m) compared to 575 m (±349 m) for available sites (Table 4). In contrast, for the post nesting period woodpeckers selected areas with higher pine and fir basal area, more open canopies, and smaller trees compared to random sites (Table 3, Fig. 3). Model validation indicated that both models performed better than random, and on average correctly predicted use in 66 and 78% of cases for the nesting and post-nesting seasons, respectively.

4. Discussion

4.1. Substrates used for foraging

White-headed woodpeckers varied their foraging behavior over the course of our study and most individuals fledged multiple young in our study stands that had been harvested multiple times and lacked large old trees (mean diameter of trees was estimated at 33 cm). This suggests that managed forests that include historic and recent thinning and prescribed fire can provide foraging habitat for this species during the breeding period. Our results also indicate that stands composed of large, old pines are not necessary for providing foraging substrates for breeding. Lacking large, old pines, white-headed woodpeckers in our study foraged on dead wood, foliage of pines and firs, and the trunks of moderately-sized pines (e.g., 40–50 cm), while seed cones were rarely used.

The varied foraging behavior of woodpeckers in our study, characterized by woodpeckers shifting among substrates as seasons changed, is similar to some accounts of white-headed woodpeckers foraging in other studies. Morrison et al. (1987) noted that more than six tree species and four substrates were used by white-headed woodpeckers during summer in central California,

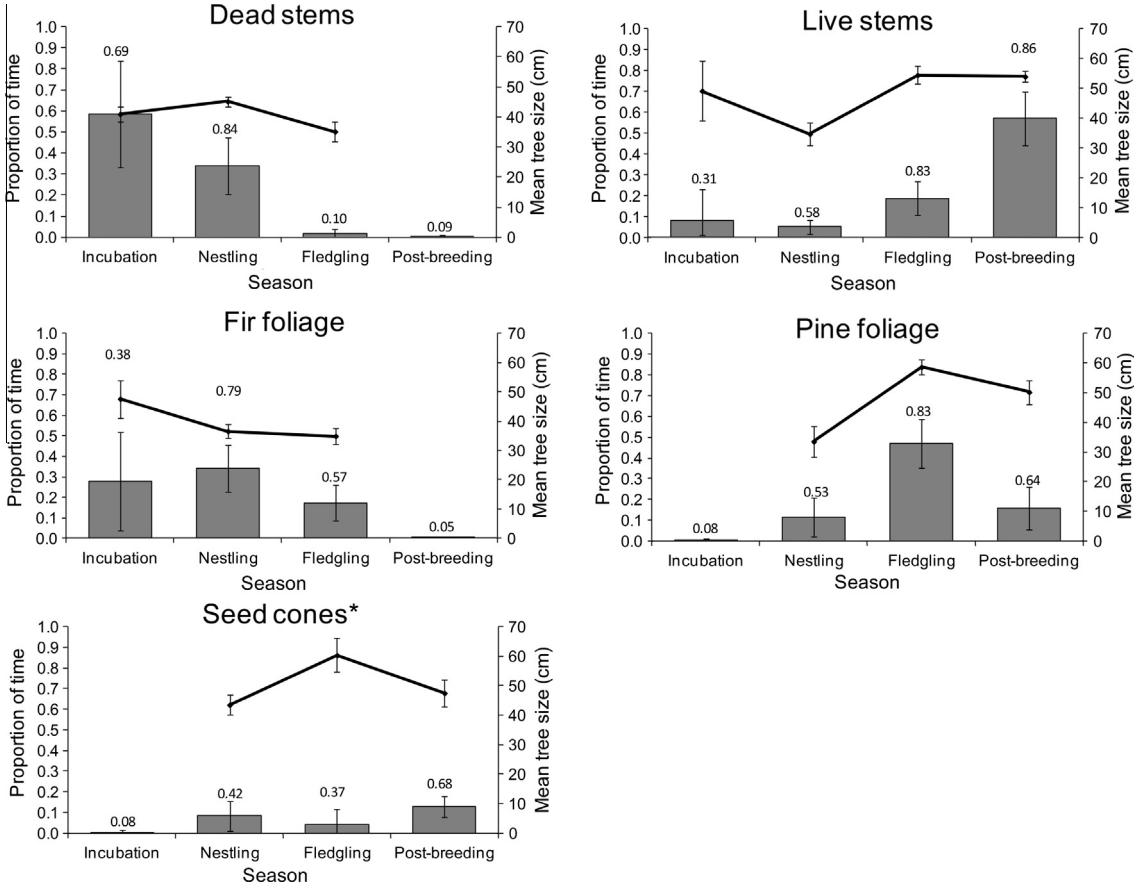

Fig. 2. Foraging substrates used by 37 white-headed woodpeckers that were radio-tracked in central Washington, 2011–2013. Shown are mean proportion of time (bars; n = 10,576 min), mean tree size (lines; n = 2435 trees), and 95% confidence intervals for each time period and substrate. Numbers above each bar represent proportion of individuals observed foraging on each substrate for each time period. ∗Only Douglas-fir seed cones were used during incubation and nestling periods, and only ponderosa pine seed cones were used during the fledgling and post-breeding periods.

Table 2
Relative support for models examining third-order forage-site selection by white-headed woodpeckers during the nesting period (n = 19 woodpeckers) and post-nesting period (n = 21 woodpeckers) in central Washington, U.S.A., 2011–2013.

Model	k	AIC_c	Δ_i	w_i
Nesting period				
Nestdistance, QMD, canopy, pineba, firba	5	492.02	0.00	0.999
Nestdistance	1	506.77	14.75	<0.001
QMD, pineba	1	520.28	28.26	<0.001
Pineba	2	520.35	28.33	<0.001
QMD	1	523.71	31.69	<0.001
QMD, canopy	1	525.61	33.59	<0.001
Firba	2	525.77	33.75	<0.001
Canopy	1	528.78	36.76	<0.001
Post-nesting period				
QMD, canopy, pineba, firba	4	406.03	0.00	0.997
QMD, pineba	2	417.32	11.29	0.004
QMD, canopy	2	428.87	22.84	<0.001
QMD	1	432.32	26.29	<0.001
Pineba	1	534.71	128.67	<0.001
Canopy	1	558.64	152.61	<0.001
Firba	1	562.17	156.13	<0.001

while Kozma and Kroll (2013) identified 16 prey items brought to nestlings in a 4-week period in central Washington. Likewise, Otvos and Stark (1985) documented more than 40 food items in the stomachs of white-headed woodpeckers from California. The substrates used in this study are also similar to at least some past studies. Hanson and North (2008) observed white-headed woodpeckers foraging predominately on dead wood during the nesting period, although dead wood in their study consisted of standing snags. Raphael and White (1984) observed them foraging on foliage throughout spring and summer months. Our study adds to this research because it is the first to link foraging with reproductive consequences. We found that neither substrate used nor distances traveled for foraging were important predictors of productivity. This is true even for woodpeckers that traveled more than 2 km from nest sites to forage – a surprising distance given the presumed sedentary life-history of this species (Garrett et al., 1996) – and we observed generally high productivity by woodpeckers nesting in our study area. Thus, the variable and plastic foraging behaviors observed in white-headed woodpeckers may be an adaptive trait.

Despite these similarities among studies, our results differ from other foraging studies of the species. For example, Dixon (1995a, 1995b) reported white-headed woodpeckers foraging mostly by gleaning on the trunks of large pine trees in Oregon, and concluded that large live pines alone were important for foraging. Others have observed them foraging on pine cones in California and Idaho (Beal, 1911; Ligon, 1973; Tevis, 1953). Some of the differences between ours and these studies may be attributed to differences in study timing, as already noted. Ligon (1973) observed woodpeckers for a very short duration (3 days) whereas Dixon (1995a, 1995b) only observed foraging in late summer and autumn. In our study, had we restricted the duration to late summer and autumn, we would never have observed dead wood or fir foliage foraging and we would have concluded that only live pines were used. Our results

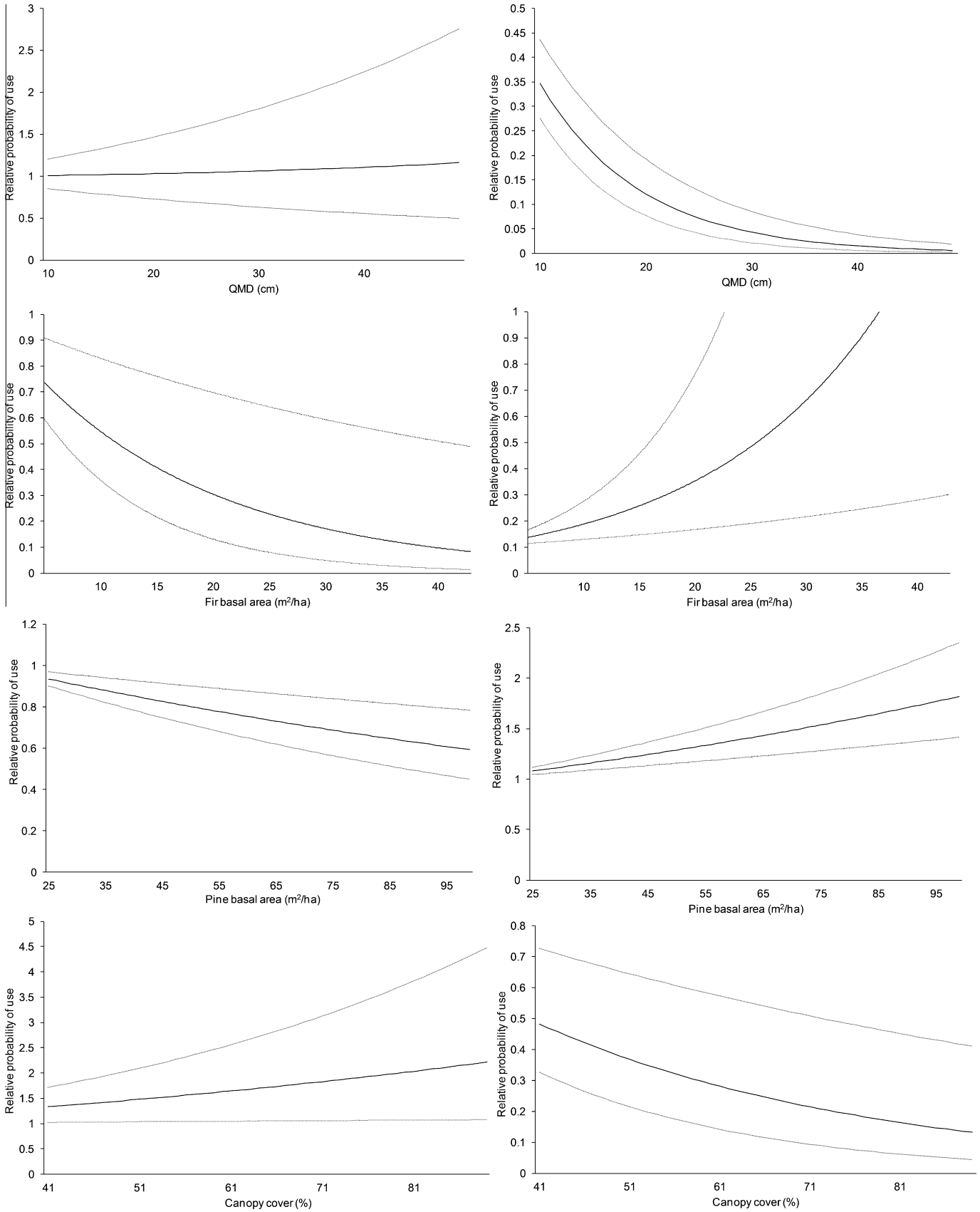

Fig. 3. Relative predicted probability of use (with 95% confidence intervals) of habitat features for foraging by white-headed woodpeckers during the nesting (left; $n = 19$ woodpeckers) and post-nesting seasons (right; $n = 23$ woodpeckers) in central Washington, 2011–2013.

Table 3
Parameter estimates, standard errors, chi-square statistics, and *P*-values explaining forage site selection by white-headed woodpeckers during the nesting and post-nesting period in Washington, U.S.A., 2011–2012.

Parameter	β	SE	z	P	Lower CI	Upper CI
Nesting period						
QMD	0.0003	0.0089	0.0062	0.973	−0.017	0.018
Pineba	−0.0615	0.0167	−3.682	<0.001	−0.094	−0.029
Firba	−0.0602	0.0212	−2.841	0.005	−0.102	−0.019
Canopy	0.0106	0.0062	1.695	0.090	0.001	0.020
Nestdistance	−0.0013	0.0003	−5.041	<0.001	−0.002	−0.001
Post-nesting period						
QMD	−0.1065	0.0117	−9.093	<0.001	−0.129	−0.084
Pineba	0.0704	0.0152	4.640	<0.001	0.041	0.100
Firba	0.0628	0.0189	3.314	<0.001	0.026	0.099
Canopy	−0.0267	0.0076	−3.536	<0.001	−0.042	−0.012

Table 4
Summary of habitat attributes from used versus available foraging sites for white-headed woodpeckers tracked in central Washington, 2011–2013. Attributes are provided only for the subsample of sites included in discrete choice models, rather than for all forage sites.

	Used	Available
Nesting season (n = 760)		
QMD (cm)	32.03 ± 10.19	33.63 ± 11.22
Fir basal area (m^2/ha)	7.38 ± 5.37	8.07 ± 6.14
Pine basal area (m^2/ha)	6.32 ± 5.34	7.41 ± 5.55
Canopy cover (%)	45.83 ± 20.98	45.98 ± 19.44
Distance from nest site (m)	467 ± 356	575 ± 349
Post-nesting season (n = 810)		
QMD (cm)	32.75 ± 10.08	33.07 ± 10.79
Fir basal area (m^2/ha)	8.57 ± 6.50	8.43 ± 7.38
Pine basal area (m^2/ha)	6.31 ± 8.02	6.28 ± 5.56
Canopy cover (%)	47.05 ± 18.88	46.56 ± 22.77

are also in contradiction to the summary of white-headed woodpecker foraging provided by Garrett et al. (1996), who concluded that white-headed woodpeckers rarely drill into dead wood and also that they forage on pine seeds year-round. In our study, drilling deep into dead wood was the most common means of foraging during the nesting period, and surface gleaning on trunks was restricted to autumn. In addition, pine seed foraging was rare in our study. It accounted for only 4% of all foraging and was observed only in the fledgling and post- fledgling autumn periods.

Given our results, we consider that the cone foraging behavior of white-headed woodpeckers may be less important than suggested in some past studies. Multiple papers on nesting ecology have described this species as dependent or reliant on pine seeds without direct observations of foraging within their populations (e.g., Hollenbeck et al., 2011; Wightman et al., 2010). Our results add to a larger body of literature that indicates that cone foraging is likely opportunistic. This literature includes studies that have reported both infrequent (Dixon, 1995b; Otvos and Stark, 1985) and no cone foraging (Grinnell and Storer, 1924; Hanson and North, 2008; Kozma and Kroll, 2013; Morrison et al., 1987; Morrison and With, 1987; Raphael and White, 1984). In support of this, white-headed woodpeckers do not exhibit adaptations that are typical for a pine-seed-dependence. Vertebrate animals that are dependent on conifer seeds evolved strategies for dealing with fluctuations in cone availability, or masting (Herrera et al., 1998). These strategies have been well-documented, and include facultative partial migration [e.g., crossbills (*Loxia* spp., Benkman, 1987), nutcrackers (*Nucifraga* spp., Formosof, 1933; Vander Wall et al., 1981)], food storage [e.g., chipmunks (*Tamias* spp.), squirrels (*Sciurus* spp. and *Tamiasciurus* spp.), jays (*Cyanocitta* spp.), reviewed in Vander Wall, 1997], and opportunistic breeding [e.g., crossbills (Hahn, 1995, 1998), pinyon jays (*Gymnorhinus cyanocephalus*, Ligon, 1974)]. With the possible exception of some local, small-scale movements (Dixon, 1995b) such behaviors have not been documented in white-headed woodpeckers. We therefore do not consider it surprising that in our study when pine seeds were presumably not available, white-headed woodpeckers switched to other substrates rather than migrating, retrieving seed caches, or foregoing breeding. However, given the plasticity of behaviors and foraging substrates found in this study and others, we encourage other studies to determine whether cone crops are important elsewhere, or improve survival or reproduction in our study area. Given that cones were rarely used in our study, we were unable to assess whether they were influential in survival or reproduction.

4.2. Foraging behavior, productivity, and selection

Our observations of foraging provide important insights into the behavioral ecology of white-headed woodpecker. Individuals in our study showed generally high productivity compared other studies, even while foraging in managed stands with environmental conditions presumably quite different from historical ones (Wright and Agee, 2004, but see Baker, 2012 and Hessburg et al., 2007); number of fledglings per nest in our study was 2.3 compared to an average of ~1.1 for >300 nests monitored in central Oregon by Frenzel (2003). In particular, the stump foraging behavior that dominated during the nesting period suggests behavioral plasticity, since cut stumps were not present for woodpeckers before ca. 1850. This may simply reflect a modification of historical foraging behavior that favored snags, and as noted above, the use of snags for foraging by white-headed woodpeckers has been observed in other studies (Hanson and North, 2008). Deadwood is an important foraging substrate for other North American woodpeckers (Nappi et al., 2015) and it should not be surprising that it can be important for some populations of white-headed woodpecker, despite accounts suggesting the opposite (e.g., Garrett et al., 1996).

Overall, our findings support suppositions of Morrison and With (1987) that this species is plastic in its foraging. Consequently, it is difficult to make generalizations about white-headed woodpecker foraging needs across large spatial or temporal scales, and studies based in one locale or in a single time period should not be used to characterize year-round foraging needs in other regions. For example, observations by Dixon (1995a) during a two- to six-month period (July onward) in one locale (central Oregon, U.S.A.) are sometimes used as evidence that white-headed woodpeckers require only large diameter pines for foraging (e.g., >60 cm DBH; Altman, 2000), and have formed part of the basis for ponderosa pine management in the northwestern U.S.A. (Hessburg et al., 2013; USFS, 2010, 2013). In our study, pines >60 cm DBH accounted for fewer than 4% of all foraging observations. While we did not measure foraging during winter, or measure availability of large pines to specifically test for selection at the tree-level, the fact remains that in our study area white-headed woodpeckers successfully breed while infrequently foraging on large diameter pines. Providing large diameter pines for foraging to the exclusion of other substrates may not be beneficial for woodpeckers during the breeding period, and management plans based on seasonal observations should be broadened. Similarly, we urge that results from our study not be used to characterize habitat needs of white-headed woodpeckers year-round, since we did not observe foraging from December through April. It is likely that white-headed woodpeckers in central Washington rely on different substrates during the winter and early spring months. Our study also should not be used to manage white-headed woodpecker habitat in other locales where they may use very different substrates. Rather, management plans should take into account the variation and plasticity in foraging by white-headed woodpeckers, and

restrict their inferences to local populations and appropriate time periods.

Given that most stands occupied by white-headed woodpeckers in this study had been harvested at least once in the last century, it is not surprising that they used smaller trees compared to those reported by Dixon (1995a, 1995b) in old-growth stands. The average size of trees used in our study was 50 cm DBH, similar to Raphael and White (1984), but smaller than the 68 and 74 cm reported by Dixon (1995a, 1995b). Additionally, we found areas of large diameter trees were not selected for. Instead during the nesting period woodpeckers selected areas of their home range that were close to nests but with low basal area of trees. During the post-nesting period woodpeckers selected areas with higher densities of pines and firs (e.g., higher basal area and lower QMD compared to non-use sites). This habitat-level selection may simply reflect substrate-level selection that we observed. Specifically, for the nesting period, woodpeckers predominately foraged on cut stumps, and it is likely that such habitats would have lower basal areas if they were recently thinned. For the post-nesting period, they foraged on foliage and live stems, resulting in selection for habitats with high tree densities.

Large-diameter trees are thought to be important for white-headed woodpecker foraging because the rugose bark is thought to harbor high densities of insect prey and more reliable cone crops. However, we could find no studies that actually compared bark arthropod abundance on forage trees of different sizes in our study areas, and as reviewed above, cones were rarely used in our study. It is possible that bark does not harbor high densities of quality prey in our study areas compared to stumps and foliage from May through October. Although we did not design this study to identify prey species, observations of food items in the bills of adults suggest that woodpeckers were foraging on very small, barely discernible arthropods while on tree trunks. In contrast, when foraging on stumps and foliage, we observed them consuming relatively large and easily visible long-horn beetle larvae (*Cerambycidae* spp.), spruce bud worms (*Choristoneura occidentalis*), and pine butterfly larva (*Neophasia menapia*; C. Mehmel, pers. comm.). Long-horn beetle larvae were obtained by drilling into the surface of cut stumps, spruce budworms by gleaning from fir foliage, and pine butterfly larva by pecking into the terminal clusters of ponderosa pines. We suggest that woodpeckers were increasing their foraging efficiency by selecting stumps and foliage for foraging, and that pine trunks were less profitable areas for foraging during the breeding period.

4.3. Management implications

This study adds to the growing body of literature indicating that white-headed woodpeckers successfully occupy and breed in forests with historic and recent timber harvest activity (Kozma and Kroll, 2013; Linden and Roloff, 2015; Lindstrand and Humes, 2009; Lorenz et al., 2015a). While they typically require snags for nesting and roosting – one potential component of old-growth (Garrett et al., 1996) – they are not necessarily dependent on large, old pines for foraging during the breeding season. Given the variability that this and other studies have noted in foraging, we suggest white-headed woodpeckers are plastic enough in their foraging that they are less limited by foraging habitat compared to nesting habitat (i.e., snags for cavity excavation) in the breeding season. Because of this, they may even preferentially select recently disturbed habitat, like burns, for breeding because they contain high snag densities for nest substrates (Lorenz et al., 2015a). Overall, we suggest that managers consider that snag availability can be an important limiting factor for this species during the breeding season (Lorenz et al., 2015b) compared to foraging habitat. As such, we encourage policies that promote the retention and creation of snags rather than a more exclusive focus on providing large diameter live pines. We also encourage studies of white-headed woodpecker foraging during the winter months to evaluate whether large pines are important during this period and whether seed cone availability enhances survival. Future studies are also needed to examine foraging in portions of the white-headed woodpecker's range where foraging information is currently limited or lacking, in order to guide region-specific management for this species.

Acknowledgements

This work was supported by the U.S. Department of Agriculture, Forest Service. We appreciate logistical support from R. Huffman with the Washington Department of Fish and Wildlife, and A. Lyons, K. Mellen-McLean, J. St. Hilaire, and D. Youkey with the U. S. Forest Service. J. Dudley, M. Kissling, C. Raley, M. Raphael, and P. Singleton loaned us equipment. We are grateful to individuals who provided advice on capturing woodpeckers and transmitter attachment, including R. Dixon, J. Dudley, C. Lehman, C. Raley, C. Rota, M. Rumble, R. Scott, and C. Werner, and to T. Johnson for providing advice on statistical methods. P. Fischer, K. Heniff, and S. Graham helped with field data collection, and P. Fischer was especially helpful in preparing transmitters and nets for trapping. C. Coffin, T. Bass, and J. Ashbaugh allowed access to their land.

References

Altman, B., 2000. Conservation Strategy for Land Birds of the East-slope of the Cascade Mountains in Oregon and Washington. American Bird Conservancy, Corvallis, OR.

Baker, W.L., 2012. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. Ecosphere 3, 23.

Beal, F.E.L., 1911. Food of the Woodpeckers of the United States. U.S. Department of Agriculture Biological Survey Bulletin 37.

Benkman, C.A., 1987. Food profitability and the foraging ecology of crossbills. Ecol. Monogr. 57, 251–267.

Beyer, H.L., 2012. Geospatial Modeling Environment. 0.7.1.0.

Bonnot, T.W., Wildhaber, M.L., Millspaugh, J.J., DeLonay, A.J., Jacobson, R.B., Bryan, J. L., 2011. Discrete choice modeling of shovelnose sturgeon habitat selection in the lower Missouri River. J. Appl. Ichthyol. 27, 291–300.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Dixon, R.D., 1995a. Ecology of White-headed Woodpeckers in the Central Oregon Cascades. M.S. Thesis. University of Idaho, Moscow, ID.

Dixon, R.D., 1995b. Density, Nest-site, and Roost-site Characteristics, Home Range, Habitat Use, and Behavior of White-headed Woodpeckers: Deschutes and Winema National Forests, Oregon. Oregon Department of Fish and Wildlife Nongame Report No. 93-3-01. Portland, OR.

Formosof, A.N., 1933. The crop of cedar nuts, invasions into Europe of the Siberan nutcracker (*Nucifraga caryocatactes macrorhynchus*) and fluctuations in numbers of the squirrel (*Sciurus vulgaris*). J. Anim. Ecol. 2, 70–81.

Frenzel, R.W., 2003. Nest-site Occupancy, Nesting Success, and Turn-over Rates of White-headed Woodpeckers on the Winema and Deschutes National Forests, Oregon, in 2003. A Report Submitted to the Fremont-Winema National Forests and the Deschutes National Forest. September 2003. 39 p.

Fuchs, J., Pons, J.M., 2015. A new classification of the pied woodpecker assemblage (Dendropicini: Picidae) based on a comprehensive multi-locus phylogeny. Mol. Phylogenet. Evol. 88, 28–37.

Gaines, W.L., Haggard, M., Lehmkuhl, J.F., Lyons, A.L., Harrod, R.J., 2007. Short-term response of land birds to ponderosa pine restoration. Restor. Ecol. 15, 670–678.

Gaines, W.L., Haggard, M., Begley, J., Lehmkuhl, J.F., Lyons, A.L., 2010. Short-term effects of thinning and burning restoration treatments on avian community composition, density, and nest survival in the eastern Cascades dry forests, Washington. For. Sci. 56, 88–99.

Garrett, K.L., Raphael, M.G., Dixon, R.D., 1996. White-headed woodpecker (*Picoides albolarvatus*). Account 252. In: Poole, A., Gill, F. (Eds.), The Birds of North America. Academy of Natural Sciences, Philadelphia, PA.

Grinnell, J., Storer, T.I., 1924. Animal Life in the Yosemite. University of California Press.

Hahn, T.P., 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostra*. J. Exp. Zool. 272, 213–226.

Hahn, T.P., 1998. Reproductive seasonality in an opportunistic breeder, the red crossbill *Loxia curvirostra*. Ecology 79, 2365–2375.

Hanson, C.T., North, M.P., 2008. Postfire woodpecker foraging in salvage-logged and unlogged forests of the Sierra Nevada. Condor, 777–782.

Herrera, C.M., Jordano, P., Guitian, J., Traveset, A., 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. Am. Nat. 152, 576–594.
Hessburg, P.F., Salter, R.B., James, K.M., 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecol. 22, 5–24.
Hessburg, P.F., Reynolds, K.M., Salter, R.B., Dickinson, J.D., Gaines, W.L., Harrod, R.J., 2013. Landscape evaluation for restoration planning on the Okanogan-Wenatchee National Forest, U.S.A. Sustainability 5, 805–840.
Hilkevitch, A.N., 1974. Sexual Differences in Foraging Behavior of White-headed Woodpeckers. M.S. Thesis. California State University, Long Beach, CA.
Hollenbeck, J.P., Saab, V.A., Frenzel, R.W., 2011. Habitat suitability and nest survival of white-headed woodpeckers in unburned forests of Oregon. J. Wildlife Manage. 75, 1061–1071.
Ibarzabal, J., Tremblay, J.A., 2006. The hole saw method for accessing woodpecker nestlings during developmental studies. Ann. Zool. Fenn. 43, 235–238.
Jackson, J.A., 1977. How to determine the status of a woodpecker nest. Living Bird 15, 205–221.
Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource performance. Ecology 61, 65–71.
Kirby, V.C., 1980. An adaptive modification in the ribs of woodpeckers and piculets (Picidae). Auk 97, 521–532.
Kozma, J.M., Kroll, A.J., 2012. Woodpecker nest survival in burned and unburned managed ponderosa pine forests of the northwestern United States. Condor 114, 1–13.
Kozma, J.M., Kroll, A.J., 2013. Nestling provisioning by hairy and white-headed woodpeckers in managed ponderosa pine forests. Wilson J. Ornithol. 125, 534–545.
Ligon, J.D., 1973. Foraging behavior of the white-headed woodpecker in Idaho. Auk 90, 862–869.
Ligon, J.D., 1974. Green cones on the pinon pine stimulate late summer breeding in the pinon jay. Nature 250, 80–82.
Linden, D.W., Roloff, G.J., 2015. Improving inferences from short-term ecological studies with Bayesian hierarchical modeling: white-headed woodpeckers in managed forests. Ecol. Evol. 5, 3378–3388.
Lindstrand, L., Humes, M., 2009. White-headed woodpecker occurrences in Sun Pass State Forest, south-central Oregon. Northwestern Nat. 90, 212–216.
Lorenz, T.J., Vierling, K.T., Kozma, J.M., Millard, J.E., 2015a. Space use by white-headed woodpeckers and selection for recent forest disturbances. J. Wildlife Manage. 79, 1286–1297.
Lorenz, T.J., Vierling, K.T., Johnson, T.R., Fischer, P.C., 2015b. The role of wood hardness in limiting nest site selection in avian cavity excavators. Ecol. Appl. 25, 1016–1033.
Mellen-McLean, K., Wales, B., Bresson, B., 2013. A Conservation Assessment for the White-headed Woodpecker (*Picoides albolarvatus*). U.S. Department of Agriculture, Forest Service, and U.S. Department of Interior, Bureau of Land Management. 41 p.
Milne, K.A., Hejl, S.J., 1989. Nest-site characteristics of white-headed woodpeckers. J. Wildlife Manage. 53, 50–55.
Morrison, M.L., With, K.A., 1987. Interseasonal and intersexual resource partitioning in hairy and white-headed woodpeckers. Auk, 225–233.
Morrison, M.L., With, K.A., Timossi, I.C., Block, W.M., Milne, K.A., 1987. Foraging behavior of bark-foraging birds in the Sierra Nevada. Condor 89, 201–204.
Nappi, A., Drapeau, P., Leduc, A., 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? For. Ecol. Manage. 346, 10–21.
Ohmann, J.L., Gregory, M.J., Henderson, E.B., Roberts, H.M., 2011. Mapping gradients of community composition with nearest-neighbor imputation: extending plot data for landscape analysis. J. Veg. Sci. 22, 660–676.
Otvos, I.S., Stark, R.W., 1985. Arthropod food of some forest-inhabiting birds. Can. Entomol. 117, 971–990.
R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Raphael, M.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monogr. 86, 3–66.
Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62, 335–337.
SAS Institute, 2011. SAS 9.3. SAS Institute, Care, North Carolina, USA.
Tarbill, G.L., Manley, P.N., White, A.M., 2015. Drill, baby, drill: the influence of woodpeckers on post-fire vertebrate communities through cavity excavation. J. Zool. 296, 95–103.
Tevis Jr., L., 1953. Effect of vertebrate animals on seed crop of sugar pine. J. Wildlife Manage. 17, 128–131.
U.S. Department of Agriculture, Forest Service, 2010. Gold Spring Restoration Project, Naches Ranger District, Okanogan-Wenatchee National Forest Environmental Assessment.
U.S. Department of Agriculture, Forest Service, 2013. Nelli Restoration Project, Naches Ranger District, Okanogan-Wenatchee National Forest Environmental Assessment.
Vander Wall, S.B., 1997. Food Hoarding in Animals. University of Chicago Press.
Vander Wall, S.B., Hoffman, S.W., Potts, W.K., 1981. Emigration behavior of Clark's nutcracker. Condor 83, 162–170.
Weibel, A.C., Moore, W.S., 2002a. Molecular phylogeny of a cosmopolitan group of woodpeckers (Genus *Picoides*) based on COI and cyt b mitochondrial gene sequences. Mol. Phylogenet. Evol. 22, 65–75.
Weibel, A.C., Moore, W.S., 2002b. A test of mitochondrial gene-based phylogeny of woodpeckers (Genus *Picoides*) using an independent nuclear gene β-Fibrinogen Intron 7. Mol. Phylogenet. Evol. 22, 247–257.
Wightman, C.S., Saab, V.A., Forristal, C., Mellen-McLean, K., Markus, A., 2010. White-headed woodpecker nesting ecology after wildfire. J. Wildlife Manage. 74, 1098–1106.
Wright, C.S., Agee, J.K., 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecol. Appl. 14, 443–459.