The role of wood hardness in limiting nest site selection in avian cavity excavators

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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.

Key words: *Black-backed Woodpecker; nest limitations; nest site selection; primary cavity excavator; resource selection; secondary cavity user; snag decay class; White-headed Woodpecker; wood hardness; wood mass density.*

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 (Martin et al. 2004, Aitken and Martin 2008, Gentry and Vierling 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, Strukelj 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, Bonnot et al. 2009, Saab 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 (Matsuoka 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, USA, in Yakima, Kittitas, and Chelan Counties (approximately 47°00′ N and 121°00′ W). Land ownership included private, state, and the United States Forest Service. We searched for nests in all major forest 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 occidentalis*) 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 10 study sites ~600–3000 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, Camarillo, California, USA) 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 reuse 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 orientation of the nest cavity entrance, a spherical densiometer 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 prefire canopy cover we used Gradient Nearest Neighbor (GNN) Classified Landsat (ETM+) satellite imagery flown between two and eight years prior to each fire (IMAP: Interagency mapping and assessment project,

Landscape Ecology Mapping Modeling and Analysis [LEMMA]; *available online*).[5] This data set averaged prefire canopy cover within 30 × 30 m pixels, and for nests we assumed that the canopy cover from each 30 × 30 m pixel was representative of canopy cover at the actual nest site. We used ArcGIS 10 (ESRI 2010) to extract these data for nest sites.

For assessing nest site selection at the territory scale, we measured all of the features mentioned in the previous paragraph at one random tree associated with each nest. We included only snags in our sample of random trees, since only a small proportion of nests occurred in live trees. We selected random snags by walking >75 m 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 the 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, so we measured hardness at 1-cm increments, beginning at the tree's surface and ending 15 cm deep toward the heartwood, similar to Farris et al. (2004) (Fig. 1). Thus, for each hardness measurement, we measured hardness at one spot on the exterior of the tree, but recorded 16 measures of wood hardness as we drilled in toward 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, Matsuo-

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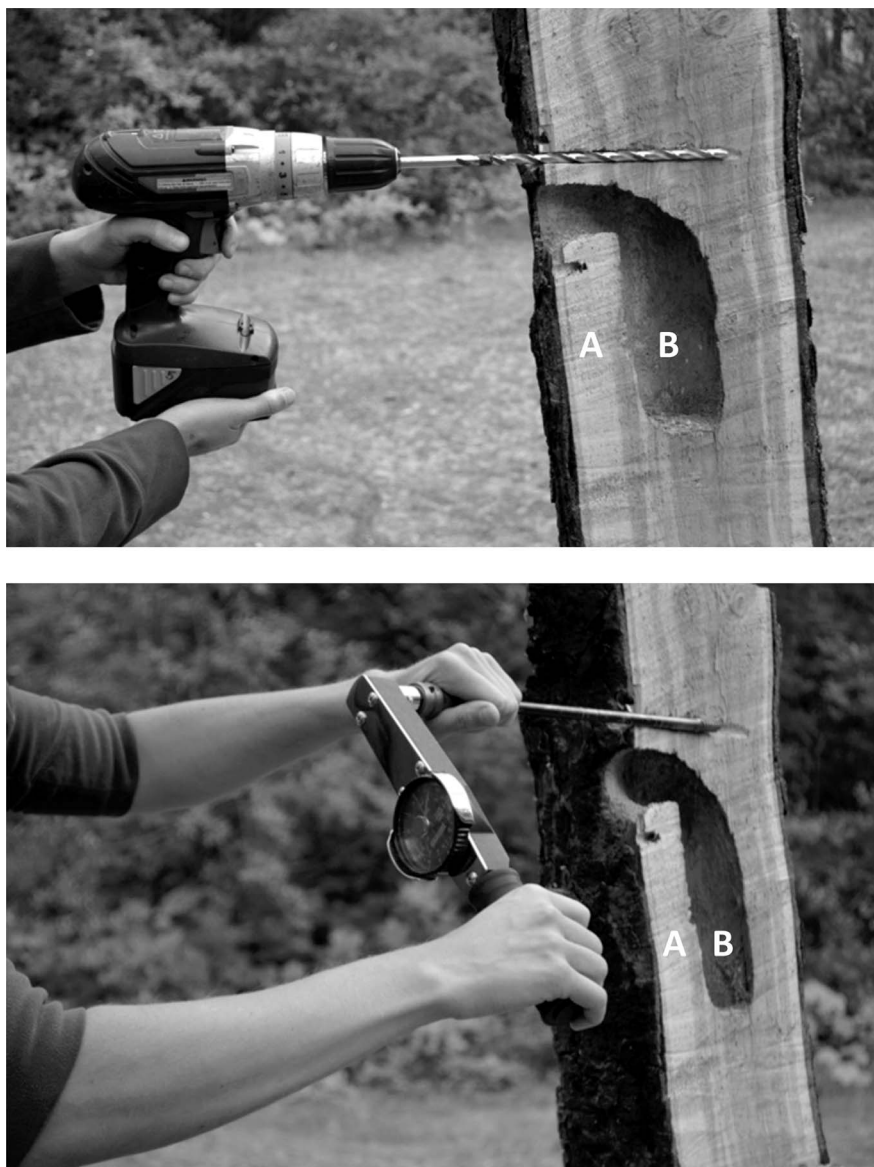[5] http://lemma.forestry.oregonstate.edu/data

Fig. 1.   Longitudinal section of an American Three-toed Woodpecker (*Picoides dorsalis*) 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 the 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 the area marked B represents the nest cavity body in our study.

ka 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 to the nest. 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") (Fig. 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 comparable to 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. Therefore, at a subsample of 10% of random trees, we 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. Therefore, whenever possible we 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 in nest territories 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, Hollenbeck et al. 2011, Nappi and Drapeau 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 nonuse 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 nonuse 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 then computed simple proportions of nonuse 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; and (6) suitable for nesting (sill and body both suitable). We omitted categories for body wood that was too soft because we found no nests with softer body wood than random sites.

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

TABLE 1. Description of model parameters used to examine nest site selection by four primary cavity excavators (PCEs) in central Washington, USA, 2011–2013.

Possible variables	Parameter	BBWO	HAWO	NOFL	WHWO	Hypothesized reason	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 (perhaps related to travel ease and thus predation)	8, 18
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	. . .	

Notes: An "x" indicates that the given parameter was included in models for that species. The PCE species are: BBWO, Black-backed Woodpecker (*Picoides arcticus*); HAWO, Hairy Woodpecker (*P. villosus*); NOFL Northern Flicker (*Colaptes auratus*); and WHWO, White-headed Woodpecker (*P. albolarvatus*). 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. An ellipsis indicates a lack of research on nest site selection; thus we included all possible parameters and did not attempt to provide a hypothesized reason. Sources are: 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, Matsuoka 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. 2010; 18, Hollenbeck et al. 2011; 19, Nappi and Drapeau 2011; 20, Straus et al. 2011; 21, Cooke and Hannon 2012; and 22, Kozma and Kroll 2012. See Appendix B for sources used to create this table and Appendix C for the set of final models.

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 as 315–45°, east as 46–115°, south as 116–205°, and west as 206–295°. 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 the 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

TABLE 2. Description of snag decay classes by Thomas, Cline, and Bull used to categorize snags in central Washington, USA, 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 has lost some bark, branches, and often a portion of the top
3	Snag missing bark, most of the branches, and has a broken top

Note: Data sources for each system are: Bull (Bull et al. 1997), Cline (Cline et al. 1980), and Thomas (Thomas et al. 1979).

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 the percentage of bark, branches, needles, limbs, and top remaining on the snag, percentage of 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" were nest sites and the "controls" were 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 the Akaike weights (w_i) for all models containing each variable, and for variables with equal representation across models

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, USA, 2011–2013.

Species	n	Sill hardness (N·m)		Cavity body hardness (N·m)	
		Mean	Range	Mean	Range
American Three-toed Woodpecker	9	5.7[cd]	0.6–13.8	2.5[a]	0.6–6.6
Black-backed Woodpecker	39	5.2[c]	0.0–11.9	1.7[a]	0.0–6.2
Hairy Woodpecker	60	3.8[ab]	0.0–9.8	1.8[a]	0.0–5.0
Northern Flicker	55	2.5[a]	0.0–9.6	1.1[a]	0.0–4.7
White-headed Woodpecker	75	2.8[a]	0.0–14.5	1.7[a]	0.0–5.1
Williamson's Sapsucker	21	4.2[bc]	0.1–16.6	1.6[a]	0.3–4.9
Random trees	259	6.6[d]	0.0–26.1	9.0[b]	0.0–27.6

Notes: The PCE species are: American Three-toed Woodpecker (*Picoides dorsalis*), Black-backed Woodpecker (*P. arcticus*), Hairy Woodpecker (*P. villosus*), Northern Flicker (*Colaptes auratus*), White-headed Woodpecker (*P. albolarvatus*), and Williamson's Sapsucker (*Sphyrapicus thyroideus*). Superscript letters indicate results of post hoc multiple comparison tests, and means with the same letter do not differ.

(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 (Hosmer 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^2 values 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 ~9 cm deep, at which point hardness leveled off (Fig. 2). Nest sites also increased in hardness beginning approximately 10 cm deep (Fig. 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
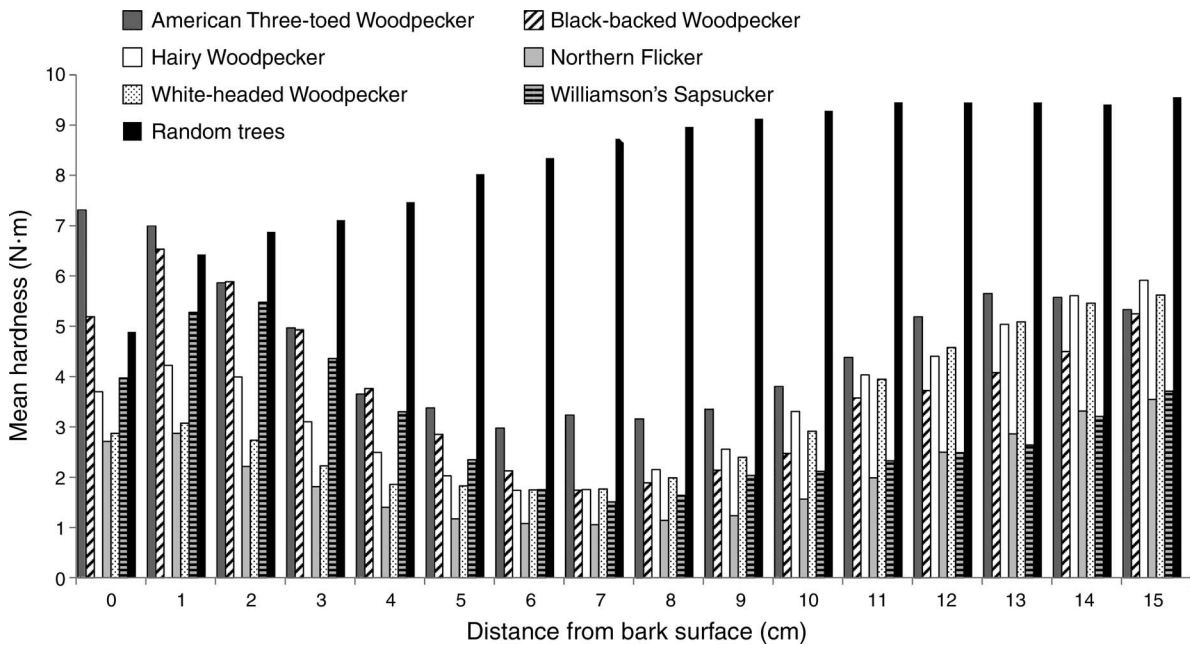
Fig. 2. Mean hardness at nests for six species of woodpecker compared to random sites in central Washington, USA, from 2011 to 2013. See Table 3 notes for full species names.

hardness did not differ within random trees by height ($F_{2,43} = 0.09$, $P = 0.9168$).

PCE nest site availability

Among 360 nonuse snags measured in White-headed and Black-backed Woodpecker territories, we classified 86% and 96% as unsuitable for nesting by these species, respectively (Fig. 3). For both species, the majority of nonuse snags (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
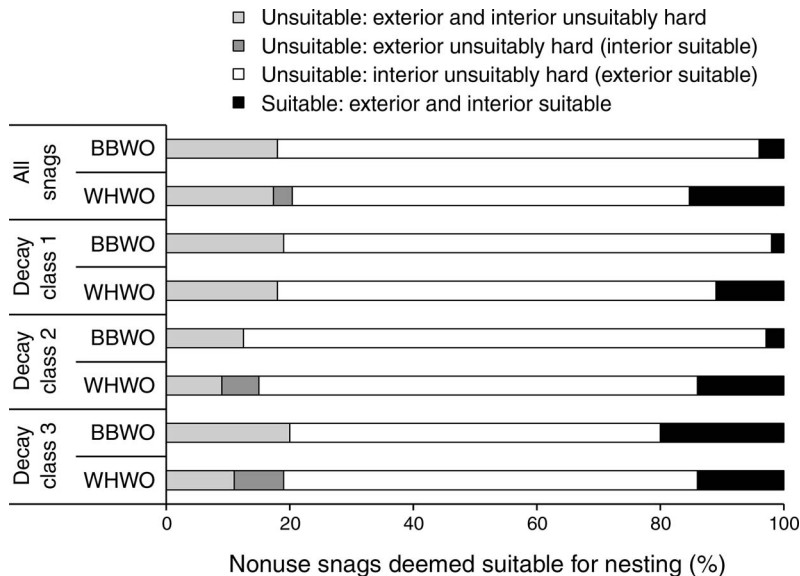

Fig. 3. Percentage of 360 nonuse snags in Black-backed Woodpecker (BBWO) and White-headed Woodpecker (WHWO) nesting territories that were deemed suitable for nesting based on wood hardness in central Washington, USA, 2011–2013. We considered all snags together, and then the percentages in each of three decay classes of Bull et al. (1997). See Table 2 for descriptions of the decay classes.

TABLE 4. Support for models in 90% confidence set explaining multi-scale nest site selection by four species of PCE in central Washington, USA, 2011–2013.

Species and 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

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

highest proportion of suitable wood was decay class 3 of Bull's system, in which 14–20% of sites were suitable for White-headed and Black-backed Woodpeckers, respectively (Fig. 3). However, when considering average wood hardness for used vs. 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 wood 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 therefore 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 pairwise comparisons (Fig. 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

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, USA, 2011–2013.

Species and 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 east	0.258	0.293	0.833	−0.317	0.53
Orientation north	−0.325	0.392	0.444	−1.095	0.53
Orientation south	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

decay classes. For example, the softest and hardest samples were both from snags in decay class 3 of Bull's system.

We found that the 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 variation 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 2004, 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 postfire) for nesting, which almost certainly lacked appreciable numbers of preburn 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 because 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, Wilkins and Ritchison 1999), 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
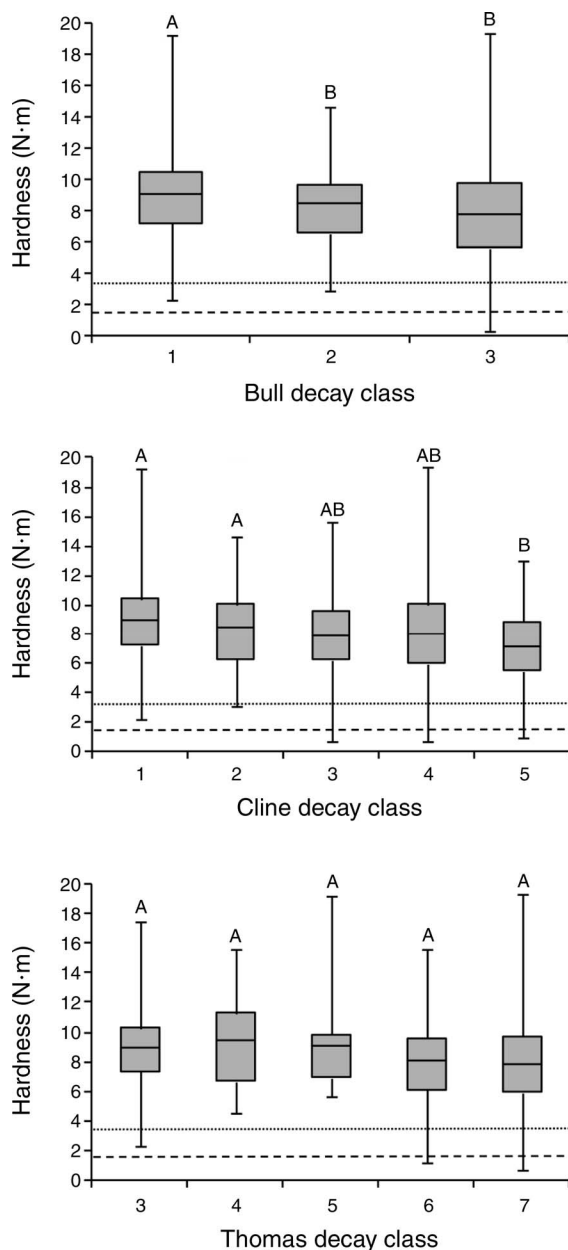

Fig. 4. Variation in wood hardness by snag decay class for 559 random snags in central Washington, USA, 2011–2103, classified by the decay class systems of Bull (top), Cline (center), and Thomas (bottom). See Table 2 for descriptions of the decay classes. Dashed and dotted lines on plots indicate mean 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.

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 trade-offs when selecting nest sites, because sites that are easy to excavate could be riskier in terms of nest predation (Kilham 1983, Tozer et al. 2009) and

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, USA, 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
Percentage of blackened bark	−0.003	0.004	−0.84	0.402
Percentage of top missing	−0.009	0.006	−1.58	0.114
Percentage of bark missing	0.011	0.007	1.60	0.110
Percentage of branches missing	−0.004	0.005	−0.71	0.476

more exposed to climate variability. We suggest that future studies examine some of these trade-offs, 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 trade-offs 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 had harder sill wood than 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 (see Plate 1) may be more limited than White-headed Woodpeckers for nest sites, possibly 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, USA, Raphael and White (1984) reported that Black-backed Woodpeckers nested in trees with an 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 are promoted for nests sites of the declining White-headed Woodpecker based on research from Oregon, USA (Wightman et al. 2010), while we found them selecting trees as small as 16 cm dbh. Since internal wood softening is likely 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.

PLATE 1.   A female Black-backed Woodpecker (*Picoides arcticus*) at a nest excavated in a small diameter (22 cm), live ponderosa pine (*Pinus ponderosa*) in central Washington, USA, 2013. While large diameter snags have been promoted for this species in some studies, we found them nesting in both live and dead trees, and across a range of tree diameters (21–86 cm). Despite this variation, woodpeckers consistently selected sites with softened interior wood. Photo credit: T. J. Lorenz.

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 USA, 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 USA, 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 in coniferous forests is particularly needed because 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*) (e.g., 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 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, because 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, Strukelj 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 should be provided for PCEs than generally recommended, because past research studies likely overestimated the abundance of suitable nest sites and underestimated the number of snags required to sustain PCE populations. 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, USA, and found no avian nest cavities eight to nine years later. Likewise, for 883 and 1111 snags created by tree-topping in western Oregon, USA, 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 "nonideal" 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 nonideal 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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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-1042.1.sm