Primary Cavity Excavator Nesting Ecology, Space Use, and Distribution:
A Multi-scale Perspective

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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

Primary Cavity Excavators (PCEs) are an influential guild of animals that excavate cavities in trees for nesting and roosting. Vacated PCE cavities provide nest and shelter sites for a large number of animals – in some regions, up to one third of all species use or rely on PCE cavities. Thus, many species of PCE are considered ecosystem engineers and ecological keystones, and conservation of PCEs is important for biodiversity and ecosystem health. In this study, I explored nesting ecology, space use, and distribution of PCEs in the northwestern U.S.A. In chapter 1, I examined the role of wood hardness in limiting nest site selection. I found that interior wood hardness at nests differed from random sites, and nests of all species contained significantly softer interior wood than random trees. Accordingly, interior wood hardness was the most influential factor in nest-site selection by the six species I included in my study. In chapters 2 and 3, I focused on one at-risk PCE, the white-headed woodpecker (*Picoides albolarvatus*), and examined summer-fall ranging behavior and foraging ecology. I found that white-headed woodpeckers selected burned patches for their home ranges and varied their foraging behavior throughout the monitoring period. Overall, this study shows the importance of providing high densities of suitable snags for PCEs, even for live-tree foragers like the white-headed woodpecker. Snag management guidelines should be revised to take into account that large numbers of snags cannot be used for nesting by PCEs.

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CHAPTER 1

THE ROLE OF WOOD HARDNESS IN LIMITING NEST-SITE SELECTION IN AVIAN CAVITY EXCAVATORS

Abstract

Woodpeckers and other primary cavity excavators (PCEs) are important worldwide for excavating cavities in trees, and a large number of studies have examined their nesting preferences. However, quantitative measures of wood hardness have been omitted from most studies, and ecologists have focused on the effects of external tree- and habitat-level features on nesting. Moreover, information is lacking on the role of wood hardness in limiting nesting opportunities for this important guild. Here, we used an information theoretic approach to examine the role of wood hardness in multi-scale nest-site selection, and in limiting nesting opportunities for six species of North American PCEs. We found that interior wood hardness at nests ($n = 259$) differed from that at random sites, and all six species of PCE had nests with significantly softer interior wood than random trees ($F_{(1,517)} = 106.15$, $P < 0.0001$). Accordingly, interior wood hardness was the most influential factor in our models of nest-site selection at both spatial scales that we examined – in the selection of trees within territories and in the selection of nest locations on trees. Moreover, regardless of hypothesized excavation abilities, all the species in our study appeared constrained by interior wood hardness, and only 4-14% of random sites were actually suitable for nesting. Our findings suggest that past studies that did not measure wood hardness counted many sites as available to PCEs when they were actually unsuitable, potentially biasing results. Moreover, by not accounting for nest-site limitations in PCEs, managers may overestimate the amount of suitable habitat. We therefore urge ecologists to incorporate quantitative measures of wood hardness into PCE nest-site selection studies, and to consider the limitations faced by avian cavity excavators in forest management decisions.

Introduction

Most woodpeckers (Piciformes: Picidae) are members of an important and influential guild called primary cavity excavators (PCEs). PCEs are ecosystem engineers that are unique among vertebrates because of their ability and propensity to excavate nest cavities in solid wood. They also differ from the majority of birds that construct nests with materials from the external environment surrounding nest-sites, because the nests of PCEs are entirely constructed by removing wood from a tree's interior. This makes the nest-sites of PCEs relatively well-protected against environmental variability and predators, and many vertebrates that cannot excavate wood themselves readily use and compete for old, vacant PCE nests (Gentry and Vierling 2008, Martin et al. 2004, Aitken and Martin 2008). This guild of animals, called secondary cavity users (SCUs), is large and diverse – in some regions, SCUs comprise up to one-third of all vertebrate species and include all major taxa (Bunnell et al. 1999). Because of this, many species of PCE are considered both ecosystem engineers and ecological keystones (Daily et al. 1993, Bednarz et al. 2004, Blanc and Walters 2008), and the presence of PCEs has well-documented and far-reaching effects on species richness and ecosystem health (Lindenmayer et al. 2000, Virkkala 2006, Drever et al. 2008).

Given their importance, a great deal of research has focused on PCE nesting ecology, especially nest-site selection. Despite this attention, however, research studies have come to different conclusions about influential factors in nest site selection. These differences began more than 50 years ago, when some early studies suggested that PCEs select sites based on external tree- or habitat-level factors, such as tree size, tree species, and vegetation cover (e.g., Lawrence 1967). Others proposed that internal wood density drove PCE nest site selection (Conner et al. 1976, Miller and Miller 1980), and PCEs selected sites with ‘soft’ or ‘decayed’ wood (Kilham 1971, Conner et al. 1976, Miller and Miller 1980, Daily 1993) rather than trees with particular external features or characteristics. More recently, research studies have come to different conclusions even for the same species of PCE. For selection of nest trees within territories (third-order selection; Johnson 1980), Saab et al. (2009) reported that tree size and surrounding snag density were important for selection by hairy woodpeckers (*Picoides villosus*), while Schepps et al. (1999) concluded hairy woodpeckers select sites based on wood hardness.

Some of this dichotomy may stem from the fact that while methods for measuring external tree- and habitat-level features have been available for decades, methods for quantifying wood density lagged behind. An economical and practical tool for estimating wood density inside PCE nest trees was not available until Matsuoka (2000) improved on Schepps et al.’s (1999) method for measuring wood hardness. In lieu of quantitative measures, studies have used visual indications of wood decay, such as the presence of fungal conks (Pasinelli 2007, Cockle et al. 2012) or tree decay classes (Martin et al. 2004, Vierling et al. 2008, Bonnot et al. 2009, Wightman et al. 2010) as a surrogate for wood density. However, recent research has revealed two downsides of such visual markers for predicting PCE use. First, PCE nest trees do not always display fungal fruiting bodies even when wood decay fungi are present (Conner et al. 1976). Secondly, when tested in forestry studies, decay classes at best only roughly correlate with wood density (Saint-Germain et al. 2007, Aakala 2010, Strukeljii et al. 2013). Probably because of these shortcomings, PCEs reportedly use a variety of decay classes, ranging from entirely live trees with no conks or defects, to trees in advanced decay classes, indicating that fungal conks and decay classes are fairly unreliable indicators of nest site availability.

While past studies have advanced our understanding of PCE nest-site selection in multiple ways, incorporating quantitative measures of wood harness might advance our understanding further. In particular, studies are needed that simultaneously consider the effects of external habitat-level factors and wood hardness on nest site selection We reviewed a large number of studies published since Schepps et al. (1999) and Matsuoka (2000) that modeled habitat-level factors in nest site selection but did not quantify wood hardness (Martin et al. 2004, Vierling et al. 2008, Saab et al. 2009, Bonnot et al. 2009, Wightman et al. 2010, Hollenbeck et al. 2011). Meanwhile, the only studies we found that quantified wood hardness restricted their analysis of nest site selection to nest-tree factors (Schepps et al. 1999), measured hardness but did not specifically examine nest site selection (Matsouka 2008, Tozer et al. 2009), or measured hardness only at the outer surface of trees (Schepps et al. 1999, Tozer et al. 2009), when early studies indicated that interior wood hardness was more important (Conner et al. 1976, Miller and Miller 1980). Assuming that wood hardness is an influential factor, information is also needed on what proportion of wood in different decay classes is suitable for PCE nesting, and whether external features of trees can be used to estimate nest-site availability for PCEs. While forestry studies have measured wood hardness for trees in different decay classes, this information has not been used to estimate PCE nest site availability because there is no quantitative information on the density of wood at nests for any North American PCE. Such information would also be important for determining whether PCEs have nest-site limitations similar to SCUs (Newton 1994, Martin et al. 2004, Wiebe 2011).

Given these information gaps, we designed a study to examine the role of wood hardness in PCE nest-site selection and in limiting nesting opportunities. We had four primary objectives. First, we compared wood hardness at nests to wood at random sites, to determine whether nest wood was distinctive and limiting in natural systems. Second, we explored variation in wood hardness for nests of different species of PCE, and we tested whether species differed in their excavation abilities. Third, we examined the relative role of wood hardness in nest-site selection by PCEs. To do this, we modeled wood hardness in comparison with external tree- and habitat-level features that have been implicated in past studies of nest-site selection by PCEs. We tested for selection at two spatial scales – selection of nest trees within territories and selection of nest cavities on trees. Lastly, we examined whether external features of trees were a reliable indicator of interior wood hardness. We did this by comparing wood hardness for random trees within different decay classes and with different external properties.

Methods

Study area and study species

We conducted this study from 2011 through 2013 in the eastern Cascade Range of Washington State, U.S.A., in Yakima, Kittitas, and Chelan Counties (approximately 47º 00’ N and 121º 00’ W). Land ownership included private, state, and United States Forest Service. We searched for nests in all major forest cover types native to the eastern Cascade

Range, including ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), subalpine fir (*Abies lasiocarpa*) and western larch (*Larix occadentalis*) forests (Lillybridge et al. 1995). Elevation ranged from 350 m to 2000 m and dominant tree species varied among sites and by elevation. In general, 1350 m elevation marked the division between lower elevation ponderosa pine and Douglas-fir forest types and higher elevation grand fir or western larch forest types (Lillybridge et al. 1995). Some forests had been burned in U.S. Forest Service prescribed burns or wildfires in the last 10 years, and nests were found in patches ranging from unburned to severely burned (100% mortality of overstory trees).

We selected six species of PCEs for our study that occur in forests of western North America: American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*P. arcticus*), hairy woodpecker, northern flicker (*Colaptes auratus*), white-headed woodpecker (*P. albolarvatus*), and Williamson's sapsucker (*Sphyrapicus thyroideus*). We chose these species because they represent two presumed but unconfirmed guilds in excavation ability among PCEs. American three-toed, black-backed, and hairy woodpeckers have been classified as 'strong' excavators (Dudley and Saab 2003, Edworthy et al. 2012), compared to northern flicker, white-headed woodpecker, and Williamson's sapsucker (Saab and Dudley 1998, Schepps et al. 1999, Bunnell 2013).

Field methods

We searched for PCE nests from March through July, 2011-2013, in ten study sites approximately 600 to 3000 ha in size. We searched for nests in both live and dead trees. To make finding nests easier, we used playbacks of calls and drumming to locate adult birds

(Johnson et al. 1981) and followed adults until we located their nest cavities. We considered nests occupied if we observed eggs or nestlings using inspection cameras (Cen-tech Inc., Camarillo, CA) or if adult behavior indicated that incubation or nestling feeding was underway (Jackson 1977), and we marked the locations of all occupied nests on portable GPS units. PCEs may re-use cavities among years, and for nests that we found after nest-excavation we looked for fresh wood chips on the ground surrounding nests to determine whether nests were current-year excavations.

After the nesting season, we returned to all current-year nests and measured vegetation features that were hypothesized to influence PCE nest-site selection in past studies. We measured the diameter at breast height (DBH) of the nest tree, nest and tree height, and noted the species of tree. Most nests were in standing dead trees (hereafter, snags) and for these nests, we examined the remaining bark, tree growth form, and other features to determine species following Parks et al. (1997). We used a compass to determine the aspect for the nest cavity entrance, a spherical densitometer to estimate canopy cover at the nest tree, and estimated the proportion of the ground covered by shrubs within a 5-m radius plot (Martin et al. 1997). We also measured the DBH and noted the species of all trees and snags within 11.3 m of the nest for trees and snags at least 1.4 m height and 8 cm DBH (Martin et al. 1997). These measures were used to calculate tree and snag density at nest-sites. We then estimated prefire canopy cover at nest-sites because Saab et al. (2009) suggested it is important for nest-site selection in black-backed woodpeckers. To estimate pre-fire canopy cover we used Gradient Nearest Neighbor (GNN) Classified Landsat (ETM+) satellite imagery flown between two and eight years prior to each fire (LEMMA 2009). This dataset averaged pre-fire canopy cover within 30x30 m pixels, and for nests we assumed that the canopy cover from each 30x30 m pixel was representative of canopy cover at the actual nest site. We used ArcGIS 10 (Environmental Research Systems Institute) to extract these data for nest sites.

For assessing nest-site selection at the territory scale, we measured all of the aforementioned features at one random tree associated with each nest. We included only snags in our sample of randoms, since only a small proportion of nests occurred in live trees. We selected random snags by walking >75m from nests in a random orientation until we encountered a snag within ~10 m of the bearing. Following Bonnot et al. (2009), we assumed that nest territories were no greater than 250 m radius. Therefore, if no snag was encountered within 250 m of a nest-site, we returned to the nest and selected another random orientation. For random snags we included only those larger than 20 cm for the large-bodied northern flicker and 15 cm for the smaller woodpeckers and sapsuckers, because this corresponded to the smallest DBH trees used in our study by the large and small-bodied PCEs, respectively.

Characterizing wood hardness at nests and random sites

At each nest-site we measured the hardness of wood using a method developed by Matsuoka (2000) in which wood mass density is proportional to torque required to spin an increment borer into a pre-drilled hole. It is similar to the more commonly used resistograph (Isik and Li 2003, Farris et al. 2004), but requires the operator to manually record torque associated with predetermined distance increments. We accessed cavities >2 m high using climbing ladders, tree climbing spikes, and by felling snags, although we minimized felling to extremely high cavities or unstable snags (<1% of all snags).

As suggested by Matsuoka (2000), we used torque measured in newton meters (N•m) for all statistical analysis involving wood hardness although we also present summary statistics on wood mass density (Appendix A). In the first year of our study, the horizontal depth of our widest cavity was 14 cm, and so we measured hardness at 1 cm increments, beginning at the tree's surface and ending 15 cm deep towards the heartwood, similar to Farris et al. (2004) (Figure 1). Thus, for each hardness measurement we measured hardness at one spot on the exterior of the tree, but took 16 measures of wood hardness as we drilled in towards the tree's center.

A fundamental problem with this method is that it is impossible to measure the hardness of wood that has already been removed by PCEs (Conner 1977, Matsuoka 2000). We therefore had to make several assumptions about how hardness of removed wood was best represented by hardness of remaining wood. Results from Matsuoka (2008) suggest that wood 5 cm above the nest cavity opening is similar to wood 10 cm below the cavity body. Furthermore, Matsuoka (2008) implied that this wood should be representative of the excavated wood since it is close in proximity. We therefore measured wood hardness within 5 cm of the top of the nest cavity entrance. For nests excavated directly under limbs where the presence of a limb made it impossible to measure from the tree surface, we measured wood hardness within 10 cm of the lowest point of the nest cavity body.

Matsuoka (2008) also showed that hardness can vary across the width of nest sites, particularly between wood excavated for the nest entrance hole (hereafter 'sill') and wood excavated for the main cavity chamber, or cavity body (hereafter 'body') (Figure 1). We therefore treated sill and body wood differently in all analyses. For woodpecker nests, we measured horizontal sill and body width using calipers, and then averaged hardness for all wood measured in the sill and body regions. Random sites of course lacked nests. Thus, for comparing nest wood with random wood, we assumed that wood in the outer three centimeters of random sites was representative of the sill wood at PCE nests, since the average sill width in our study was 3 cm. Similarly, we assumed that wood 3 to 13 cm deep was representative of body wood, since across all nests, the average horizontal width of the nest cavity body was 10 cm. For random sites, we measured wood hardness at a random height and orientation on each snag. For logistical reasons, we selected random heights no greater than 12 m, which was the maximum extent of our climbing ladder. Since the average height of nests in our study was much lower than this (mean = 4.26 m; SD = 3.51 m), we assumed that this would not inordinately bias our results.

Pyle and Brown (1999) found that wood hardness varied across the bole of logs, and therefore it is possible that hardness varies across the bole of snags. If this is the case, a measurement taken at one location on random snags may not be representative of hardness throughout the bole. At a subsample of 10% of random trees, we therefore compared three measures of hardness within three strata of the tree’s height: the upper third, the middle third, and the lower third of the bole. Within each of these strata, we measured hardness at one random height and orientation. Although we conducted this test in order to measure the extent of hardness variation within trees, it is likely that our sample-scheme was not extensive enough to detect small or rare pockets of rot within the sampled trees. We therefore restricted our inferences on wood availability to actual measurement points, rather than assuming that our samples described hardness in the entire bole of random trees.

PCE nest-site availability

To calculate the availability of suitable wood, we compared the range of hardness between nest and random sites. We limited this analysis to two focal species, black-backed and white-headed woodpeckers, because we did not have time to measure hardness intensively at nest sites for all six PCEs before snowfall limited access to field sites. We chose these two species because they represent both the strong and weak excavator guilds, but are also at-risk species that have been the focus of much research attention recently (Bonnot et al. 2009, Wightman et al. 2010, Nappi and Drapeau 2011, Hollenbeck et al. 2011). For this particular objective, we selected a subsample of 50% of all black-backed and white-headed woodpecker nest-sites, returned to those nest-sites in autumn, and measured the wood hardness at the six nearest unused snags to each nest tree. We then calculated the minimum and maximum hardness values from nest-sites for the two species separately. Then for each of the six nearest non-use snags, we determined whether the range of hardness values in the sill and body region fell within the range of values for nest-sites. If the non-use site contained harder or softer wood than nests for that species, we considered it unusable (or unsuitable or unavailable) for nesting. Otherwise, we considered the sample usable (or suitable or available). We found no nests with softer body wood than random sites, and therefore omitted categories for body wood that was too soft. We then computed simple proportions of non-use samples that fell within each of six categories:

1 – sill too hard, body suitable

2 – sill suitable, body too hard

3 – sill too hard, body too hard

4 – sill too soft, body suitable

5 – sill too soft, body too hard

6 – suitable for nesting (sill and body both suitable)

We computed these proportions for all snags together, and then by snag decay class based on the system by Bull et al. (1997). Assuming that hard wood is more common than soft wood, we expected that the strong excavator guild, represented by the black-backed woodpecker would be less limited; i.e. they would have a higher proportion of excavatable wood available in nest territories, compared to a weak excavator, the white-headed woodpecker.

Nest-site selection model development

We evaluated multi-scale nest-site selection only for species with at least 30 nest locations. We used an information-theoretic approach (Burnham and Anderson 2002) to develop candidate models for each species based on hypotheses of nest-site selection from past research. Thus, for territory-scale selection we first conducted a literature search to determine features that were hypothesized to influence PCE nest-site selection and nest survival in past studies (Table 1; Appendix B). Some features implicated in past studies were highly correlated in our study because they essentially measured the same thing, but at slightly different scales. For example, Saab et al. (2009) and Forristal (2009) suggested that black-backed woodpeckers selected nest-sites with high densities of snags >23 cm DBH, whereas Bonnot et al. (2009) reported that they selected sites with high densities of snags >15 cm DBH. For such factors, we selected one parameter to include in our models, generally the factor that was implicated in the largest number of studies. Some other potentially influential features were not present in our study areas. For example, Bonnot et al. (2009) found that black-backed woodpeckers selected nest patches with high densities of aspens, which we did not ever record among 821 sampled trees in black-backed woodpecker territories. Thus, after combining some factors and omitting others, we retained 11 parameters that we considered might influence territory scale nest-site selection in our study area. We then built candidate models for each species that considered the potential effects of these factors on nest predation, adult foraging opportunities, and ease of excavation (Table 1), and we limited our candidate set to 20 models for all species (Johnson and Omland 2004). Because the literature indicates that the different species respond differently to various habitat features, the number of candidate models differed by species and ranged from 12 to 18 models.

For most species in this study, selection for a site on a tree had not been examined in past research studies. Thus, for the selection of a site on a nest tree, we included four covariates for all species: cavity orientation, cavity height, body wood hardness, and sill wood hardness. For this analysis, orientation was divided into four categories around the ordinal directions: north = 315-45º, east = 46-115º, south = 116-205º, west = 206-295º. Similar to territory scale selection, we built models for each species that considered the effects of nest predation, ease of excavation, and also nest thermoregulation on nest-site selection.

Tree external appearance and wood hardness

Snag decay classification systems are a common means of grouping snags into categories that are assumed to reflect underlying wood hardness and associated decay. However, we could find no past woodpecker studies that tested whether snag decay classes provided accurate information on wood hardness in a tree's interior. Therefore, we noted the decay class for every tree and snag sampled in our study using three established classification systems that have been used in past studies with our focal species. For these systems, trees are classified into three (Bull et al. 1997; hereafter Bull), five (Cline et al. 1980; hereafter Cline), or nine classes (Thomas et al. 1979, hereafter Thomas) based on whether they are alive or dead, the amount of bark remaining, condition of the top (intact or broken), and condition of the limbs (limbs or branches intact or broken), and higher numbers are supposed to indicate more advanced stages of decay (Table 2). We then tested whether wood hardness varied by decay class.

As noted by others (e.g., Larjavaara and Muller-Landau 2010), snag decay classes are inherently subjective; many trees are difficult to place into categories because they do not lose their bark, top, or limbs following the progression described by the various decay classes. Therefore, for each tree we also noted the approximate percentage of each of these features remaining. We then counted the number of old woodpecker cavities and starts, estimated the proportion of the tree surface that was blackened from fire, and noted the presence of fungal conks and woodpecker foraging evidence, using Farris et al. (2004) as a guide. We then related wood hardness at these trees with their external characteristics to determine if any external features were reliable predictors of internal wood hardness.

Statistical analysis

We used two-way repeated-measures ANOVA to compare hardness between the nest sill and body, and between nests of different species and random samples, where sill and body wood were treated as repeated, or within-subjects factors, and species was treated as a between-subjects factor. For this analysis we combined all random samples into a separate group to compare with samples from the nests of the different PCE species. Thus, our between subjects factor had seven levels, one for nests of each of the six species of PCE and one for random samples. We used one-way repeated measures ANOVA to test for differences in wood hardness at different heights within random trees, and simple, one-way ANOVA to compare wood hardness for trees within different snag decay classes. Whenever appropriate, data were assessed for normality. When overall F-statistics indicated a significant difference among means, we used post-hoc multiple comparison Tukey-Kramer tests.

We used multiple regression to determine whether any external features of random snags were reliable predictors of wood hardness. Variables considered as possible predictors were percent bark, branches, needles, limbs, and top remaining on the snag, percent bark that was blackened from fire, and the presence of fungal conks, woodpecker foraging evidence, and old cavities or cavity starts. We looked for correlations among explanatory variables beforehand, and found that branches, needles, and limbs were correlated. Consequently, we omitted limbs and needles from our final model. We assessed model fit using R^2 and looked for violations of model assumptions using standard residual tests and diagnostic plots.

To compare different models of nest-site selection by PCEs, we used conditional logistic regression models with matched-pairs case-control sampling, and where the “cases” are nest-sites and the “controls” are random sites (Keating and Cherry 2004). Prior to building our models we assessed possible correlations between all pairwise combinations of covariates and omitted covariates if their coefficient >0.5. We used Akaike’s Information

Criterion corrected for small sample sizes (AIC_c) to assess the amount of support for the different models. Based on Akaike weights, we considered models in the 90% confidence set of candidate models as the best approximating models given the data. For each variable in the 90% confidence set we computed model averaged parameter estimates, their standard errors, and 95% confidence intervals (± 1.96 SE), following Mazerolle (2006) and Symonds and Moussalli (2011). When confidence intervals did not include 0, we concluded that the associated parameter had an effect on nest-site selection. To assess the importance of variables, we computed a relative importance value by summing w_i for all models containing each variable, and for variables with equal representation across models (Burnham and Anderson 2002). For variables that showed quasi-complete separation, we computed parameter estimates using Firth's penalized maximum likelihood-method (Firth 1993) following recommendations by Allison (2008).

Goodness-of-fit tests for conditional logistic regression in case-control studies have not been well developed except for very special cases (Homer and Lemeshow 1985, Arbogast and Lin 2004), and the lack of predicted probabilities preclude the use of tools like prediction error and cross-validation. For all models in our 90% confidence set we therefore provided likelihood-based pseudo R^2 measures based on McFadden's proposed measures of goodness-of-fit (McFadden 1973), with the caveat that these do not necessarily have the same properties as R^2values in linear regression with least squares estimation, but they are roughly analogous. We computed McFadden's adjusted pseudo R^2, which penalizes models for including too many predictors, and we considered values close to 1 as indicative of adequate model predictive power.

We used SAS version 9.3 statistical software (SAS Institute 2011) for all statistical analyses, and we considered statistical results significant at $\alpha = 0.05$.

Results

General characteristics of nest and random sites

We found 259 PCE nests across a range of forest types and substrates. Most were in dead ponderosa pines (53%) or Douglas-firs (24%). Seven nests (3%) occurred in live trees, including live trembling aspen (*Populus tremuloides*), ponderosa pine, and Douglas-fir. One nest was excavated into the cedar siding of a cabin, two were in cut stumps, and one was in a fallen log on the ground. The remaining 19% of nests were in snags representing seven other tree species: grand fir, subalpine fir, trembling aspen, western red cedar (*Thuja plicata*), western larch, lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*). Average cavity height was 4.26 m (range 0.00-23.68 m) and average nest tree DBH was 41.90 cm (range 15.67-104.49 cm). The smallest nest tree in our sample was used by a white-headed woodpecker (DBH = 15.67 cm) and the largest by a hairy woodpecker (DBH = 104.49 cm). For comparison, average height of random sample locations was 4.12 m (range 0.76-16.74 m), and average DBH of random trees was 38.40 cm (range 15.49-108.20 cm).

Characteristics of wood hardness at nests and random sites

Mean wood hardness differed between the nest sill and body regions ($F_{(1,517)} = 65.66$, $P < 0.0001$), and between nests and random sites ($F_{(1,517)} = 106.15$, $P < 0.0001$). For all PCE nests, wood in the sill region was harder than wood in the body region, but for random sites wood in the body region was harder (Table 3). This resulted in a different hardness profile between nests and random sites where nests showed a distinctive drop in wood hardness in the tree interior, but samples from random snags increased in hardness from the bark surface until approximately 9 cm deep, at which point hardness leveled-off (Figure 2). Nest sites also increased in hardness beginning approximately 10 cm deep (Figure 1), and overall woodpeckers appeared to align the nest cavity body with the patch of softest wood at each site.

For wood in the body region, we found no differences in hardness by species, although random samples had significantly harder body wood than nests for all species (Table 3). For wood in the sill region, on average American three-toed woodpecker nests had the hardest sills among all species, and northern flicker had the softest sills. However, we observed considerable overlap in minimum and maximum sill hardness among species. For example, on average Williamson's sapsucker and white-headed woodpecker had sills of intermediate hardness, but they also had the hardest recorded sills of any species (16.61 and 14.46 N•m, respectively) (Table 3).

For assessing variation in hardness within trees, we randomly selected a subsample of 23 random trees (~10%) from our larger sample of all random trees. For logistical reasons, we restricted this subsampling to snags within 200 m of roads. For this subsample, wood hardness did not differ within random trees by height ($F_{(2,43)} = 0.09$, $P = 0.9168$).

PCE nest-site availability

Among 360 non-use samples obtained from white-headed and black-backed woodpecker territories, we classified 86% and 96% of wood samples as unsuitable for nesting by these species, respectively (Figure 3). For both species, the majority of non-use samples (63 and 78%) were deemed unsuitable because interior wood was too hard to be excavated for a nest cavity body, even though the exterior wood was suitable for nesting.

When considering snag suitability based on decay classification systems, the decay class that provided the highest proportion of suitable wood was decay class 3 of Bull's system, in which 14 to 20% of wood samples were suitable for white-headed and black-backed woodpeckers respectively (Figure 3). However, when considering average wood hardness for used versus unused snags, wood from decay class 3 was 4.6 times harder than wood from black-backed and white-headed woodpecker nest sites. Additionally, the majority of snags were too hard to be used for nesting by either species based on interior wood hardness and regardless of snag decay class. Decay class 1 of Bull performed especially poorly for black-backed woodpecker: 2% of snags in this class were usable, and on average wood from snags in this decay class was five times harder than wood at black-backed woodpecker nest sites.

Nest-site selection

We found at least 30 nest-sites for four species: black-backed woodpecker, hairy woodpecker, northern flicker, and white-headed woodpecker. For territory scale selection, the best fitting model describing nest-site selection included only body wood hardness for all species except white-headed woodpecker, which also included sill wood hardness in the top model (Table 4). For nest-tree selection, the top model included body wood hardness for all species (Table 4). For all species and at both spatial scales, the importance value for body wood hardness was 0.99, and body woody hardness was the only statistically significant parameter estimate in all models (Table 5). McFadden's pseudo R^2 ranged between 0.926 and 0.951 for models explaining nest-site selection, and 0.607 and 0.928 for nest-tree selection (Table 5), suggesting adequate predictive power for all models.

Tree external appearances and wood hardness

We classified 559 random snags into decay classes based on the systems of Bull, Cline, and Thomas. We had small sample sizes of snags in decay classes 1, 2, 8, and 9 (live trees and stumps) of the system used by Thomas, and thus only compared decay classes 3-7 for this classification system. Hardness of wood sampled from snags differed among classes for Bull ($F_{(2, 556)} = 10.93$, $P < 0.0001$) and Cline ($F_{(4, 554)} = 6.76$, $P < 0.0001$), but not for Thomas where we found an overall significant F-test ($F_{(4, 554)} = 5.72$, $P = 0.0002$) but no significant pair-wise comparisons (Figure 4). For Bull's system, average wood hardness decreased predictably by decay class. However, for Cline, wood hardness did not decrease predictably among decay classes, and snags in decay class 4 were harder than those in decay class 3. Overall, there was much overlap in hardness within decay classes. For example, the softest and hardest samples were both from snags in decay class 3 of Bull's system.

We found that external characteristics of snags were poorly correlated with wood hardness at sample locations ($R^2 = 0.074$). The only significant predictor of wood hardness for random sites was the presence of old woodpecker nest cavities and starts ($\beta = -1.31$, $p = 0.0032$), and for each cavity or start observed on a tree, mean wood hardness decreased by 1.3 N•m (Table 6). Woodpecker foraging evidence and the proportion of blackened bark, intact bark, intact top, and intact branches on a snag were not associated with changes in wood hardness (Table 6). Residuals plots and the Durbin-Watson test ($d = 1.97$) suggested that the model assumptions were not violated. We intended to consider whether the presence of fungal conks was associated with variation in wood hardness, but we found too few snags with conks (3.9%) to include them in our analysis. All of these conks (100%) were fruiting bodies of pouch fungus (*Cryptoporus volvatus*) and they occurred only on blackened and burned conifer snags.

Discussion

Characteristics of nest wood and differences among species

All six species of PCE in our study occupied nests that had a distinctive wood hardness profile, in which the nest cavity body was aligned with a patch of interior soft wood. This is similar to qualitative descriptions of wood at woodpecker nests by Conner et al. (1976) and Miller and Miller (1980), and more recent quantitative measures by Matsuoka (2008) for the Eurasian greater spotted woodpecker (*Dendrocopos major*). Our study confirms that soft interior wood is important for many North American PCEs since we observed this pattern at nest sites for all six species of PCE in our study.

There are several possible reasons for this distinctive profile of wood hardness. A few studies have suggested that woodpeckers do not select soft wood, but rather create soft wood by foraging or drilling starts, introducing fungi on their bills (Farris et al. 2004) and then returning to these locations to nest in later years. But most research indicates that woodpeckers instead locate and select soft spots that were independently created by wood decay fungi (Kilham 1983, Jackson and Jackson, Losin et al. 2006). Our results support this. First, woodpecker foraging evidence was not associated with softened wood on random snags. Second, many woodpeckers were attracted to recent burns (<1 year post-fire) for nesting, which almost certainly lacked appreciable numbers of pre-burn excavations. Third, some snags in our study were monitored as part of a concurrent study on woodpecker space use, and for these snags we knew the locations of past starts and observed woodpeckers creating cavities from start to finish within a single breeding season. Losin et al. (2006) pointed out that even if woodpeckers carry fungi on their bill tips (Farris et al. 2004), cavity starts are an unlikely medium for fungal growth since they are exposed to drying effects of wind and sun. Also, early studies noted the tapping behavior of woodpeckers in spring near future excavations (Kilham 1983), indicating that PCEs search for and detect subtle changes in wood resonance while pecking or climbing trees (Conner et al. 1976). Given the rarity of soft wood in our study, and the absence of obvious visual cues associated with soft wood, our findings support these suppositions that PCEs find soft spots as they visit trees and snags, and they possess sensory abilities lacking in humans that enable them to perceive changes in wood density within a tree's interior.

Assuming that PCEs find, rather than create soft spots, Kilham (1968, 1971) suggested that PCEs prefer sites with soft interior wood for excavation-ease, but which also had hard exteriors to protect future nest contents from predators. It is also possible that PCEs select sites based on future cavity microclimate. Wood hardness may directly or indirectly (by constraining sill or body thickness, or cavity orientation; Losin et al. 2006) affect microclimate of nests, which in turn may affect clutch size under some environmental conditions (Wiebe 2001). PCEs may also simply prefer wood with the maximum hardness they are capable of excavating. However, they are likely capable of leveraging more power when they are positioned vertically on the outside of the tree rather than when head and body movements are confined and horizontal inside of a cavity start (Miller and Miller

1980). This might force them to select trees with soft interiors. Alternatively, they may instead prefer the softest, easiest sites available and trees with soft interiors often have hard exteriors.

After measuring large numbers of random sites, our findings indicate that ease of excavation is a major factor driving nest wood hardness and site selection. We observed a consistent preference for sites with soft interiors, despite their rarity on the landscape. Additionally not all nests followed the pattern of hard exterior/soft interior. Some nests had soft exteriors and interiors, although no nests followed the reverse pattern (soft exterior and hard interior). The notion that PCEs select sites that are easy to excavate is supported by Losin et al. (2006), who reported that red-naped sapsuckers (*Syphrapicus nuchalis*) preferred nest sites with thin sapwood and that would be easier to excavate. However, within the range of wood hardness that they are physically capable of excavating, PCEs probably also face tradeoffs when selecting nest sites, because as noted above, sites that are easy to excavate could be riskier in terms of nest predation (Kilham 1983, Tozer et al. 2009) and more exposed to climate variability. We suggest that future studies examine some of these tradeoffs, and determine the extent to which PCEs are limited by excavation abilities that may force them to compromise on thermal benefits and safety. An important first-step in this process is to measure wood hardness in available trees to more accurately estimate the number of potential nest sites, which prior to this study has probably been grossly overestimated.

Another important consideration is that species likely differ in their excavation abilities, and this may affect tradeoffs in nest-site selection decisions. In support of this, while we found no difference in internal wood hardness, we did observe differences in exterior, or sill wood hardness among the six species in this study. On average, nests of three-toed woodpeckers (*P. dorsalis* and *P. arcticus*) had harder sills than those of sapsuckers, which in turn hard harder sill wood than the hairy woodpecker, white-headed woodpecker, and northern flicker nests. Despite these differences and their implications for nest site selection, our results suggest that researchers should be cautious about using excavator guilds (e.g., Ingold 1994, Dudley and Saab 2003, Bunnell 2013) without more study, particularly controlled tests in laboratory settings. This is partly because despite differences in mean sill hardness, we observed a lot of overlap suggesting excavator guilds are overly simplistic. Moreover, even if guilds reflect biological differences in ability, they may not be realized in natural settings where birds appear most limited by soft interior wood. For example, our results suggest that in some locations black-backed woodpeckers may be more limited than white-headed woodpeckers for nest-sites, presumably because black-backed woodpeckers nest in recent burns where less wood has had time to soften following death. Thus, even if excavator guilds provide biologically accurate information, they may not provide reliable information for management or conservation purposes, and therefore should be used with caution.

Nest-site selection

We found that interior wood hardness was the most important predictor of nest-site selection at the nest tree and territory scale for all species examined suggesting that PCEs are limited to a small subset of trees on the landscape for nesting. These findings may explain why some species that do not forage on snags are nevertheless attracted to patches of burned forest, or other areas of high snag density. For example, aerial insectivores like

Lewis's woodpecker (*Melanerpes lewis*), ground-foragers like northern flicker, and live-tree specialists like white-headed woodpecker are all known to converge in burned forests during the nesting season (Saab et al. 2009). If soft wood is rare, then the probability of soft wood occurring in any given area is probably somewhat proportional to the sheer amount of dead or diseased wood. The more snags that occur in an area, the higher the probability that at least a few have suitable soft spots, and these PCEs may be attracted to burns because they provide opportunities for nesting that are not commonly found in nearby unburned forests.

Our findings may also explain previously inexplicable regional variation in woodpecker nesting preferences noted by others. For example, Bonnot et al. (2009) called attention to regional variation in nest tree size for the at-risk black-backed woodpecker – in California, U.S.A., Raphael and White (1984) reported that black-backed woodpeckers nested in trees with average DBH of 45 cm, whereas in Quebec, Canada, Nappi and Drapeau (2011) found them nesting in trees half that size (mean DBH = 22 cm). Similarly, large diameter snags (>38-50cm DBH) are promoted for nests sites of the declining white-headed woodpecker (Mellen-McClean et al. 2013) based on research from Oregon, U.S.A., while we found them selecting trees as small as 16 cm DBH. Since internal wood softening is caused by wood rotting fungi, and since fungi likely grow differently in different trees and regions, woodpeckers in different regions might select sites with highly variable external properties, but to them, very similar internal properties. If this is the case, it is not possible to make generalizations about nest-site selection across regions without accounting for wood hardness or decay fungi – providing large diameter snags in a region where PCEs are using rot in small diameter trees could be detrimental. It also suggests that it would be more beneficial for PCEs if managers focus on providing trees with rot, or which are susceptible to rot, rather than trees with particular external features or dimensions.

The notion that wood-rotting fungi are important to PCE nesting ecology is not new. Jackson and Jackson (2004) provided a review of the evidence that wood rotting fungi are central for PCE nesting ecology, and suggested that woodpeckers select for sites with rot or with fungal conks. However, we propose that PCEs do not select specifically for rot or fungal conks, but rather that they select trees with soft interiors, and soft interior wood is often caused by wood decay fungi. This would explain why PCEs sometimes use manufactured nest boxes or human buildings for nesting, which should contain little or no trace of wood-rotting fungi, but which are filled with soft materials such as wood shavings or insulation. If this is the case, then wood hardness is ultimately the mode by which PCEs select nest-sites, and it just so happens that in natural systems, wood rotting fungi are a common mechanism by which wood is softened.

Nevertheless, we do not intend to downplay the role of wood rotting fungi in PCE nesting ecology. On the contrary, we agree with Jackson and Jackson (2004) that more research is needed on the species of fungi that cause wood softening at PCE nests, and how they can be promoted. This is especially true for coniferous forests. With the exception of the endangered red-cockaded woodpecker (*Picoides borealis*) of the southeastern U.S.A., past research has focused on PCE use of heart rot-infected deciduous trees (Conner et al. 1976, Daily 1993, Schepps et al. 1999, Matsuoka 2008). In coniferous forests of the northwestern U.S.A., we observed that many nests were excavated into the sapwood of conifer snags, indicating that sapwood rot is an underappreciated mechanism of wood softening in some regions. Research on rot coniferous forests is particularly needed since several at-risk PCEs rely on coniferous forests for population persistence, including the white-headed, black-backed, Lewis's, and American and Eurasian three-toed woodpecker (*Picoides tridactylus*) (Garrett et al. 1996, Dixon and Saab 2000, Vierling et al. 2013).

Tree external appearances and wood hardness

We found that commonly used snag decay classes were a poor predictor of nest-site selection compared to wood hardness. There are several reasons why decay classes poorly predict PCE use in this and past studies (Chambers and Mast 2005, Bagne et al. 2008). First, decay classes attempt to categorize and simplify a continuous and complex phenomenon (Creed et al. 2004, Angers et al. 2012). Second, factors that enable trees to compartmentalize decay can function long after a tree's death (Shigo 1984). Thus, indicators of decay class that should be used to identify localized pockets of decay are in practice are applied to describe decay in the entire bole of a tree. Third, snag decay classes group snags based on their exterior features, whereas woodpeckers appear to select snags based on internal features, specifically wood hardness. Factors that cause a tree to take on the outward appearance of a snag decay class are not necessarily those that cause fungal colonization and wood softening in the interior. For example, top breakage is often listed as a major factor associated with advanced snag decay (Cline et al. 1980, Bull et al. 1997). Yet top breakage may occur from factors besides decay, such as from excessive wind, snow, mechanical thinning, or fire, and thus a broken-top snag may contain hard wood in all of its bole. When tops do break from decay, the portion of bole containing soft wood may fall to the ground. Although dead-topped trees are said to provide a good surface for fungal colonization (Haggard and Gaines 2001), we could not find studies that specifically tested this hypothesis, and fungal growth could be inhibited in some broken-topped trees, since they subject the bole's interior to the drying effects of wind and sun (Losin et al. 2006). In sum, a broken-top tree or snag would be favorable for PCE use only under fairly specific conditions. It is not surprising therefore that while PCEs consistently selected soft interior wood in our study, nests occurred in sites ranging from entirely live trees to live trees with dead tops, and snags with both intact and broken tops.

Snag decay classes have likely enjoyed such popularity because they are easy to use. However, they can be fairly subjective (Larjavaara and Muller-Landau 2010), and their limitations for predicting wood density were appreciated early on by foresters (Gale 1973). Since then, the majority of studies on snag decay classes report findings very similar to ours; for random spots on snags, there is large variation within and overlap among decay classes in wood density. Thus while decay classes may sometimes point to localized pockets of decay, for describing wood in the entire bole of a tree they only indicate changes in wood mass density at coarse scales – for example between the two most extreme decay classes within one system – and they poorly describe variation at finer scales (Saint-Germain et al. 2007, Aakala 2010, Paletto and Tosi 2010, Strukeljii et al. 2013). This is potentially problematic for studies of PCE nest-site selection, since PCEs appear to perceive changes in wood density at very fine scales (Matsuoka 2008, Zahner et al. 2012).

Despite these concerns, we could find no other studies of PCE nest-site selection that acknowledged the shortcomings of decay classes and tested their accuracy. Additionally, ours is the first study to relate hardness of snag decay classes with hardness at PCE nests. We found that regardless of snag decay class, the majority of wood in nesting territories was unsuitably hard for nesting by our two focal species, the black-backed and white-headed woodpecker. We also found no external features of snags that were associated with interior wood softness at our random measurement points. While we acknowledge that sampling at random spots on snags, rather than near broken tops or limbs, likely led to a conservative estimate of soft wood, we recommend that ecologists avoid using snag decay classifications for determining the suitability of sites for PCE nests until more intensive sampling of snags is done. When decay classes are used, ecologists should recognize that the majority of wood on all snags is likely unsuitable for nesting.

Implications for research and management

Our findings suggest that higher densities of snags and other nest substrates be provided for PCEs than generally recommended, because past research studies likely underestimated the abundance of suitable nest sites. Accordingly, the felling or removal of snags for any purpose, including commercial salvage logging and home firewood gathering, should not be permitted where conservation and management of PCEs or SCUs is a concern (Scott 1978, Hutto 2006). Managers should also take particular care that programs designed to increase the number of nesting substrates do not end up providing large numbers of unusable sites. Several studies attempting to create nest snags for PCEs have reported low use by woodpeckers, indicating that this should be a major concern. For example, Bednarz et al. (2013) inoculated 330 trees with *Fomitopsis pinicola* in western Washington, U.S.A., and found no avian nest cavities 8 to 9 years later. Likewise, for 883 and 1111 snags created by tree-topping in western Oregon, U.S.A., by Walter and Maguire (2005) and Kroll et al. (2012), only 2-3% were used by woodpeckers for nesting 10 to 12 years later. In these cases, managers may have unknowingly provided large numbers of unsuitably hard snags that PCEs were not physically capable of excavating. Yet the alternative situation could also be detrimental. If managers provide large numbers of unsuitably soft snags, PCEs may experience high depredation rates and be incapable of successfully fledging broods (Conner 1977, Tozer et al. 2009). This second case could have significant population-wide ramifications for rare or sensitive species since it could attract nesting birds to sink habitats. But either situation may be costly for managers while not beneficial for PCEs.

For researchers, future studies of PCE nesting ecology must include quantitative measures of wood hardness for unbiased results. Past research studies that did not measure wood hardness probably counted some trees as available for PCEs that were not actually available. In addition to causing bias (Jones 2001), this may explain 'non-ideal' selection decisions reported by PCEs in past studies. Sadoti and Vierling (2010) and Frei et al. (2013) reported that woodpeckers selected sites where they experienced low productivity, and then concluded that PCEs made maladaptive or non-ideal selection decisions. But these studies did not measure wood hardness and therefore some sites counted as available were probably not available. In order to determine the extent and frequency of bias, new studies should be conducted to revisit old research questions, and these new studies should quantitatively measure wood hardness to obtain a more accurate assessment of nest site availability. Additionally, until wood hardness is incorporated into nest-site selection models, ecologists should remain cautious of interpretations made without measures of wood hardness, at least at the territory scale and smaller. We also encourage researchers to further explore the role of wood hardness in PCE nest site limitations and nest survival (Tozer et al. 2009), and to conduct intensive studies of wood hardness to better estimate the availability of suitable nest wood in different forest types. Lastly, as suggested by Jackson and Jackson (2004), much could be gained by identifying and promoting wood decay fungi associated with PCE nest-sites, rather than simply measuring and modeling patterns in external features.

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Table 1. Description of model parameters used to examine nest-site selection by PCEs in central Washington, U.S.A., 2011-2013.

Possible variables	Parameter	Black-backed woodpecker	Hairy woodpecker	Northern flicker	White-headed woodpecker	Hypothesized reason and source
Territory scale						
Nest tree DBH	DBH	x	x	x	x	Protection from predation and/or search image[3, 4, 8, 9, 10, 12, 13, 15, 17, 19, 20, 21]
Snag decay class from Cline	Cline	x	x	x	x	Protection from predation, ease of excavation, and/or search image[3,4,9,10,13,17,19]
Nest tree sill wood hardness	Sill	x	x	x	x	Protection from predation, thermoregulation, or ease-of-excavation[1,5,16,20]
Nest tree body wood hardness	Body	x	x	x	x	Ease of excavation[2,11]
Density of live trees >50 cm DBH near nest	Dlive50				x	Preferred foraging habitat[8,18]
Density of live trees >10 cm DBH near nest	Dlive10	x	x	x		Protection from predation[4,22]
Density of snags >23 cm DBH near nest	Dsnag	x	x	x		Preferred foraging habitat[4,7, 13,14,15,19,22]
Prefire canopy cover	Prefire	x				Preferred foraging habitat[15]
Shrub cover around nest	Shrub				x	Protection from predation[22]
Percent slope at nest	Slope				x	Unknown[8,18] (perhaps related to travel ease and thus predation)

Percent canopy cover at nest	Canopy			x	x	Protection from predation, thermoregulation, and/or preferred foraging habitat[6,18]
Nest tree scale						
Nest cavity orientation	Orientation	x	x	x	x	-
Nest cavity height	Height	x	x	x	x	-
Nest tree sill wood hardness	Sill	x	x	x	x	-
Nest tree body wood hardness	Body	x	x	x	x	-

[1]Conner 1977, [2]Miller and Miller 1980, [3]Raphael and White 1984, [4]Saab and Dudley 1998, [5]Schepps et al. 1999, [6]Wiebe 2001, [7]Saab et al. 2002, [8]Buchanan et al. 2003, [9]Spiering and Knight 2005, [10]Bagne et al. 2008, [11]Matsouka 2008, [12]Vierling et al. 2008, [13]Bonnot et al. 2009, [14]Forristal 2009, [15]Saab et al. 2009, [16]Tozer et al. 2009, [17]Wightman et al. 2009, [18]Hollenbeck et al. 2011, [19]Nappi and Drapeau 2011, [20]Straus et al. 2011, [21]Cooke and Hannon 2012, [22]Kozma and Kroll 2012

Notes: An ‘x’ indicates that the given parameter was included in models for that species. The hypothesized reason for including a given parameter was sometimes based on our interpretation of study results; the sources used to create this table did not always provide a reason for the importance of the different parameters. See Appendix B for sources used to create this table and Appendix C and D for the set of final models.

Table 2. Description of snag decay classes by Thomas, Cline, and Bull used to categorize snags in central Washington, U.S.A., 2011-2013.

Class	Description
Thomas	
1	Live tree with no defects
2	Live tree with defects
3	Snag with limbs bark and top present
4	Snag with top remaining but some bark and limbs absent
5	Snag with top remaining, some limbs absent, and all bark absent
6	Snag with some top missing, and all limbs and bark absent
7	Snag with most of top missing, and all limbs and bark absent
8	Stump-sized snag (no bark or limbs) with top lying at base
9	Stump-sized snag (no bark or limbs) with top disintegrated
Cline	
1	Snag with top, branches, limbs and bark 100% intact
2	Snag with few limbs, no fine branches, broken top, and variable bark sloughing
3	Snag with limb stubs only, broken top, and variable bark sloughing
4	Snag with few or no limb stubs, broken top, and variable bark sloughing
5	Snag with no limb stubs, broken top, and 20% bark remaining
Bull	
1	Snag retaining 100% of its bark, branches, and top
2	Snag that have lost some bark, branches, and often a portion of the top
3	Snag missing bark, most of the branches, and have a broken top

Table 3. Mean and range of sill and body wood hardness at nests for six species of woodpecker compared to random trees in central Washington, U.S.A., 2011-2013.

Species	Mean (range) sill hardness (N•m)[1]	Mean (range) cavity body hardness (N•m)[1]
American three-toed woodpecker (*n* = 9)	5.7 (0.6-13.8) cd	2.5 (0.6-6.6) a
Black-backed woodpecker (*n* = 39)	5.2 (0.0-11.9) c	1.7 (0.0-6.2) a
Hairy woodpecker (*n* = 60)	3.8 (0.0-9.8) ab	1.8 (0.0-5.0) a
Northern flicker (*n* = 55)	2.5 (0.0-9.6) a	1.1 (0.0-4.7) a
White-headed woodpecker (*n* = 75)	2.8 (0.0-14.5) a	1.7 (0.0-5.1) a
Williamson’s sapsucker (*n* = 21)	4.2 (0.1-16.6) bc	1.6 (0.3-4.9) a
Random trees (*n* = 259)	6.6 (0.0-26.1) d	9.0 (0.0-27.6) b

[1] Letters indicate results of post-hoc multiple comparison tests and means with the same letter do not differ.

Table 4. Support for models in 90% confidence set explaining multi-scale nest-site selection by four species of PCE in central Washington, U.S.A., 2011-2013.

Species	Model	k	AIC_c	Δ_i	w_i	Pseudo R^2
Territory scale						
Black-backed woodpecker	body	2	2.333	0.000	0.665	0.926
	sill body	3	4.686	2.352	0.205	0.889
	sill body dsnag	4	7.176	4.843	0.059	0.852
Hairy woodpecker	body	2	2.211	0.000	0.647	0.951
	sill body	3	4.429	2.218	0.213	0.928
	sill body dsnag	4	6.727	4.517	0.068	0.904
Northern flicker	body	2	2.231	0.000	0.584	0.947
	sill body	3	4.471	2.240	0.191	0.921
	cline sill body	4	4.800	2.569	0.162	0.895
White-headed woodpecker	sill body	3	4.338	0.000	0.891	0.940
	body	2	8.865	4.527	0.093	0.894
Nest-tree scale						
Black-backed woodpecker	body	2	7.120	0.000	0.749	0.837
	sill body	3	9.310	2.189	0.251	0.803
Hairy woodpecker	body orientation	3	4.429	0.000	0.894	0.928
	body	2	9.805	5.376	0.061	0.861
Northern flicker	height sill body orientation	5	33.156	0.000	0.472	0.607
	body	2	33.730	0.573	0.354	0.534
	sill body	3	35.959	2.802	0.116	0.508
White-headed woodpecker	sill body	3	25.364	0.000	0.533	0.729
	body	2	25.805	0.441	0.427	0.723

Notes: Variables used in models are defined in Table 1, and full set of models is listed in Appendix C and D.

Table 5. Model averaged parameter estimates, unconditional standard errors, 95% confidence intervals, and importance values explaining multi-scale nest-site selection by four species of PCE in central Washington, U.S.A., 2011-2013.

Species	Parameter	Estimate	SE	Upper CI	Lower CI	Importance
Territory scale						
Black-backed woodpecker	body	-0.412	0.089	-0.237	-0.587	0.99
	sill	-0.045	0.055	0.153	-0.063	0.27
	dsnag	0.001	0.001	0.001	-0.001	0.19
Hairy woodpecker	body	-0.377	0.072	-0.237	-0.518	0.99
	sill	-0.015	0.031	0.075	-0.044	0.29
	dsnag	0.001	0.001	0.002	-0.001	0.14
Northern flicker	body	-0.399	0.082	-0.237	-0.560	0.99
	sill	-0.002	0.061	0.122	-0.119	0.42
	cline 1	-0.037	0.139	0.235	-0.310	0.17
	cline 2	0.020	0.180	0.315	-0.390	0.17
	cline 3	-0.038	0.147	0.307	-0.268	0.17
	cline 4	0.048	0.127	0.297	-0.202	0.17
White-headed woodpecker	body	-0.365	0.060	-0.247	-0.483	0.99
	sill	-0.026	0.099	0.167	-0.219	0.90
Nest-tree scale						
Black-backed woodpecker	body	-0.627	0.143	0.908	0.347	0.99
	sill	-0.001	0.044	0.086	-0.086	0.25
Hairy woodpecker	body	-0.502	0.092	0.683	0.321	0.99
	sill	-0.004	0.007	0.011	-0.018	0.04
Northern flicker	body	-0.592	0.155	0.895	0.288	0.99
	sill	-0.044	0.092	0.225	-0.137	0.59
	height	-0.134	0.092	0.046	-0.313	0.47
	orientation e	0.258	0.293	0.833	-0.317	0.53
	orientation n	-0.325	0.392	0.444	-1.095	0.53
	orientation s	0.353	0.360	1.059	-0.353	0.53
White-headed woodpecker	body	-0.537	0.104	0.740	0.333	0.99
	sill	-0.098	0.087	0.072	-0.268	0.55

Table 6. Parameter estimates, standard errors, and P-values for multiple regression associating wood hardness with external features of 559 random snags in central Washington, U.S.A., 2011-2012.

Variable	Estimate	SE	T	*P*
Presence of foraging sign	0.368	0.327	1.12	0.261
Presence of cavities	-1.31	0.440	-2.98	0.003
Percent blackened bark	-0.003	0.004	-0.84	0.402
Percent top missing	-0.009	0.006	-1.58	0.114
Percent bark missing	0.011	0.007	1.60	0.110
Percent branches missing	-0.004	0.005	-0.71	0.476

Figure 1. Longitudinal section of an American three-toed woodpecker nest showing the procedure we used to quantify wood hardness. First, we used a drill to create a 9-mm diameter hole above the nest cavity opening (Top), and then recorded torque (N•m) required to spin an increment borer into the pre-drilled hole (Bottom) following Matsuoka (2000). The area marked *A* represents the nest sill and area marked *B* represents the nest cavity body in our study.

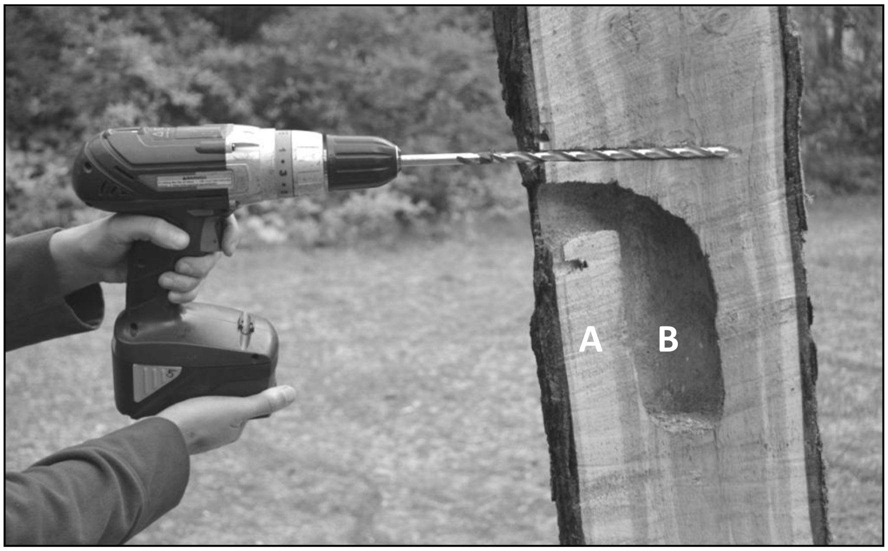


Figure 2. Mean hardness at nests for six species of woodpecker compared to random sites in central Washington, U.S.A., 2011-2013.

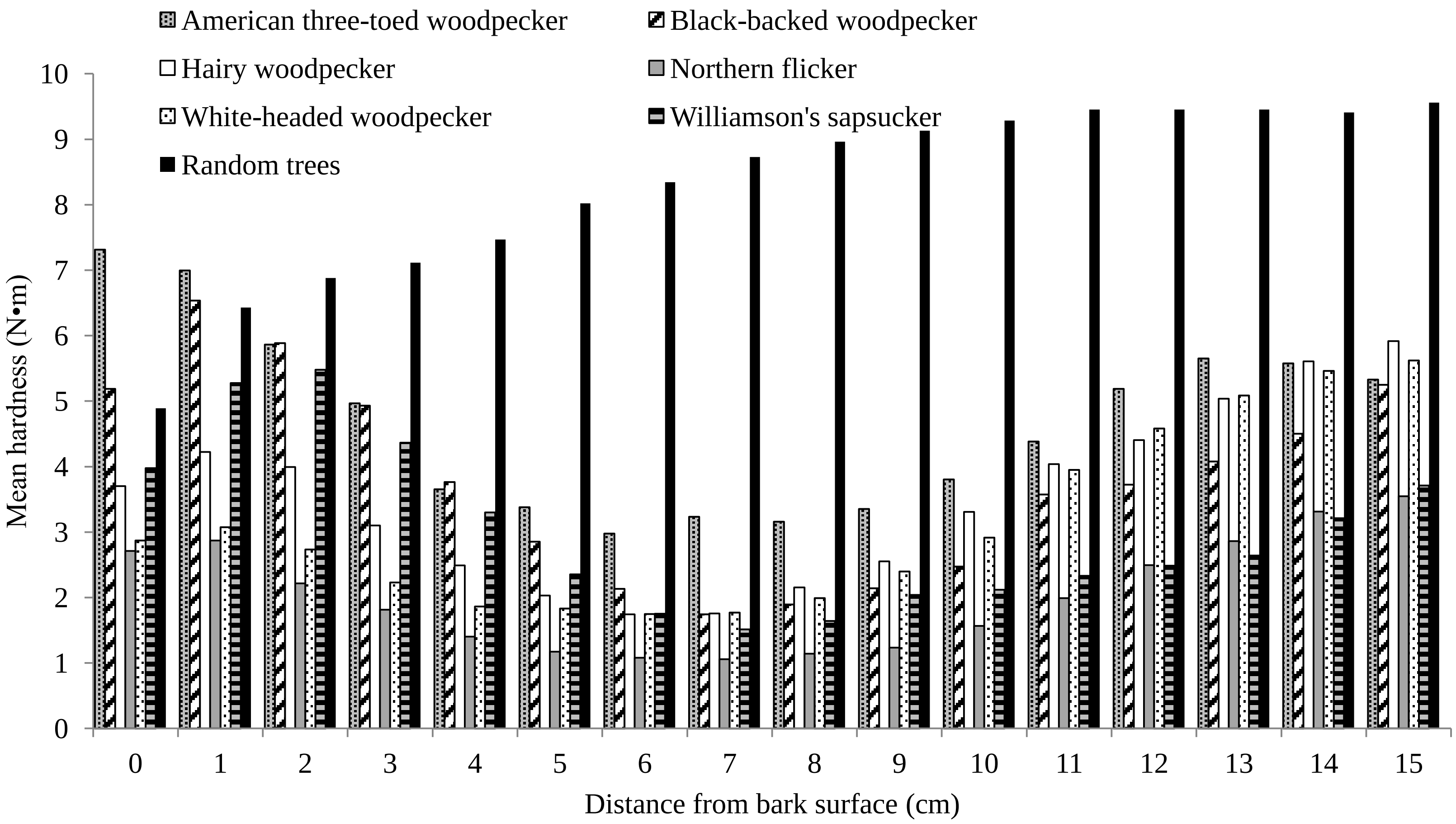


Figure 3. Proportion of 360 non-use snags in black-backed (BBWO) and white-headed woodpecker (WHWO) nesting territories that were deemed suitable for nesting based on wood hardness in central Washington, U.S.A., 2011-2013. We considered all snags together, and then proportions in each of three decay classes of Bull et al. (1997).

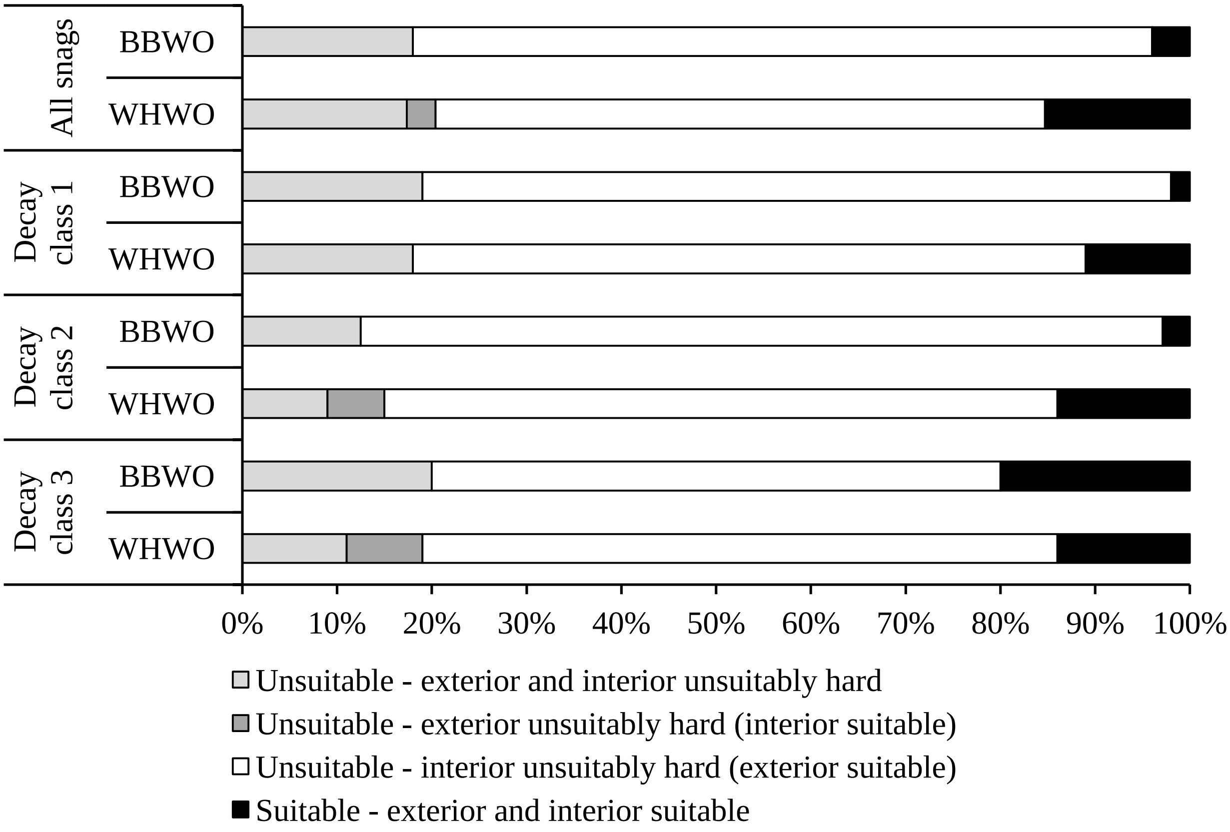
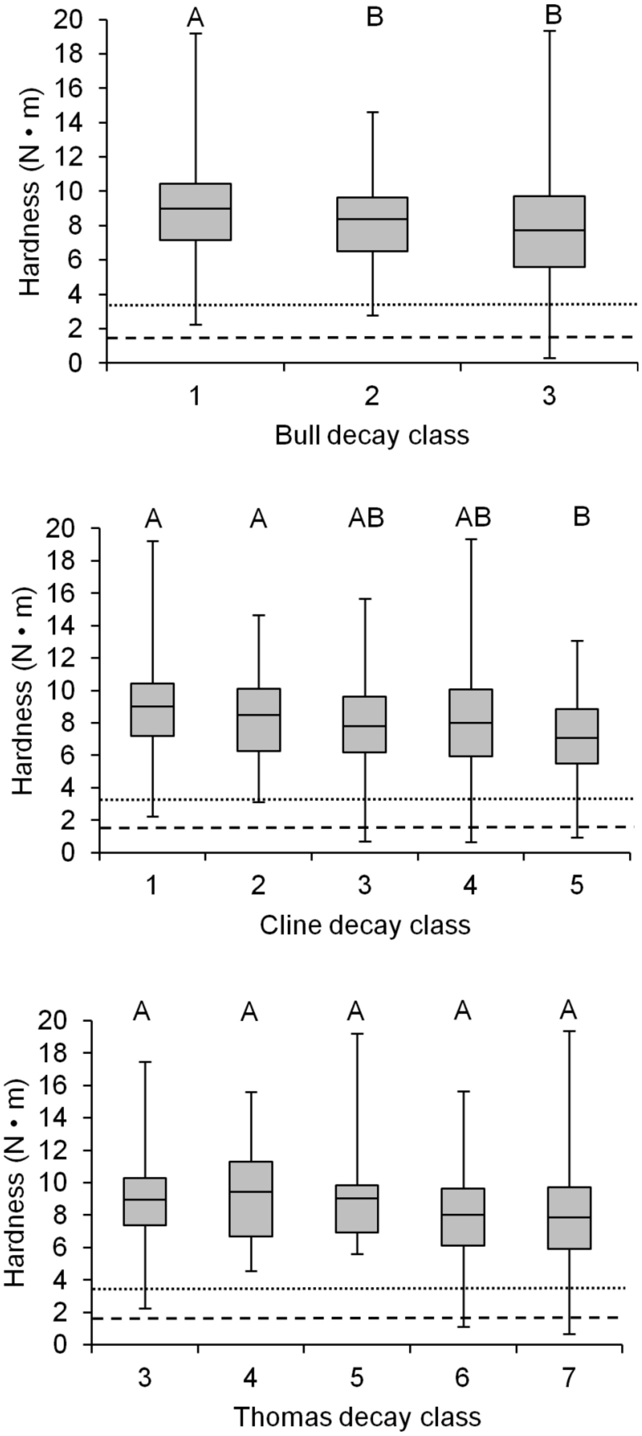


Figure 4. Variation in wood hardness by snag decay class for 559 random snags in central Washington, 2011-2103, classified by the decay class systems of Bull (top), Cline (center), and Thomas (bottom). Dashed and dotted lines on plots indicate mean body and sill wood hardness at nests, respectively. Letters show the results of post-hoc multiple comparison tests and means with the same letter do not differ.



CHAPTER 2

VARIATION IN SPACE USE BY AN AT-RISK ECOSYSTEM ENGINEER, THE WHITE-HEADED WOODPECKER: EVALUATING THE ROLE OF SOCIODEMOGRAPHIC VERSUS ENVIRONMENTAL FACTORS

Abstract

White-headed woodpeckers (*Picoides albolarvatus*) are important cavity excavators that have recently been the focus of much research because of concerns over population declines. However, most past studies have focused on their nesting ecology and information is needed on factors influencing space use especially in forests lacking old-growth pine. We conducted a study of space use by white-headed woodpeckers during the nesting (May-July) and post-nesting autumn (July-October) seasons in stands historically used for timber production. Our objectives were to examine home range characteristics and selection, and to compare the role of environmental versus sociodemographic factors in space use. Average size of 99% kernel home ranges was 125 ha (n = 19) in the nesting and 137 ha (n = 30) post-nesting seasons, and we found no differences in home range size by sex in either season. We observed considerable overlap in home ranges by some neighboring woodpeckers, including an extreme case of 91% overlap for one female during the nesting period. The best model explaining home range size included only bird weight and age and no habitat predictors, although neither of these parameter estimates were significant. Thus, although the weight and age model ranked higher than others in our study, home range size was apparently largely influenced by factors that we did not measure. Productivity was not influential in ranging behavior, and most birds (71%) successfully fledged at least two young. For selection of home ranges on the landscape, the best model included only a single predictor for recent disturbances, and woodpeckers selected areas that had recently been burned, thinned and burned, or subject to disease. Our results suggest that recent forest disturbance, particularly burns, may benefit white-headed woodpeckers possibly by increasing the number of snags for nesting. Meanwhile, home range size is highly variable, and range size should not be used as an indication of habitat quality without more detailed studies on causal relationships between ranging behavior and factors such body condition and life experience.

Introduction

The white-headed woodpecker (*Picoides albolarvatus*) is a member of an important guild of animals called primary cavity excavators because their cavities provide nest and shelter sites for a variety of small-bodied secondary cavity users (Tarbill 2010). They occupy dry pine forests in western North America, and in the northwestern U.S.A. they are considered a sensitive species associated with late-seral ponderosa pine (*Pinus ponderosa*) forests (Garrett et al. 1996). Large, old pines are considered important for providing reliable food, and large diameter snags for nesting (Raphael and White 1984, Dixon 1995a). It is thought that the selective logging of large diameter pines by European settlers in the 19th and 20th centuries contributed to wide-spread population declines (Dixon 1995a, Wisdom et al. 2000), although quantitative information is lacking to evaluate this contention. Because of their association with mature pine stands in some areas (Dixon 1995a, 1995b), white-headed woodpeckers have also been used as a management indicator species for forest management practices aimed at restoring old-growth conditions in ponderosa pine forests in the northwestern U.S.A. (Altman 2000, Wisdom et al. 2000, Gaines et al. 2007).

Given this status as a sensitive species, white-headed woodpeckers have become the focus of numerous research studies in recent years. Somewhat surprisingly, several of these studies have found white-headed woodpeckers in a variety of disturbed and managed habitats including recent burns (Hanson and North 2008, Saab et al. 2009, Wightman et al. 2010, Tarbill 2010), young (<75 yrs) forests managed for timber production and grazing (Lindstrand and Humes 2009, Kozma 2011), and salvage logged burns (Kozma 2011). In some of these areas, nest success and productivity rates are similar to rates for older stands. For example, Kozma (2009) reported nest success of 84.6% in recently harvested stands in Washington, which is nearly identical to nest success of 84% reported in mature ponderosa pine stands in Oregon in Garrett et al. (1996).

Although comparisons across studies must be done with caution, these findings suggest that white-headed woodpeckers may be less restricted to old forests than originally thought. Unfortunately, however, all studies on white-headed woodpeckers in disturbed, young, or managed forests have been limited to observations at nest sites or detections during surveys. Thus, there is limited information on space use by white-headed woodpeckers in managed forests. Additionally, no past studies have simultaneously related environmental, demographic, and social factors to white-headed woodpecker space use; past studies have only considered the effects of habitat on home range size (Dixon 1995a, 1995b), even though sociodemographic factors such as population density and productivity are important in ranging behavior for other picids (Hooper et al. 1982, Elchuk and Wiebe 2003, Leniowski and Wegrzyn 2013).

Given these information gaps, we designed a study to explore white-headed woodpecker space use in managed forest types, particularly those subject to both historic (pre-1990) and recent (post-1990) timber harvest. We had three primary objectives. First, we obtained base-line information on home range size and overlap in managed stands, since past studies have focused on white-headed woodpecker space use in old-growth stands. Second, we modeled variation in home range size to assess factors associated with spacing. We were particularly interested in the degree to which sociodemographic factors such as bird age, population density, and nest productivity were influential in space use compared to habitat features such as stand age, tree size, and availability of old-growth forest. Lastly, we examined the role of habitat features and forest disturbance on selection of home ranges during the nesting and post-nesting periods. In our study areas, old-growth forest (defined as forests with >10% canopy cover and >50.8 quadratic mean diameter) was rare and so we especially were interested in determining features selected by white-headed woodpeckers in landscapes lacking large, old trees.

Methods

Study area

We selected six sites for this study on the east slopes of the Cascade Range in Yakima, Kittitas, and Chelan counties in Washington State (approximately 46º 45′ N, 120º 58′ W and 47º 30′ N, 120 º 33′ W) (Figure 1). Study sites were between 1500 and 3500 ha in size (mean = 2404 ha ±833 ha). Five sites were on National Forest land, and one encompassed both state (Washington Department of Natural Resources and Washington Department of Fish and Wildlife) and private lands. White-headed woodpeckers are generally considered rare in Washington, and so we initially relied on previously published information on white-headed woodpeckers to locate study areas. Thus, we selected Mission, Wenas, Nile, and Rimrock study sites (Figure 1) because they contained known populations of woodpeckers from past research (Buchanan et al. 2003, Gaines et al. 2007, Kozma 2009). We added Oak and Rattle as additional sites because reconnaissance surveys revealed breeding pairs of woodpeckers.

The composition of forests in our study sites varied considerably based on aspect, slope, elevation, and longitudinal distance from the Cascade Crest. Rather than defining and searching only in particular forest types as has been done in some past studies (e.g., Buchanan et al. 2003, Hollenbeck et al. 2011), we instead searched the entirety of each study site for woodpeckers. Generally, ponderosa pine was dominant or co-dominant with Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*). Other common tree species included western larch (*Larix occidentalis*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*).

We estimated that more than 92% of the area within our sites had been harvested for timber at least once since 1950 based on U.S. Forest Service Timber Harvest activity reports and Washington State Department of Natural Resources Forest Practice Permits. Most harvests were described as overstory removal cuts (removal of entire mature overstory) or partial removal cuts (removal of part of the overstory). Approximately 39% of the area within our sites had been burned with prescribed fire and/or thinned an additional time within ten years of the start of this study. Four sites were actively grazed by domestic livestock every summer during this study. Two study areas fell within domestic sheep grazing allotments on the Okanogan-Wenatchee National Forest (Nile and Rattle), and one site each contained a U.S. Forest Service and Washington Department of Natural Resources cattle grazing allotment (Rimrock and Wenas, respectively).

Field methods

From March through May we searched for territorial, adult white-headed woodpeckers in our study sites by broadcasting playback calls and drumming. Beginning in mid-May, we returned to these territories and searched for nests by following adults to nest sites. We recorded the locations of all nest sites on portable GPS units (location error ±5-6 m). 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. Whenever possible, we weighed woodpeckers although because of concerns over handling stress during the nesting season, nine individuals were released without being weighed. 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.

We aged all captured woodpeckers as second-year, third-year, and after-third-year using Pyle and Howell (1995). Since some woodpeckers were aged one to two years prior to radio tracking during concurrent research studies, we were able to assign some birds to higher age categories during the year they were radio tracked; thus some adults color-banded and aged as after-third-year in 2011 were not radio tracked until 2012 or 2013 and were classed as after-fourth- and after-fifth-year in our analysis. All handling was in accordance with Institutional Animal Care and Use Committee guidelines (University of Idaho Protocol #2011-30) and in compliance with the Ornithological Council Guidelines for the Use of Wild Birds in Research (Fair et al. 2010).

To estimate productivity, we checked nest contents using a hole saw (Ibarzabal and Tremblay 2006) or video inspection probe within 5 days of nest fledging and counted the number of nestlings. We took several precautions to avoid affecting productivity and nest success of radio tagged adults. First, adults were captured at nests only after incubation was underway to avoid nest abandonment. Second, we assumed that after capture, adults would need up to several hours to grow accustomed to their transmitters and return to nest sites. Therefore during incubation, we captured woodpeckers at nest sites only on sunny, calm afternoons to minimize exposure by eggs to cool temperatures. We also monitored nests for up to 250 minutes prior to trapping to ensure eggs were well-attended. We waited to capture incubating adults only once we determined that the second adult was present nearby to take over incubation duties while we were working with the captured bird. We also avoided capturing males after approximately 1600 hrs, since males incubate and brood nestlings overnight. With these precautions in place, it is unlikely that we adversely affected productivity. We observed no cases of nest abandonment following radio tagging, and across all years, productivity of radio tagged woodpeckers (mean fledglings = 2.17) did not differ from productivity of non-radio tagged woodpeckers (mean fledglings = 1.85) monitored in the same study areas (t = 1.999, df = 62, *P* = 0.370).

We began tracking radio tagged woodpeckers 1-4 days after trapping. We obtained point locations by homing to individuals and recorded the locations visited by individuals using portable GPS units. We followed woodpeckers no more than 2 hours at a time, and recorded point locations every five minutes following Dixon (1995a, 1995b). We considered these locations independent since we observed that white-headed woodpeckers were capable of traversing their home range within minutes (White and Garrott 1990). We revisited each individual woodpecker every 1-4 days. Since white-headed woodpeckers are sensitive to human disturbance at nest sites, we intentionally tracked woodpeckers only when they were at least 25 m from nest sites. When our presence obviously influenced adult behavior (e.g., incessant calls and refusal to leave the nest vicinity), we moved out-of-sight until the radio signal or vocalizations indicated that the woodpecker had resumed its normal activities. Since white-headed woodpeckers commonly travel out-of-sight of their nests while foraging (e.g., >50 m), most telemetry tracking was done without disturbance to nests.

Following Elchuk and Wiebe (2003) we calculated nearest neighbor distances between nests for those in which we documented eggs or nestlings. While it is possible that we missed some nests, this is unlikely for several reasons. First, in addition to searches for territorial white-headed woodpecker pairs, study areas were typically visited every 1-2 days for concurrent research on nest site selection, nest survival, adult survival, and juvenile dispersal and survival, making it unlikely that pairs were missed or nests initiated in between visits. Second, white-headed woodpeckers are territorial during this period making them likely to respond to our call playbacks, which are a widespread and recommended tool for locating such species (Dudley and Saab 2003). Third, white-headed woodpeckers are generally rare in this region and thus the probability of missing large numbers of breeders is low. Additionally, our average nearest neighbor distance of 878 m (range 106-2723 m; n = 19 nests) is similar to an eight-year average from central Oregon with a robust sample of nests (mean = 817 m, range 126-2424 m; *n* = 127 nests), corroborating our conclusion that few, if any, nests were missed.

Home-range analysis

We estimated home ranges for two seasons separately – the nesting and post-nesting seasons. We defined the nest season as the period between the start of nest excavation and the date of nest fledging. The post-nesting season extended from the date of nest fledging through either molt of the tail feathers, or the first frost, whichever came first. Since different individuals initiate nests and molt at different times, the start and end dates of each season varied by individual, although in general the nesting season extended from May through mid-July, and the post-nesting season from mid-July through October.

For both seasons we delineated home ranges using the 99% contour interval of the fixed kernel distribution and plug-in bandwidth estimator in Geospatial Modeling Environment (Beyer 2012). Although 95% fixed kernels with Least Squares Cross-Validation (LSCV) are used more commonly and sometimes recommended for estimating home range size (e.g., Laver and Kelly 2008, but see Beyer 2012), we used 99% kernels with the plugin estimator in our analyses because they were more apt to include distant foraging excursions by our woodpeckers during the nesting season. We found that such forays were excluded in the more commonly used 95% fixed kernels with LSCV. However, for comparison with other studies, we also reported 95% fixed kernels computed with LSCV.

We constructed area observation curves (Odum and Kuenzler 1955) for seven individuals and documented that 99% kernels for both seasons reached an asymptote between 25 and 30 point relocations. Therefore, we estimated home ranges only for individuals with at least 30 point locations per season. Previous studies of woodpecker space use have used several home range estimation methods, including minimum convex polygons and 50% kernels (Dixon 1995a, 1995b, Elchuk and Wiebe 2003). We therefore reported 50% fixed kernels, 95% fixed kernels (as mentioned above), and 100% minimum convex polygons for comparative purposes, but did not include them in any analyses.

We calculated the area of home range overlap between nesting and post-nesting seasons for the same individual following Kernohan et al. (2001). We also separately computed the area of home range overlap for all woodpeckers radio tracked in neighboring territories and in the same year and season. Similar to home range estimation, we computed areas of overlap only for comparison with other studies, and did not use them in any analysis.

Measuring land-cover

To estimate land cover characteristics within home ranges we used Gradient Nearest Neighbor (GNN) models derived from a combination of field plots, mapped environmental data, and Landsat Thematic Mapper (TM) satellite imagery from 2012 (Ohmann et al. 2011). This dataset provided spatially explicit information on vegetation features at a 30-m resolution for all study sites. Based on a review of the literature, habitat variables that we considered important to woodpecker spacing behavior were mean basal area for ponderosa pine and Douglas-fir (Buchanan et al. 2003), canopy cover (Buchanan et al. 2003, Hollenbeck et al. 2011), proportion of late-successional old-growth forest (LSOG; Dixon 1995a, 1995b), proportion of the range with >40% canopy cover (Hollenbeck et al. 2011), variation in canopy coverage (Hollenbeck et al. 2011), average quadratic mean diameter of trees (Hollenbeck et al. 2011), elevation, and average stand age (Dixon 1995a, 1995b, Buchanan et al. 2003) (Table 1). We derived mean slope within home ranges using a digital elevation model (DEM), since Buchanan et al. (2003) and Hollenbeck et al. (2011) suggested that white-headed woodpecker select level ground for nesting. Wightman et al. (2010) found white-headed woodpeckers nesting in recent burns, and so we obtained data on forest disturbances from LandTrendr (Landsat-based detection of Trends in Disturbance and Recovery methods; Kennedy et al. 2010). LandTrendr uses repeat flown Landsat imagery to categorize forest disturbance based on magnitude and duration, and we considered recent (<10 year), short duration (<1 year), high magnitude disturbance events from LandTrendr as representative of disturbances important in white-headed woodpecker space use. These data cannot reliably distinguish between thinning, burning, and disease as different short-term disturbance agents, and so we overlaid our LandTrendr layer with the U.S. Department of Agriculture Forest Service Activity Tracking System (FACTS) database and Washington Department of Natural Resources Forest Practice Permits to determine which disturbance events were caused by thinning, burning, combination of thinning and burning, or none of these, in which case we attributed the disturbance to disease. We then used ArcGIS 10 (Environmental Research Systems Institute) to extract these remotely sensed data for woodpecker home ranges in our study areas.

Determining availability

For assessing second-order selection (Johnson 1980), we defined availability for white-headed woodpeckers based on juvenile dispersal distances, since white-headed woodpeckers are considered non-migratory residents (Garrett et al. 1996) that likely select ranges during their first year or two of life. We used a hole saw to access nestling woodpeckers at nest sites and placed a unique combination of color-bands on each nestling. In subsequent years, we returned to study areas and used call playbacks to elicit responses from woodpeckers banded as nestlings. For each relocated juvenile, we estimated the distance between natal sites and site of farthest dispersal, and used the mean dispersal distance across all juveniles to estimate dispersal distance for our population. For each radio tagged adult we then placed a circular buffer around the home range centroid of equal radius to the mean juvenile dispersal distance. We considered this buffer as the area potentially 'available' for each adult for second-order selection. Because we likely missed many dispersing juveniles and were probably more likely to resight short-distance dispersers, these buffers should be considered conservative estimates of the area available to each adult. However, we documented two woodpeckers banded as nestlings that settled and attempted to breed within the area of mean dispersal distance (one of these woodpeckers successfully fledged young) and so we deemed that this buffer was a plausible, though potentially conservative, definition of availability, given the information currently available on white-headed woodpecker home range selection in the literature.

Since white-headed woodpeckers are a territorial species that only occur in lowland forests in Washington, we further restricted availability to areas outside of known territories for other white-headed woodpeckers and to forests below 1300 m elevation, the approximate maximum elevation for a white-headed woodpecker nest in Washington. Then we used a random sample tool in ArcGIS to generate two random, non-use circular areas within this buffer but outside of the actual home range for each individual. The size of each circular, non-use range was equal to the average range size for that season. Even though it is more common to compare a single non-use polygon to each used one, we generated two random polygons for comparison with each used home range because we were concerned that a single non-use polygon would not capture the variability in features within our study areas. We then determined the proportions of each of the aforementioned habitat variables within these ‘available’ polygons for comparison with used home ranges.

Model development

We used an information theoretic approach (Burnham and Anderson 2002) to evaluate factors influencing home range size and second-order selection. We developed a set of *a priori* models based on published literature and our observations of woodpecker space use with the aforementioned habitat variables and four social-demographic parameters: distance to the nearest neighbor’s nest, bird age, number of fledglings, and weight at time of capture, as an indication of body condition. Although we captured individuals over a two-month period and body weight may change as the season progresses (but see Koening et al. 2005), we found no significant correlation in mass by capture day for males (t = -0.301, df = 17, P = 0.7671) or females (t = 0.992, df = 17, P = 0.3351). We also found no significant correlation between date of capture and the ratio of weight to tarsus length (t = -1.322, df = 31, P = 0.1957), and therefore we considered a single measure of weight as representative of body condition regardless of day of capture.

Prior to building our models we looked for correlations between all pairwise combinations of covariates and omitted covariates if their coefficient was >0.5. For our analysis of range size, among our ten potential habitat covariates, elevation, proportion of the range with recent disturbance, and basal area of both ponderosa pine and Douglas-fir were correlated with canopy cover, and therefore we included only canopy cover in our final models. Likewise, stand age, QMD, and proportion of the home range with LSOG were likewise correlated. We consequently included only QMD in our models, since QMD was implicated in Hollenbeck et al. (2011) as an influential variable for this species. Lastly, the proportion of the home range that was thinned and burned was also highly correlated, and 78% of the area that had been burned had also been thinned. As a result, we lumped thinning, burning, and disease into a single variable, disturbance. For our analysis of home range size, we therefore included eight covariates: QMD, slope, canopy cover, standard deviation of canopy cover, nearest-neighbor distance, bird age, bird weight, and productivity.

For assessing second-order selection, we omitted the four social-demographic variables. We found no correlations between old-growth, QMD, and ponderosa basal area and included all three covariates along with disturbance, slope, and canopy cover (Table 1). We then created between eight and ten models with combinations of these variables to test for the importance of open canopied forests, tree size, forest disturbance, and social-demographic factors on home range size and selection by white-headed woodpeckers.

Analysis

To examine whether range size differed by sex and study site we used two-way t-tests and one-way ANOVA. We assessed data beforehand using histograms, boxplots, and normal probability plots and found no violations of normality. To assess second-order selection for home ranges within our landscape, we used a case-control logistic model

(Keating and Cherry 2004) to compare habitats within used home ranges to randomly selected, non-use ranges. We used linear mixed models to evaluate importance of habitat versus socio-demographic factors on white-headed woodpecker range size. Woodpecker ID was included as a random effect in these models to account for patterns in the residuals owing to repeated observations of the same individual. Home range size was log-transformed prior to analyses to better meet assumptions of normality and equal variance among groups.

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to assess the amount of support for the different models. Based on Akaike weights, we considered models in the 90% confidence set of candidate models as the best approximating models given the data. Wherever applicable, for each variable in the 90% confidence set of models we computed model averaged parameter estimates, their standard errors, and 95% confidence intervals (± 1.96 SE), following Mazerolle (2006) and Symonds and Moussalli (2011). We also report non-averaged parameter estimates from the models in the 90% confidence set. When confidence intervals did not include 0, we concluded that the associated parameter had an effect on selection or range size. We used SAS version 9.3 statistical software (SAS Institute 2011) for all statistical analyses, and we considered statistical results significant at $\alpha = 0.05$. We report means ±SD unless otherwise noted.

Results

General home range characteristics

We obtained 3994 point locations on 39 breeding adult white-headed woodpeckers ($n = 19$ females, 20 males). We obtained at least 30 point locations on 19 adults during the nesting season, and 30 adults during the post-nesting season. Home range size was not correlated with the number of tracking relocations for either the nesting (r = 0.236) or post nesting seasons (r = -0.008). Mean 99% kernels were 125 ± 59.4 ha and 137 ± 69.5 ha for the nesting and post nesting seasons, respectively, although home range size varied considerably among individuals (Table 2). For the nesting season, home range size varied by a factor 5.5, and for the post nesting season by a factor of 7.3 among individuals. Home range size did not differ by sex for the nesting (t = 1.0896, df = 17, *P* = 0.2911) or post-nesting (t = 1.054, df = 28, *P* = 0.3010) seasons (Table 2). Size also did not differ by study area for either nesting ($F_{(4,14)} = 2.24$, *P* = 0.1170) or post-nesting ($F_{(5,24)} = 1.38$, *P* = 0.2680) seasons.

For individuals that we tracked during both nesting and post-nesting seasons (*n* = 14) post-nesting home ranges overlapped nesting ranges on average by 55.8% (range 12.7-97.5%). We separately computed home range overlap for neighboring woodpeckers tracked in the same year and season. During the nesting season, home ranges for 11 neighbors overlapped on average by 22.6% (range 0.1%-91.0%; Figure 2). For the post-nesting season, home ranges for 15 neighboring woodpeckers overlapped 28.7% (range 7.3-56.5%).

On average, home ranges contained more ponderosa pine than Douglas-fir (Table 3). Old-growth was uncommon in home ranges in both the nesting and post-nesting periods, and the dominant forested layer in home ranges averaged approximately 100 years old (Table 3). Average slope within nesting and post-nesting home ranges was 12% (range 3-21% slope) and 13% (range 5-23%), respectively (Table 3), although some home ranges contained slopes as steep as 237% and 151% for the two seasons.

Factors influencing home range size

In both nesting and post-nesting seasons, the best models predicting home range size included woodpecker weight and age (Table 4). Parameter estimates indicated that older, lighter woodpeckers occupied larger ranges, although confidence intervals show that these parameter estimates were not significant (Table 5). Models that included environmental predictors QMD, slope, and canopy cover were poorly supported compared to our top models, ranking lower than our null model (Table 4). Likewise, productivity and nearest neighbor distances were not influential in predicting white-headed woodpecker home range size in either season. Productivity was generally high in our study and 71% of individuals fledged at least two young. Nearest neighbor distances were highly variable, and ranged from 106 m between two nests in a small burned patch to 2723 m for one isolated nest that was off-shore a peninsula in Rimrock Lake.

Selection of home ranges in the landscape

We banded 56 nestlings at 23 nest sites in 2011 and 2012. Five of these woodpeckers were resighted in subsequent years as adults, and one female banded by an independent research group as a juvenile was resighted at a nest site in 2012. Average dispersal distance from natal sites for these six dispersers was 5.42 ±1.21 km (range 4.1-7.4 km).

On a landscape scale, the best model explaining home range selection in both seasons included forest disturbance (Table 6) and woodpeckers selected for forests with higher portions of disturbance than the surrounding landscape (nesting season: $\beta = 7.54$, 95% CI = [3.17-11.91]; post-nesting season: $\beta = 5.86$, 95% CI = [2.97-8.75]; Figure 3).

Although our disturbance layer could not distinguish between the effects of thinning, burning and disease, the FACTS database and Forest Practice Permits indicated that 19% of selected disturbances had been burned with prescribed burns, 16% subject to recent disease, and 63% both thinned and burned. None of the disturbances selected by woodpeckers in this study had only been thinned. Only one woodpecker home range occurred in an area that did not contain recent disturbance.

Discussion

White-headed woodpeckers home range size was highly variable in our study for both the nesting and post-nesting periods. Even for neighboring individuals of the same sex and tracked within the same year, home range size differed by a factor of seven. Large intraspecific variation in home range size has been noted in all major taxa, including mammals [e.g., moose (*Alces alces*; van Beest et al. 2011)], birds [e.g., Swainson's warbler (*Limnothlypis swainsonii*; Anich et al. 2010), bald eagle (*Haliaeetus leucocephalus*; Garrett et al. 1993)], reptiles [e.g., milk snakes (*Lampropeltis triangulum*; Row and Blouin-Demers 2006)], and amphibians [e.g., gold-spotted frog (*Rana chosenica*; Ra et al. 2008)]. In woodpeckers, numerous studies have likewise reported large variation in home range size among individuals. Elchuk and Wiebe (2003) reported northern flicker (*Colaptes auratus*) home range size varied from 5 to 109 ha, whereas Rota et al. (2014) reported that black-backed woodpecker (*Picoides arcticus*) home range size varied from 20 to 1248 ha.

Reasons for wide variation in sizes of woodpecker home ranges are poorly understood, and past studies have linked variation to habitat (Tremblay et al. 2009, Rota et al 2014, Tingley et al. 2014), dependent young (Mellen et al. 1992), nearest-neighbor distance (Elchuk and Wiebe 2003), and a combination of factors [e.g., habitat and population density (Hooper et al. 1982)]. For white-headed woodpecker specifically, Dixon (1995a, 1995b) linked home range size variation to habitat fragmentation, where large ranges occurred in sites where old-growth ponderosa pine was fragmented by younger forest types. However, in our study we observed variation in home range size even though younger, second-growth stands dominated our landscape, suggesting that other factors are responsible for this variation in home range size. Also, despite occurring in young forest types, average home range size in our study was similar to or smaller than averages reported by Dixon (1995a, 1995b) for stands containing old-growth pine. Instead, our results suggest that non-habitat factors including adult age and weight are more influential. Nonetheless, it is important to note that since our parameter estimates for age and weight were not significant, these two factors are not highly influential overall, and white-headed woodpecker home range size was largely driven by factors not measured in our study.

While we did not necessarily expect adult age and weight to strongly influence ranging behavior, as these factors have not been important for related woodpecker species, we were surprised that nearest neighbor distance was not influential. Population density is important for home range size in other woodpeckers (Elchuk and Wiebe 2003) and white-headed woodpeckers are generally considered territorial during the breeding season (Garrett et al. 1996). However, in our study white-headed woodpeckers appeared to compensate for close-proximity and small nearest-neighbor distances by overlapping their home ranges. For example, during the nesting season, one female in our Oak study site had 91% of her home range overlapped by her two nearest neighbors, and only 9% of her range was used exclusively by her. While we observed some territorial aggression within ~50 m of nest sites we did not observe aggression when woodpeckers were foraging away from nests. Thus, it appears that white-headed woodpeckers may restrict their territorial behavior to the area closest to nest sites, or to a type B territory (Nice 1941), at least while they are busy tending eggs and young. This would allow them to save time and resources for their reproductive efforts, rather than potentially futile attempts to defend the entirety of a 100+ ha home range. This also means that individuals nesting in areas of high population density would not need to shrink their range size to avoid neighboring conspecifics.

While past studies have reported home range size in white-headed woodpeckers, ours is the first to consider potential demographic consequences of this ranging behavior. We found that home range size was not correlated with one important measure of quality, number of fledglings. Moreover, the association between home range size and adult age was positive, indicating that older woodpeckers with higher survival and presumably more experience occupied larger ranges than younger, less experienced birds. This was contrary to our expectations from Dixon (1995a, 1995b), who implied that large home ranges occurred in poor quality habitat, where one would expect corresponding low productivity and young birds. Our findings suggest that wide-ranging behavior may not be maladaptive in white-headed woodpecker, and it is possible that the large ranges observed by older birds in our study resulted from exploratory behaviors, which can have long-term fitness benefits. Wandering individuals may gain important information on food, shelter, and future mates or rivals that is not gained by more sedentary individuals, and thereby enhance their long-term reproductive success (Forkman 1991, Inglis and Ferguson 1986, MacLean et al. 2005). The large home ranges defined by older birds in our study thus may reflect differences in exploratory tendencies among individuals or age-classes, rather than an indication of habitat quality, and future studies should investigate the role of life experience and socio-demographic factors in space use by woodpeckers.

Since home range size was not affected by environmental factors such as stand age, tree size, and slope, we did not find it surprising that these factors were unimportant for home range selection. Our findings on tree size and stand age are similar to those of Hollenbeck et al. (2011) who reported tree size did not differ between nest and available sites. However, regarding slope and steepness of home ranges, our results differ from the combined conclusions of Buchanan et al. (2003) and Hollenbeck et al. (2011) that woodpeckers select sites on level ground. In our study, slope did not differ between used and unused locations, and several woodpeckers occupied ranges in exceptionally steep terrain, where it was not uncommon to track them across slopes >30 %. Differences between our study and past studies may be due to differences in study area or methodology. In our study, slope at both used (12%) and random sites (14%) was greater than the landscape average slope reported by Hollenbeck et al.'s (2011) of 11%, indicating that our study sites were steeper overall. Meanwhile, nesting slopes reported by Buchanan et al. (2003) may have been biased low, because many of their nests were located via citizen science efforts, and sites with steep terrain were probably not explored by these groups. Additionally, neither Buchanan et al. (2003) nor Hollenbeck et al. (2011) measured spatially explicit home ranges with radio-telemetry. Instead, they placed circular buffers 0.1-314 ha in size around nest sites and quantified habitats within these buffers. Thus, it is probable that some of the areas considered used in these studies were not actually used by woodpeckers, while others classified as unused were actually used.

As the first study to investigate selection for spatially explicit home ranges, we did not find tree size or slope important for home range selection. In fact, rather than selecting for old-growth forests, white-headed woodpeckers in our study selected recently disturbed habitats irrespective of the terrain. Although we were unable to distinguish among disturbance types in our models because of high correlations, using records of timber sales and burns we estimated that 81% of home ranges occurred in a burned patch (both thinned and unthinned), compared 16% in diseased patches. No white-headed woodpeckers nested in areas that had only been thinned, and only one nested in an area that did not contain a recent (< 10 year) disturbance. These data suggest that while white-headed woodpeckers can occur in undisturbed forests, recent disturbances, particularly burns, are attractive to them.

Our findings are similar to those of Wightman et al. (2010), who reported that white-headed woodpeckers selected nest sites in burned patches in central Oregon. Wightman et al. (2010) suggested that white-headed woodpeckers select burned patches for nesting because burns contain lower densities of potential nest predators such as chipmunks (*Tamias* spp.), squirrels (*Tamiasciurus* spp.), and mice (*Peromyscus* spp.) compared to nearby live forest. However, Wightman et al. (2010) did not actually measure mammal abundance in burns, and research studies have found that mammals do not always decrease following fire (Sullivan and Boateng 1996, Amacher et al. 2008, Maguire et al. 2008, Russell et al. 2010). In fact, we could find no studies of woodpecker nest site selection that measured mammal abundance in used versus unused sites, and some studies have reported that small mammal abundance is actually higher in post-fire habitats compared to nearby live forests (Krefting and Ahlgren 1974, Converse et al. 2006, Zwolak and Foresman 2007, 2008).

We suggest instead that recent burns are attractive for nesting because woodpeckers are limited by suitable snag availability. In a concurrent study, we estimated that up to 96% of snags on the landscape may be too hard to be used by woodpeckers for nesting, and since burns provide high densities of snags, they also may offer high densities of suitably soft snags (Chapter 1). White-headed woodpeckers may be especially dependent on patches of high snag density in areas where they must compete with other woodpecker species for nest sites. In our study areas, we found that up to five other species of woodpecker may occupy the same areas for nesting. All species selected snags with soft interior wood and which were rare (Chapter 1). At the same time, white-headed woodpeckers are among the latest nesters in our study area, and their nest phenology is delayed by as much as a month compared to other woodpecker species in the region (Kozma 2009). Thus, from the limited number of suitably soft snags on the landscape, white-headed woodpeckers have to choose a site that is not first occupied by one of the other woodpecker species nesting in these patches. Given these considerations, we suggest that white-headed woodpeckers may be attracted to disturbed patches because they provided higher densities of suitable snags and thus opportunities for nesting that are not always available in nearby live forests. We suggest that future studies on white-headed woodpecker test some of these hypotheses, since they may be pivotal for successful management of this important species. In the meantime, managers should update management plans to account for the growing body of research that indicates white-headed woodpeckers occur and persist in managed forests (Kozma 2009, Kozma and Kroll 2012) as long as large numbers of suitable snags for nesting are provided.

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Table 1. Description of parameters considered for examining variation in home range size and second-order selection by white-headed woodpeckers in central Washington, U.S.A., 2011-2013.

Parameter	Description	Considered for home range size model?	Considered for second order selection model?
prod	Productivity, or number of nestlings within 5 days of nest fledging	x	
age	Adult age	x	
neighbor	Distance (m) to nearest neighbor's nest-site	x	
weight	Adult weight (g) at time of capture	x	
slope	Mean percent slope within home range	x	x
elevation	Mean elevation (m) within home range	x[1]	x[1]
LSOG	Proportion of home range composed of late-successional old-growth forest (equivalent to forests with >10% canopy cover and >50.8 QMD)	x[1]	x
agedom	Mean age of stands within home range	x[1]	x[1]
sdcanopy	Standard deviation of percent canopy coverage within home range	x	x
canopy	Mean percent canopy coverage within home range	x	x
pipoba	Mean basal area (m^2/ha) of ponderosa pine within home range	x[1]	x
psmeba	Mean basal area (m^2/ha) of Douglas-fir within home range	x[1]	x[1]
qmd	Mean quadratic mean diameter (cm) of trees within home range	x	x
disturbed	Proportion of home range thinned or burned within 10 years	x[1]	x
prop40cc	Proportion of home range with >40% canopy cover	x[1]	x[1]

[1] Denotes variables that were considered for model but omitted because of high correlations (>0.5) with other variables.

Table 2. Mean (range) home range size (ha) for 35 breeding adult white-headed woodpeckers in central Washington, U.S.A., 2011-2013. Only 99% kernels were used in our analyses of space use, whereas 95% kernels, 50% kernels, and 100% MCPs are provided for comparison with other studies.

	99% kernel	95% kernel	50% kernel	100% MCP
Nesting				
Females (*n* = 9)	109.3 ±49.5 (51.6-193.8)	104.6 ±48.5(44.5-193.4)	20.1 ±11.3 (8.9-39.3)	58.3 ±34.7 (28.9-137.6)
Males (*n* = 10)	138.9 ±66.5 (71.0-284.9)	137.9 ± 51.7 (64.3-231.1)	26.3 ±14.2 (9.5-59.0)	68.9 ±29.1(39.9-130.5)
All birds (*n* = 19)	124.9 ±59.4 (51.6-284.9)	124.9 ±50.71 (44.5-231.1)	23.4 ±13.0 (8.9-59.0)	63.9 ±31.5 (28.9-137.6)
Post-nesting				
Females (*n* = 13)	152.3 ±94.4 (58.5-411.1)	144.9 ±100.8 (54.4-427.2)	24.5 ±12.8 (9.6-76.9)	80.6 ±56.7 (23.7-238.4)
Males (*n* = 17)	125.3 ±41.6 (56.7-199.3)	122.7 ±45.1 (48.9-198.6)	27.1 ±17.5 (9.6-76.9)	58.6 ±30.5 (19.6-130.9)
All birds (*n* = 30)	137.0 ±69.5 (56.7-411.1)	137.0 ±72.9 (48.9-427.2)	22.5 ±7.6 (10.3-38.2)	68.2 ±44.4 (19.6-238.4)

Table 3. Mean values (SD) for habitat features measured within used home ranges of white-headed woodpeckers versus non-use polygons in central Washington, U.S.A., 2011-2013. Means designated with *,**, and *** are significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

	Nesting season		Post-nesting season	
	Used ranges	Non-use polygons	Used ranges	Non-use polygons
Proportion >40% canopy cover	0.62 ±0.24	0.47 ±0.27	0.60 ±0.32	0.57 ±0.25
Proportion disturbed	0.45 ±0.25***	0.05 ±0.07***	0.32 ±0.21***	0.08 ±0.10***
Proportion LSOG	0.07 ±0.12	0.07 ±0.08	0.06 ±0.09	0.05 ±0.05
Slope (%)	12.18 ±4.72	14.47 ±4.96	12.58 ±4.23	13.76 ±5.89
QMD (cm)	24.33 ±4.34	26.17 ±6.57	23.72 ±5.37	23.82 ±5.01
Douglas-fir basal area (m^2/ha)	6.75 ±2.32	7.52 ±3.98	6.82 ±2.84**	7.97 ±3.56**
Ponderosa pine basal area (m^2/ha)	8.08 ±2.95*	6.21 ±2.64*	8.39 ±2.84**	6.85 ±2.80**
Canopy cover (%)	42.86 ±11.83	40.76 ±18.00	42.08 ±13.83	42.96 ±14.98
Dominant tree age (years)	99.82 ±14.41	102.69 ±21.34	94.27 ±22.43*	100.91 ±22.29*

Table 4. Support for models explaining variation in home range size by white-headed woodpeckers in central Washington, U.S.A., 2011-2013.

Parameters	AIC$_c$	Δ_i	w_i
Nesting season			
weight	26.76	0	0.60
age, weight	28.24	1.48	0.29
null (intercept only)	31.31	4.55	0.06
prod	33.05	6.29	0.03
age	33.51	6.75	0.02
QMD	36.44	9.68	<0.01
neighbor	46.21	19.45	<0.01
QMD, canopy, sdcanopy, slope	47.2	20.44	<0.01
QMD, canopy, sdcanopy, slope, neighbor, age, weight, prod	63.77	37.01	<0.01
Post-nesting season			
age, weight	32.99	0	0.59
weight	33.82	0.83	0.39
null (intercept only)	41.09	8.10	0.01
age	42.68	9.69	<0.01
prod	44.12	11.13	<0.01
qmd	45.91	12.92	<0.01
neighbor	57.86	24.87	<0.01
QMD, canopy, sdcanopy, slope	64.72	31.73	<0.01
QMD, canopy, sdcanopy, slope, neighbor, age, weight, prod	72.42	39.43	<0.01

Table 5. Parameter estimates for models in 90% confidence set, model averaged parameter estimates, unconditional standard errors, and 95% confidence intervals explaining variation in home range size by white-headed woodpeckers in central Washington, U.S.A., 2011-2013.

Model	Parameter	Estimate	SE	Lower CI	Upper CI
Nesting season					
Weight	weight	-0.004	0.024	-0.052	0.043
Weight+age	weight	-0.011	0.024	-0.057	0.035
	age	0.143	0.154	-0.159	0.445
Averaged model	weight	-0.006	0.021	-0.047	0.035
	age	0.143	0.154	-0.302	0.445
Post-nesting season					
Weight+age	weight	-0.006	0.017	-0.039	0.026
	age	0.059	0.154	-0.243	0.361
Weight	weight	-0.004	0.016	-0.033	0.027
Averaged model	weight	-0.005	0.016	-0.036	0.026
	age	0.059	0.154	-0.302	0.302

Table 6. Comparison of models explaining second-order selection by white-headed woodpeckers during the nesting and post-nesting seasons in central Washington, U.S.A., 2011-2013.

Parameters	AIC_c	Δ_i	w_i
Nesting season			
disturbed	69.10	0.00	0.99
disturbed, pipoba, canopy, sdcanopy, QMD, slope, LSOG	90.72	21.63	0.01
pipoba	94.48	25.38	<0.01
null (intercept only)	94.66	25.57	<0.01
canopy	96.90	27.80	<0.01
sdcanopy	97.12	28.03	<0.01
canopy, pipoba	97.21	28.12	<0.01
QMD, slope, sdcanopy, canopy	98.56	29.46	<0.01
LSOG, QMD	99.21	30.11	<0.01
canopy, pipoba, LSOG, QMD	102.40	33.30	<0.01
Post-nesting season			
disturbed	127.09	0.00	0.98
disturbed, pipoba, canopy, sdcanopy, QMD, slope, LSOG	140.64	13.55	0.01
pipoba	147.91	20.82	0.01
null (intercept only)	149.24	22.15	<0.01
sdcanopy	149.87	22.79	<0.01
canopy, pipoba	149.96	22.87	<0.01
canopy	151.45	24.36	<0.01
LSOG, QMD	153.96	26.88	<0.01
QMD, slope, sdcanopy, canopy	154.09	27.00	<0.01
canopy, pipoba, LSOG, QMD	154.19	27.11	<0.01

Figure 1. Location of six study sites used to examine white-headed woodpecker space use in central Washington, U.S.A., from 2011-2013. The polygons show the outline each study site, and dots represent telemetry tracking locations from 39 radio tagged woodpeckers.

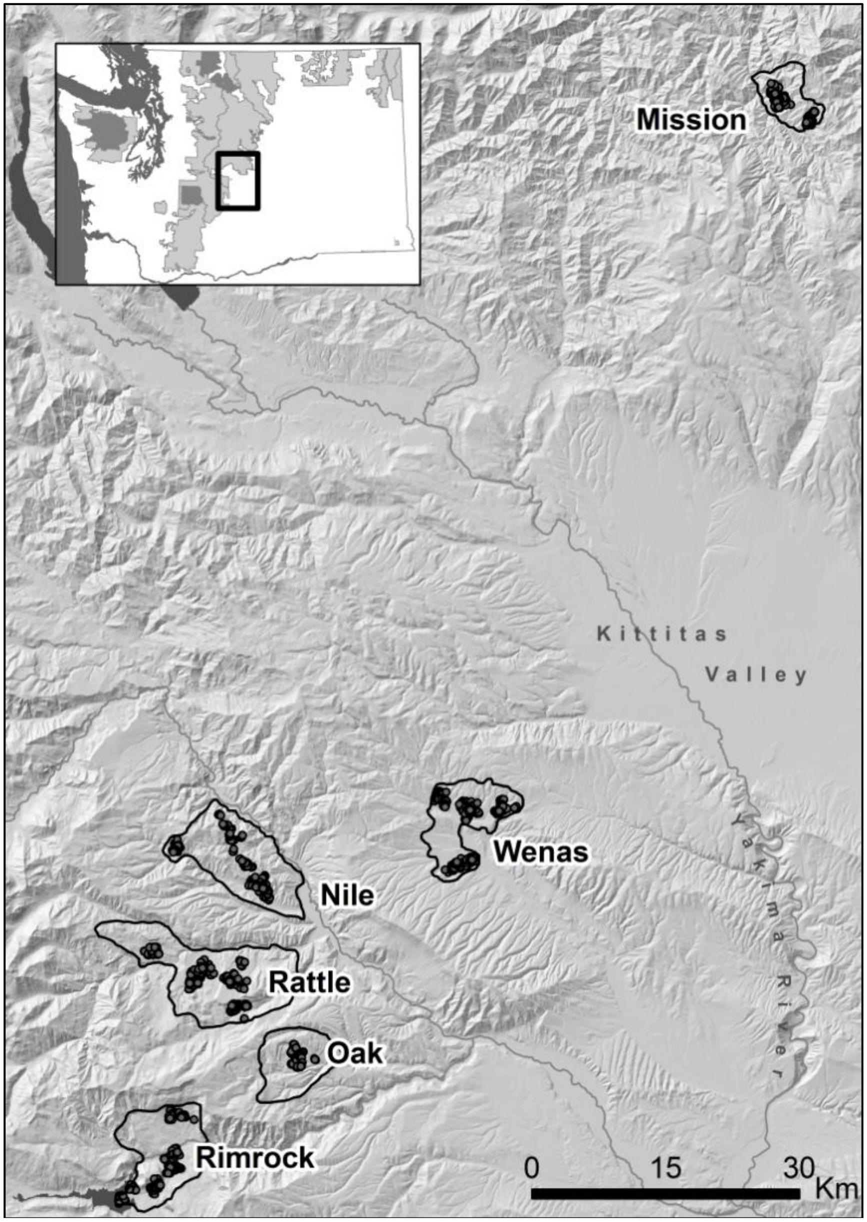


Figure 2. Overlap of home range kernels by three adult white-headed woodpeckers in the Oak study site during the nesting season in 2013. Arrows point to nest sites for three individuals (from left to right, woodpeckers male #530, female #500, and female #511), and black, gray, and white dots and lines represent points and 99-75% contours for male #530, female #500, and female# 511, respectively.

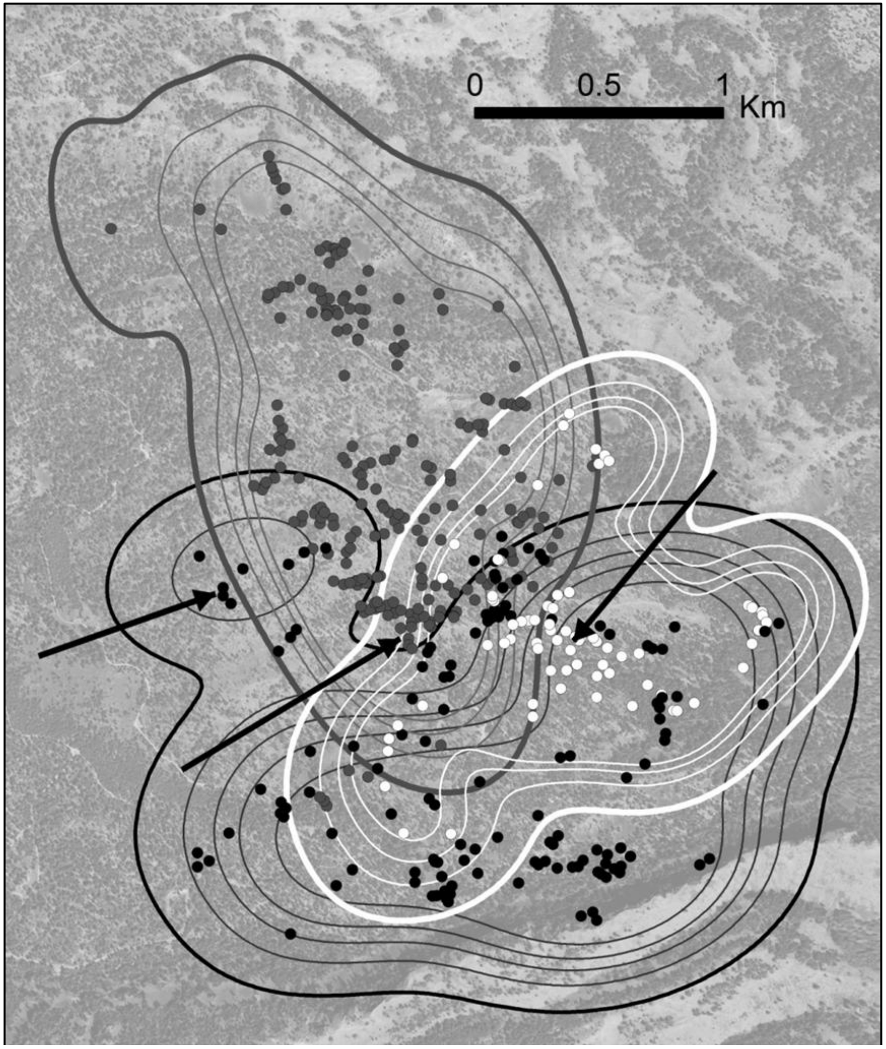
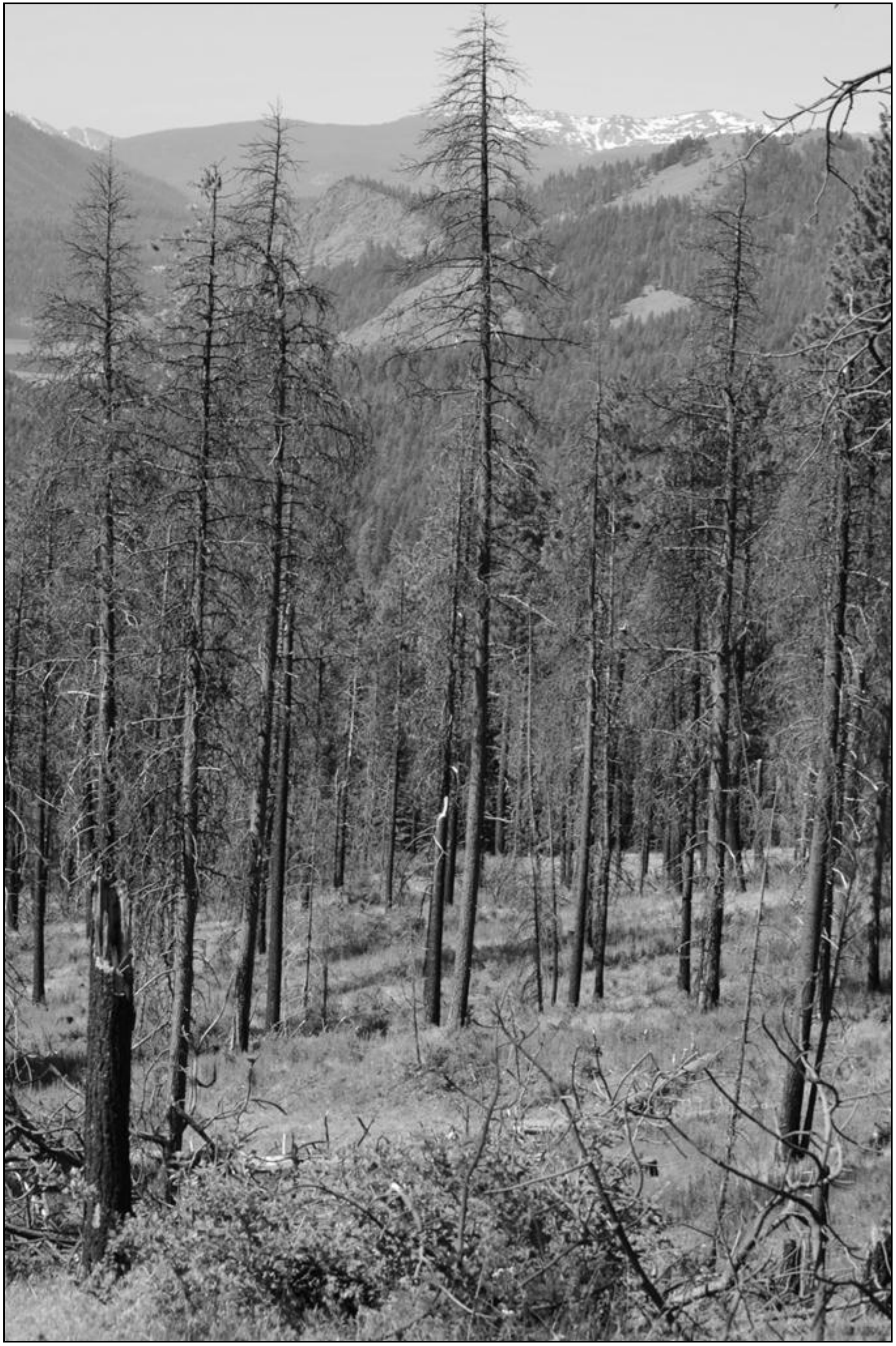


Figure 3. Example of a disturbed, burned patch used by white-headed woodpeckers for nesting in the Rimrock study area in central Washington, 2011-2013.



CHAPTER 3

FORAGING PLASTICITY BY A KEYSTONE INDICATOR SPECIES, THE WHITE-HEADED WOODPECKER

Abstract

Information on the foraging ecology of animals is important for conservation and management, particularly for at-risk species. Here, we examined foraging by the white-headed woodpecker (*Picoides albolarvatus*), an at-risk primary cavity excavator in conifer forests of western North America. Our objectives were to measure substrate use, forage site selection, distance traveled from nests for foraging, and demographic consequences of foraging, particularly for productivity. We used radio-telemetry to track woodpeckers (n = 37) as they foraged from May through October of 2011-2013 (n = 10,576 minutes foraging), which encompassed all of the incubation, nestling, and fledgling periods in their annual cycle. We also measured distances traveled from nests by foraging woodpeckers, and related substrate use and forage distance to productivity. Woodpeckers foraged on more than ten individual substrates and species of plant from May through October and switched their foraging seasonally, presumably to take advantage of prey availability. Dead wood and fir foliage [from Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*)] 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).   During the nesting season, distances traveled from nests for foraging did not affect productivity ($F_{(3,16)} = 0.61$, $P = 0.6156$), which was high even for birds with the longest (2.08 km) and shortest maximum forage distances (0.394 km).

Habitats selected for foraging matched substrate use, where woodpeckers selected areas near nests and with low live tree basal area while foraging during the nesting period, and high live tree densities for in the post-nesting period. The variable foraging patterns that we observed in our study suggested that white-headed woodpeckers are plastic in their foraging during the breeding season. Future studies should explore their foraging behavior during the winter and examine the influence of winter foraging on survivorship.

Introduction

Understanding the ecological and behavioral drivers of habitat selection by animals is essential for informing conservation and management (Morrison 2001), especially in the face of wide-spread, human-induced environmental change. Among all behaviors, an understanding of foraging is considered one of the most important for effective management, because foraging has direct demographic consequences for populations. Information on foraging and forage-site selection is particularly important for ecosystem engineers and keystone species, since their presence has consequences for the larger ecosystem in which they live. For instance, information on foraging by Red-cockaded woodpeckers (*Picoides borealis*; Engstrom and Sanders 1997), a keystone species in southeastern U.S.A. pine forests, has been used to aid management of long leaf pine forests throughout this region and preserve the keystone functions of red-cockaded woodpeckers as primary cavity excavators (Blanc and Walters 2008a, 2008b).

White-headed woodpeckers (*Picoides albolarvatus*) are important ecosystem engineers and potential keystone species in dry pine forests of the western U.S.A.. Like red-cockaded woodpeckers, white-headed woodpeckers are an important primary cavity excavator for creating cavities in trees. Throughout their range they are considered a sensitive or endangered species that has declined in the last century owing to intensive forest management practices (reviewed in Mellen-McClean et al. 2013). They are also a management indicator species for ponderosa pine (*Pinus ponderosa*) restoration in the northwestern U.S.A. (Altman 2000, Gaines et al. 2007, 2010), because their presence is thought to reflect ecosystem health and habitat quality for other pine-associated species. Previous research has indicated that white-headed woodpeckers require high densities of suitable snags for nesting and large diameter pines for foraging, both of which are components of old ponderosa pine stands (Garrett et al. 1996). Because of their indicator species status, management of large tracts of ponderosa pine forest in the northwestern U.S.A. is currently based at least partially on nesting and foraging needs of the white-headed woodpecker.

While their nesting has been well-studied range-wide (Raphael and White 1984, Milne and Hejl 1987, Wightman et al. 2010, Kozma 2011, Hollenbeck et al. 2011, Kozma and Kroll 2012), studies of white-headed woodpecker foraging have mostly focused on southern populations (Morrison et al. 1987, Morrison and With 1987, Raphael and White 1984, Hanson and North 2008). Four foraging studies have been conducted in the northwestern states of Oregon, Washington, and Idaho. These studies have helped advance our understanding of foraging, but were limited to relatively small sample sizes (3 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, since others have noted considerable spatial and temporal variation in white-headed woodpecker foraging. For example, Morrison and With (1987) observed significant differences between winter and summer foraging in California, and 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). Although it is widely recognized that accurate information on foraging is important for management and conservation, there is a lack of regionally appropriate data on foraging by white-headed woodpeckers with which to assess and 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 (Raphael and White 1984). Information on use alone can lead to biased conclusions on resources that are important for animals (Johnson 1980). Additionally, we could find no past studies that examined demographic consequences of foraging decisions. Thus it is not known whether observed differences in foraging by woodpeckers contribute to local population declines noted 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 had three objectives. First, we measured substrate use by white-headed woodpeckers during a six-month period that encompassed the incubation, nestling, fledgling, and post-fledgling seasons in their annual cycle. Our goal was to characterize not only substrate use but size of trees in forest types that had been harvested multiple times and which generally lacked large trees important for foraging in other studies (e.g., 68 cm DBH; Dixon 1995a). Second, we modeled third-order selection (Johnson 1980) by foraging white-headed woodpeckers during two time periods: the nesting period (combining the incubation and nestling seasons) and post-nesting period (combining the fledgling and post-breeding autumn seasons). Third, we examined whether differences in foraging behavior affected one important measure of population growth, productivity. Such information is important both for conserving white-headed woodpeckers, and for assessing their role as indicator species in northwestern pine forests.

Methods

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 46º 45′ N, 120º 58′ W and 47º 30′ N, 120 º 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 National Forest land, and one site encompassed both state (Washington Department of Natural Resources, and Washington Department of Fish and Wildlife) and private lands. Ponderosa pine was dominant or co-dominant with Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*) in all study areas. Other common tree species included western larch (*Larix occidentalis*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). Forests in all study areas had been harvested for timber at least once since 1950, and approximately 39 percent of the area within these study sites had been thinned and/or burned an additional time, and within ten years of the start of this study. Four study sites were used for livestock grazing during the course of this study.

Field methods

We used radio telemetry to collect foraging observations on white-headed woodpeckers. In May and June we captured adult woodpeckers in breeding territories and near nest sites using hoop nets, noose traps, and mist-nets. We attached transmitters to woodpeckers using tail mounts and leg harnesses (Rappole and Tipton 1991), and all activities were performed under University of Idaho Animal Use and Care protocol #2011-30. We alternated the sex that was radio-tagged to ensure equal representation by both sexes in our sample, and we radio-tagged only one individual from each territory or nest site for independence among individuals. Additional details on the methods for finding and selecting territories and attaching transmitters are available in Chapter 2.

We located nest sites of all radio-tagged birds either by nest searching or radio-tracking. 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 snowfall. 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).

Foraging observations

We obtained foraging observations of 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 (location error ±5-6 m). We then noted the plant species on which the birds were foraging, as well as the foraging substrate (e.g., 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 seasons, corresponding to changes in the breeding cycle between May and October: incubation season, nestling season, fledgling season, and post-fledgling autumn season. Since the length of each season varied following the biology of the species and the number of days each individual was tracked, the lengths of each season 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).

Forage site selection

We used an information theoretic approach (Burnham and Anderson 2002) to investigate whether white-headed woodpeckers selected habitats for foraging within home ranges. For this particular analysis, we combined observations from the incubation and nestling periods into a single season, which we called the nesting period. We then combined observations from the fledgling and post-fledgling autumn season into a second period, called the post-nesting period. We then 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 territory-scale nest-site selection studies. 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 season, 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 season we also included a covariate for distance to nest. 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 seasons ($r > 0.70$). We therefore omitted grand fir and used Douglas-fir basal area to represent basal area by both species for foraging woodpeckers.

To determine available habitats for comparison with those used, we first obtained 99% kernel home ranges computed in a concurrent study of space use (Chapter 2). Within each 99% kernel home range, we used the ArcGIS random sample tool to select 20 random locations for comparison with used forage locations. We then overlaid GIS layers for canopy cover, QMD, and tree basal area from Gradient Nearest Neighbor (GNN) models and extracted these data for each used and available forage point. The GNN models were derived from a combination of field plots, mapped data, and Landsat Thematic Mapper (TM) satellite imagery from 2012 (Ohmann et al. 2011), and provided spatially explicit information on vegetation for all study sites.

We restricted this analysis 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 and 21 woodpeckers during the post-nesting season. To avoid potential autocorrelation in our dataset caused by tracking woodpeckers continuously for 1 hour time blocks, we randomly selected from all forage points of each woodpecker a subset of 20 forage observations to use in this analysis.

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 seasons by sex, where season 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 a 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 multi-response logistic regression to determine whether distances traveled for foraging or substrate influenced productivity (# of fledglings/nest). Variables considered as possible predictors were maximum forage distance, mean forage distance, and proportion of time spent on the two most commonly used 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.

For examining forage site selection, we used matched case control logistic regression and treated used forage sites as cases and random points within home ranges as controls. This design requires that the probability of use be ‘small’ (Keating and Cherry 2004), such that controls are not contaminated with used sites. Given that white-headed woodpecker home ranges are large (~100-200 ha on average; Dixon 1995a, 1995b; Chapter 2), and we sampled only 20 point locations within home ranges, we assumed that this assumption was met. We compared models for the nesting and post-nesting period using Akaike’s Information Criterion corrected for small sample sizes (AICc) and Akaike weights (Burnham and Anderson 2002), where models with lowest AICc and highest weights are better supported than other models in the candidate set. For the top model, we then presented parameter estimate, their standard errors, and p-values.

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

Results

Substrates used for foraging

We recorded 10,576 minutes of foraging by 37 breeding white-headed woodpeckers from May through October, 2011-2013. 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 (trunk 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 seasons, we observed no overall differences in foraging substrate by sex ($F_{(1,32)} = 0.06$, $P = 0.8120$) and consequently combined sexes in subsequent analyses. We also observed no differences in foraging substrate use between morning and afternoon ($F_{(1,32)} = 0.023$, $P = 0.8796$), and therefore combined morning and afternoon observations in our analyses.

Dead stems and foliage were the most commonly used substrates for foraging across all seasons and individuals, and accounted for 62% of all foraging observations. Most (92%) dead stem foraging was on cut stumps from past timber harvests (Figure 1), and 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’ 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 the seasons within the monitoring period (Figure 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; Figure 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 season (Figure 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 seasons or substrates (Figure 2). One exception was that smaller trees were used during the nestling season for live-stem and foliage foraging.

Distances traveled from nests

Mean distance traveled from nests for foraging did not differ by season ($F_{(1,19)}$ = 3.00, P = 0.0994), sex ($F_{(2,19)}$ = 1.05, P = 0.3682), or substrate ($F_{(1,12)}$ = 1.03, P = 0.3312). Distance traveled averaged 0.435 km (±0.323 km; range 0.02-2.08 km) for females and 0.464 km (±0.353 km; range 0.02-1.46 km) for males. Grouping both sexes, white-headed woodpeckers traveled 0.466 km (±0.321 km) while foraging on deadwood and 0.454 km (±0.362) while foraging on fir foliage.

We found that productivity was not influenced by foraging behavior. The number of you fledged from nests was poorly correlated with mean (r = -0.1899) and maximum (r = -0.1624) foraging distance. Additionally, type 3 effects indicated that mean forage distance (χ^2 = 2.980, df = 4, P = 0.561), maximum forage distance (χ^2 = 1.786, df = 4, P = 0.775), and proportion of time spent foraging on dead wood (χ^2= 1.486, df = 4, P = 0.829) during the nesting seasons did not affect productivity. Productivity was generally high, despite the variation we observed in foraging. Only one out of 37 monitored nests 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).

Forage site selection

White-headed woodpeckers selected different habitats for foraging in the nesting versus post nesting periods. White the top-ranked model in both seasons was the global model (w_i = 0.954 and 0.998, respectively) (Table 2), parameter estimates indicated that during the nesting season, white-headed woodpeckers selected locations with low pine and fir basal area but which were close to nest sites (Table 3). In contrast, for the post nesting season woodpeckers selected areas with high pine and fir basal area, open canopies, and small trees compared to random sites (Table 3).

Discussion

White-headed woodpeckers in our study varied their foraging behavior considerably both within and among seasons, and this variation is similar to published accounts of spring and summer foraging observed by others. Morrison et al. (1987) noted that more than six tree species and four substrates were used during summer in central California, 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 season, while 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 generally 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. 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, Tevis 1953, Ligon 1973). Some of the differences between ours and these studies may be attributed to differences in study duration, 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 fall, we would never have observed dead wood or fir foliage foraging and we would have concluded that only live pines were used for foraging. Our results 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 forage on pine seeds year-round. In our study, drilling deep into dead wood was the most common means of foraging during the nesting season, and surface gleaning on trunks was restricted to autumn. In addition, pine seed foraging accounted for less than 7% of all foraging and was observed only in the fledgling and post-fledgling autumn seasons.

Given our results, we consider that the cone foraging behavior of white-headed woodpeckers in particular has received a considerable and probably unwarranted amount of attention in the past literature. Several recent reviews have described white-headed woodpeckers as ‘dependent’ or ‘reliant’ on pine seeds or cones (Garrett et al. 1996, Hollenbeck et al. 2011, Wightman et al. 2010), while our results add to a larger body of literature that indicates that cone foraging is opportunistic. This literature includes studies that have reported both infrequent (Otvos and Stark 1985, Dixon 1995b, current study) and no cone foraging (Grinnell and Storer 1924, Morrison and With 1987, Morrison et al. 1987, Raphael and White 1984, Hanson and North 2008, Kozma and Kroll 2013). Furthermore, 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* and *Tamiasciurus*), jays (*Cyanocitta* spp.), reviewed in Vander Wall 1997], and opportunistic breeding [e.g., crossbills (Hahn 1995, 1198), pinyon jays (*Gymnorhinus cyanocephalus*, Ligon 1974)]. Such behaviors have never been observed 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. While it is possible that seed cones improve survival, we observed high survival in our study despite the lack of cone foraging, and thus our findings indicate that in this study site and time period, cone crops are not likely to be important. 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 for survival elsewhere or in other seasons.

Our observations of foraging provide important insights into the behavioral ecology of white-headed woodpecker. First, individuals in our study showed generally high productivity while foraging in managed stands with environmental conditions presumably quite different from historical ones (Wright and Agee 2004, but see Hessburg et al. 2007 and Baker 2012). In particular, the stump foraging behavior that dominated during the nesting period must be a recent adaptation, since cut stumps were not present for woodpeckers before ca. 1850. Additionally, 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 season should not be used to characterize year-round foraging needs in other regions. For example, observations by Dixon (1995a; Garrett et al. 1996) during a two- to six-month period (July onward) in one locale (Sisters, Oregon, U.S.A.) are often used as evidence that white-headed woodpeckers require 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. (e.g., USFS 2010; 2013, Hessburg et al 2013). However, in our study, pines >60 cm DBH accounted for fewer than 4% of all foraging observations. Instead woodpeckers foraged on cut stumps, fir trees, and moderate-sized pines. Providing large diameter pines for foraging to the exclusion of these other substrates may not be beneficial for woodpeckers in central Washington, and management plans based on short, seasonal observations should be reconsidered. Along similar lines, 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 possible, and even likely, that white-headed woodpeckers in central Washington rely on different substrates during the winter and spring months. For example, Kozma (2010) documented sapwell feeding in our study areas in April, May, and June that we did not observe in our study of foraging from May onwards. 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-sized 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 season woodpeckers selected areas of their home range that were close to nests but with low basal area of trees. During the post-nesting season woodpeckers selected areas with higher densities pines and firs. This selection likely simply reflects substrate use we observed by woodpeckers; for the nesting season, woodpeckers heavily used cut stumps for foraging, and it makes sense that these in areas would have low tree density, since they were recently thinned. However, for the post-nesting season, they foraged on fir and pine foliage, and live stems, resulting in selection for locations with high tree densities. Probably because these patches had high tree densities, they also had lower QMD on average than random sites. This differs from our expectations based on Dixon (1995a), but is supported by observations by Hollenbeck et al. (2011). Although Hollenbeck et al. (2011) did not observe foraging, they reported that woodpeckers nested in patches with lower QMD than the landscape, similar to our study. As the first study to model forage site selection in white-headed woodpecker, our results suggest that such patches may provide important forage habitat for this species.

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, 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, at least 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 pulling out 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..). Wood boring 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. These observations 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 season.

This study adds to the growing body of literature indicating that white-headed woodpeckers successfully occupy and breed in managed stands. While they largely appear dependent on snags – one potential component of old-growth – for nesting (Garrett et al. 1996), they are not dependent on large, old pines for foraging, at least during the time periods that we examined in our study. 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, particularly snags. Because of this, they may even preferentially select recently disturbed habitats like burns for the breeding season because they contain high snag densities for nest substrates (Chapter 1). We suggest future studies examine white-headed woodpecker foraging during the winter months, to evaluate whether they are limited by foraging habitat in the non-breeding seasons, and also to examine specifically whether seed cone availability enhances survival. We also encourage other studies be conducted in a variety of managed and unmanaged forests across the range of this species to better assess differences in foraging behaviors, and to further explore relationships between foraging and demographic parameters such as productivity and survivorship.

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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 season selection?	Considered for post-nesting season selection?
canopy	Mean percent canopy coverage	x	x
pipoba	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
distance	Straight-line distance from nest site (m)	x	

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

Model	Parameters	k	AIC$_c$	Δ_i	w_i
Nesting season					
Global	distance, QMD, canopy, pineba, firba	6	946.27	0.00	0.954
Travel distance	distance	2	952.35	6.09	0.046
Pine trees	pineba	2	969.15	22.89	<0.001
Large pine trees	QMD, pineba	3	970.27	24.01	<0.001
Large trees	QMD	2	972.57	26.30	<0.001
Fir trees	firba	2	974.33	28.06	<0.001
Unmeasured factors	none (interecept only)	1	974.91	28.65	<0.001
Dense forests of large trees	QMD, canopy	3	975.22	28.95	<0.001
Closed-canopy forests	canopy	2	977.41	31.15	<0.001
Post-nesting season					
Global	QMD, canopy, pineba, firba	5	862.05	0.00	0.998
Large pine trees	QMD, pineba	3	878.92	16.87	0.001
Dense forests of large trees	QMD, canopy	3	892.61	30.56	<0.001
Large trees	QMD	2	898.62	36.57	<0.001
Pine trees	pineba	2	1026.43	164.37	<0.001
Closed-canopy forests	canopy	2	1051.76	189.70	<0.001
Unmeasured factors	none (intercept only)	1	1054.70	192.65	<0.001
Fir trees	firba	2	1056.14	194.09	<0.001

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 season in Washington, U.S.A., 2011-2012.

Parameter	β	SE	χ^2	P
Nesting season				
QMD	0.00	0.01	0.01	0.904
pineba	-0.06	0.02	12.52	0.000
firba	-0.05	0.02	6.79	0.009
canopy	0.01	0.01	2.32	0.128
distance	<0.01	0.00	27.38	<0.001
Post-nesting season				
QMD	-0.13	0.01	116.89	<0.001
pineba	0.08	0.01	30.20	<0.001
firba	0.07	0.02	15.19	<0.001
canopy	-0.03	0.01	20.62	<0.001

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

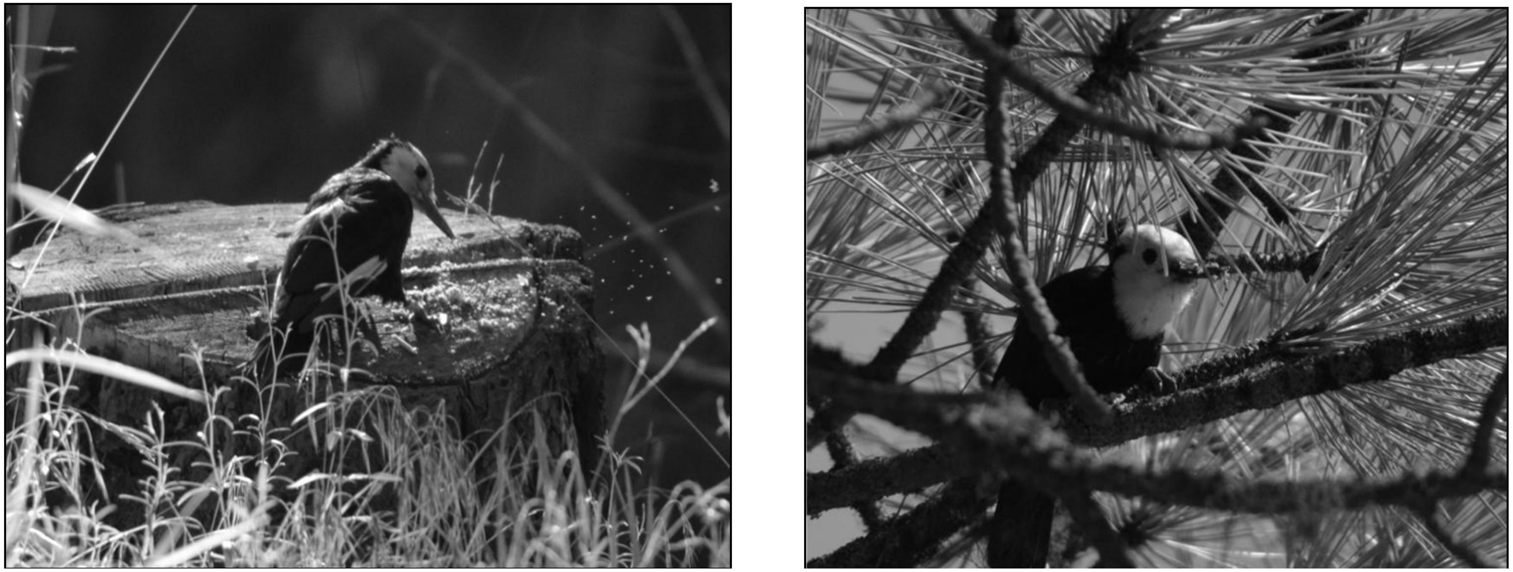
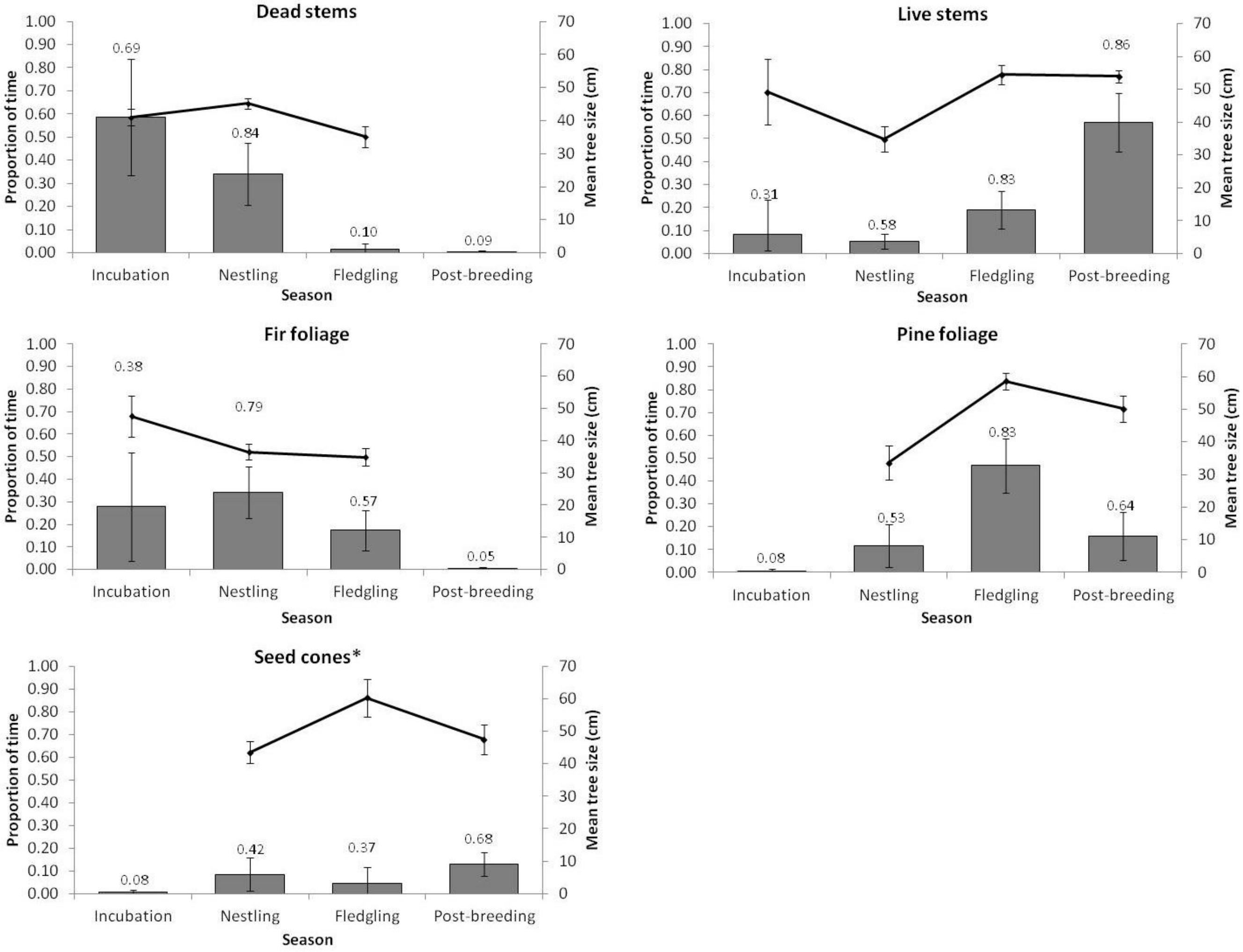


Figure 2. Foraging substrates used by 37 white-headed woodpeckers that were radio-tracked in central Washington, 2011-2013. Shown are mean proportion of time (bars; *n* = 10,576 minutes), mean tree size (lines; *n* = 2,435 trees), and 95% confidence intervals for each season and substrate. Numbers above each bar represent proportion of individuals observed foraging on each substrate. *Note that 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 seasons.



APPENDIX A

ESTIMATED WOOD MASS DENSITY FROM WOODPECKER NESTS AND RANDOM SITES, CALCULATED FROM FIGURE 3 OF MATSUOKA (2000)

Species	Sill mean (range) wood density (g/cm^3)	Body mean (range) wood density (g/cm^3)
Northern Flicker	0.226 (0.167-0.394)	0.194 (0.167-0.278)
White-headed	0.233 (0.167-0.510)	0.208 (0.167-0.289)
Williamson’s sapsucker	0.268 (0.174-0.561)	0.205 (0.175-0.285)
Hairy woodpecker	0.256 (0.169-0.400)	0.210 (0.169-0.286)
Black-backed	0.291 (0.167-0.449)	0.208 (0.167-0.313)
American three-toed	0.303 (0.181-0.495)	0.227 (0.181-0.322)
Random trees	0.323 (0.167-0.786)	0.380 (0.167-0.821)

APPENDIX B

LITERATURE REVIEWED FOR NEST-SITE SELECTION MODELS

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APPENDIX C

SUPPORT FOR ALL MODELS EXPLAINING TERRITORY-SCALE SELECTION BY FOUR WOODPECKER SPECIES IN CENTRAL WASHINGTON, 2011-2013

Model	k	AIC$_c$	Δ_i	w_i
Black-backed woodpecker				
body	2	2.33	0.00	0.665
sill body	3	4.69	2.35	0.205
sill body dsnag	4	7.18	4.84	0.059
dsnag body dlive10	4	7.18	4.84	0.059
DBH*DBH cline body dsnag	6	10.63	8.29	0.011
DBH cline sill body prefire dlive10 dsnag	8	14.80	12.47	0.001
dlive10 sill	3	47.41	45.08	0.000
dlive10	2	47.64	45.31	0.000
dsnag dlive10 sill	4	49.58	47.25	0.000
dsnag dlive10	3	49.73	47.39	0.000
sill	2	51.10	48.76	0.000
none	1	54.17	51.84	0.000
dsnag	2	55.27	52.94	0.000
DBH	2	56.35	54.02	0.000
prefire dsnag	3	57.62	55.28	0.000
cline DBH	3	57.82	55.49	0.000
DBH*DBH cline	4	61.17	58.83	0.000
Hairy woodpecker				
body	2	2.21	0.00	0.647
sill body	3	4.43	2.22	0.213
sill body dsnag	4	6.73	4.52	0.068
DBH dsnag body	4	6.73	4.52	0.068
DBH cline sill body dlive10 dsnag	7	12.15	9.94	0.004
dlive10 sill	3	48.77	46.56	0.000
sill	2	48.93	46.72	0.000
cline DBH	3	74.65	72.44	0.000
DBH	2	79.51	77.30	0.000
DBH dsnag	3	79.62	77.41	0.000
none	1	83.25	81.04	0.000
dsnag dlive10	3	187.88	185.67	0.000
Northern flicker				
body	2	2.23	0.00	0.584
sill body	3	4.47	2.24	0.191
cline sill body	4	4.80	2.57	0.162

canopy sill body	4	6.80	4.57	0.060
DBH cline sill body dlive10 canopy	7	12.38	10.15	0.004
sill	2	41.33	39.10	0.000
DBH cline	3	50.61	48.38	0.000
cline DBH dlive10 canopy	5	53.41	51.18	0.000
cline	2	55.05	52.82	0.000
none	1	76.32	74.09	0.000
canopy	2	77.92	75.69	0.000
DBH	2	78.18	75.95	0.000
canopy dlive10	3	79.83	77.60	0.000
White-headed woodpecker				
sill body	3	4.34	0.00	0.891
body	2	8.86	4.53	0.093
body dlive50 canopy shrub	5	13.07	8.73	0.011
DBH dlive50 cline sill body shrub slope	9	14.77	10.43	0.005
canopy sill	3	54.14	49.80	0.000
sill	2	54.91	50.57	0.000
cline	2	99.43	95.09	0.000
shrub cline	3	100.81	96.47	0.000
canopy	2	101.30	96.97	0.000
DBH cline	3	101.60	97.26	0.000
canopy shrub	3	101.88	97.54	0.000
none	1	102.64	98.30	0.000
slope	2	103.10	98.77	0.000
canopy shrub dlive50	4	103.91	99.57	0.000
dlive50	2	104.92	100.58	0.000
slope dlive50 DBH	4	105.18	100.84	0.000
DBH	2	106.11	101.77	0.000
dlive50 DBH	3	107.06	102.73	0.000

APPENDIX D

SUPPORT FOR ALL MODELS EXPLAINING NEST-TREE SELECTION BY FOUR WOODPECKER SPECIES IN CENTRAL WASHINGTON, 2011-2013

Model	k	AIC_c	Δ_i	w_i
Black-backed woodpecker				
body	2	7.12	0.00	0.749
sill body	3	9.31	2.19	0.251
orientation height	3	46.30	39.18	0.000
orientation	2	49.14	42.02	0.000
body orientation	3	52.81	45.69	0.000
sill	2	54.17	47.05	0.000
none	1	54.17	47.05	0.000
height	2	55.61	48.49	0.000
sill height	3	56.21	49.09	0.000
height sill body orientation	5	57.34	50.22	0.000
Hairy woodpecker				
body orientation	3	4.43	0.00	0.894
body	2	9.80	5.38	0.061
sill body	3	11.11	6.69	0.032
height sill body orientation	5	12.86	8.43	0.013
sill height	3	71.96	67.53	0.000
height	2	74.33	69.90	0.000
sill	2	77.13	72.70	0.000
orientation height	3	77.54	73.11	0.000
none	1	83.25	78.82	0.000
orientation	2	86.44	82.01	0.000
Northern flicker				
height sill body orientation	5	33.16	0.00	0.472
body	2	33.73	0.57	0.354
sill body	3	35.96	2.80	0.116
body orientation	3	37.34	4.18	0.058
sill height	3	66.27	33.11	0.000
sill	2	68.19	35.03	0.000
height	2	73.46	40.31	0.000
none	1	76.32	43.16	0.000
orientation	2	77.26	44.10	0.000
orientation height	3	80.34	47.19	0.000
White-headed woodpecker				
sill body	3	25.36	0.00	0.533

body	2	25.80	0.44	0.427
body orientation	3	31.86	6.49	0.021
height sill body orientation	5	31.97	6.60	0.020
none	1	48.93	23.57	0.000
sill height	3	73.16	47.80	0.000
orientation height	3	80.23	54.86	0.000
height	2	84.14	58.77	0.000
sill	2	86.11	60.75	0.000
orientation	2	93.94	68.58	0.000