

NEST-SITE SELECTION AND NEST SURVIVAL OF TWO WOODPECKER  
SPECIES IN PONDEROSA-PINE DOMINATED FORESTS

by

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## ABSTRACT

Management of woodpecker populations requires knowledge of nesting habitat and vital rates in different forest conditions. We examined nest-site selection and nest survival for two woodpeckers, northern flicker (*Colaptes auratus*) and hairy woodpecker (*Picoides villosus*) at three locations in ponderosa-pine forests of the interior Columbia River Basin. Our goals were to: (1) characterize the range of habitat conditions available to nesting woodpeckers in our study area; (2) determine which habitat features best discriminated between nest and non-nest plots, and (3) establish which habitat features most influenced daily nest survival. Northern flickers and hairy woodpeckers were more likely to choose snags than live trees. Both species used larger diameter snags than those available at random. Nest snags tended to be in plots that had higher snag densities and lower live tree densities. For northern flickers, a model of constant daily survival received more support than any model containing habitat covariates. Daily nest survival from the best model for northern flickers was estimated to be 0.55 (95% CI: 0.46-0.64). Increasing live tree density and coarse woody debris volume were included in the most well supported model for hairy woodpeckers. Results from this study did not provide support for the "nest-quality" hypothesis. Nest survival for woodpeckers in this study was low, especially at the Idaho location; we hypothesize that this could be because of differences in predator abundance among the three locations. In ponderosa pine forests that have not been recently disturbed, we recommend maintaining clumps of snags, especially those that contain large snags. Further research is needed to understand the mechanisms that dictate woodpecker nest survival in ponderosa pine forests.

## INTRODUCTION

Woodpeckers (family Picidae) have unique ecological roles in forested ecosystems (Virkkala 2006). The niche of woodpeckers is defined by their use of rare forest features such as snags for nesting and roosting and downed wood for foraging. The exploitation of these forest features by woodpeckers creates habitat for other cavity-nesting species and a variety of other vertebrates (Aubry and Raley 2002a, Martin et al. 2004). Because of their important roles in forests, several woodpeckers are designated as indicator species, or considered species at-risk by state and federal agencies. Maintaining populations of woodpeckers requires explicit knowledge of their nesting habitat requirements as well as knowledge of key demographic rates such as nest survival and fledging rate. Information regarding habitat use is available for many woodpecker species in a variety of habitats; however, few studies have included estimates of nest survival as well as quantification of habitat selection. The recent development of analytical tools that allow for habitat covariates to be modeled with daily nest survival provide for more meaningful comparisons of habitat use and reproductive outcome. To link changes in fitness to habitat selection, nest survival and nest-site selection should be measured concurrently (Clark and Shutler 1999). To begin, we place nest survival in the context of other important life-history considerations.

Nest survival is an important part of overall reproduction for birds, though it does not solely describe this demographic rate. Furthermore, reproductive rate is only one of several components that determine population dynamics. Change in population size in its simplest form can be described by the equation:

$$N(t+1) = N(t) + B(t) + I(t) - D(t) - E(t) ,$$

which represents change in population size as a result of: birth rate, immigration rate, death rate, and emigration rate (Williams et al. 2002). Nest survival can be considered an important part of the birth rate for birds, but clutch and brood size, seasonal fecundity, and juvenile survival are parts of "birth rate" as well. Demographic rates for birds are available to differing degrees. Below, we consider information on these rates for the two woodpecker species of interest, northern flicker (*Colaptes auratus*) and hairy woodpecker (*Picoides villosus*).

Rates relating to reproduction are more readily available for most bird species, including woodpeckers. Clutch sizes for northern flicker ( $\bar{X} = 6.5$ ; range = 3-12 eggs, n=411; (Moore and Koenig 1986)) and hairy woodpecker ( $\bar{X} = 4.09$ ; range = 3-7 eggs, n=461; (McNair 1987)) have been well established, yet there is evidence of latitudinal and seasonal variation in clutch size (Moore 1995, Jackson et al. 2002). Little information exists for brood sizes, but they are probably approximately one less than the clutch size (Moore 1995, Jackson et al. 2002). Both species are likely single brooded though re-nesting may occur upon failure of the nest (Moore 1995, Jackson et al. 2002). Juvenile survival is known for a handful of North American woodpeckers (Koenig and Mumme 1987, DeLotelle and Epting 1992, Stacey and Taper 1992) and some European species (Virkkala et al. 1993); reported values of this rate varied from 0.35 to 0.78. Adult survival rates for woodpeckers are available for just over half of the North American species, and just less than a third of European species; average adult survival rate is 0.58 with a range from 0.30 to 0.93 for these studies (Wiebe 2006). Information on

immigration and emigration rates is virtually non-existent for woodpeckers. Nest survival, fledgling rate, and other similar metrics are more prevalent in the literature although these rates are not necessarily directly comparable. A literature review of North American cavity-nesting birds revealed that "woodpeckers have the highest mean rate of [nest] success (77%)" as compared to other cavity-nesting birds (Johnson and Kermott 1994). It should be noted though, that nest survival estimates that simply reflect the number of successful nests out of the total number of nests found produce nest survival estimates that may be biased high (Mayfield 1961). The demographic parameters mentioned above likely differ depending on the habitat considered and/or the geographic area considered..

We investigated nest survival for the two common woodpecker species in our study. We chose this demographic rate because it is relatively easy to obtain for a large number of nests (> 100). Estimates of adult and juvenile survival, immigration, and emigration are difficult to obtain for woodpeckers because adults are difficult to capture (especially when nests are placed high in trees) and re-sighting rates for woodpeckers can be low between years (V. Saab, pers. comm.). Individual members of a population may not choose habitat in the breeding season solely for the purpose of successfully fledging young. Tradeoffs will exist between adult survival, nest survival, and survival of post-fledging juveniles during the breeding season. The quality of habitat for over-winter survival may also be a consideration in nest-site selection.

Long-term evolutionary pressure informs habitat selection, and species are constrained largely by this evolutionary history; however, behavioral plasticity allows for

some degree of variation in selection of habitat (see Hansen 1992). Several facts complicate the relationships that may be drawn between habitat and demographic rates. Demographic rates can vary with habitat features (Dufour and Clark 2002, Ward et al. 2004). For example, exposure of foraging adults to predators may be expected to vary with habitat (Ostrand et al. 1996, Elchuk and Wiebe 2002). Habitat can also influence reproductive output through differential availability/quality of food and the availability of "safe" nest sites (Gates and Gysel 1978, White 1996). Habitat selection probably varies throughout the annual cycle, further complicating the relationship between habitat selection and demographic rates. Habitat selection can differ seasonally (i.e. in the breeding vs. over-wintering period) and may reflect tradeoffs between maximized adult and juvenile survival, over-winter survival of these age-classes, and maximal reproduction. Implicit in any study of habitat selection is the assumption that individuals in a population can evaluate the "quality" of the habitat; this assumption may not always be tenable (Delibes et al. 2001). Habitat selection may also be limited by access to very specific habitat features, such as cavities for secondary cavity-nesting birds (Newton 1994). Finally, habitat selection can be considered a hierarchical process (Hutto 1985), and the ability to tease apart the variation in habitat selection attributable to a specific scale may not always be possible (Battin and Lawler 2006). Habitat selection is a complex process that probably involves choices by organisms at a variety of spatial and temporal scales (Orians and Wittenberger 1991) in response to a variety of competing forces (Cody 1981). Though woodpeckers may choose nesting habitat in an attempt to



maximize reproductive output, this choice clearly must involve tradeoffs with other demographic parameters such as adult and juvenile survival.

Woodpeckers in North America are predominantly insectivorous (with the exception of the most frugivorous group, *Melanerpes*, and the sapsucking *Sphyrapicus* group). The two species that we consider in this study, northern flicker and hairy woodpecker, typically forage for ants and bark-dwelling (Scolytidae) or wood-boring (Cerambycidae and Buprestidae) beetles, respectively. Because woodpeckers behave as central-place foragers during the breeding season, nest-site selection could reflect selection for areas with a more abundant or higher quality food (Green and Anthony 1989). Conversely, feeding adults may instead adjust the amount of time and distance traveled to foraging sites depending upon perceived threats to the nest (Martindale 1982). Selection of nesting habitat could potentially reflect food availability in the post-fledging stage (Poysa et al. 2000). The amount of time spent by woodpeckers feeding newly fledged young varies, and for the two species we considered, this time period ranges from 22 days for northern flicker (Moore 1995) to at least 3-4 weeks for hairy woodpecker (Jackson et al. 2002).

Habitat usage varies temporally for many vertebrate species; especially iteroparous vertebrates such as birds. Northern flickers (red-shafted subspecies; *C. a. cafer*) are somewhat migratory, especially those individuals in northern populations (Moore 1995). Hairy woodpeckers are considered primarily non-migratory, though movements of up to 160 km from banding stations have been noted (Jackson et al. 2002). If hairy woodpeckers remain resident in an area throughout the winter, then nest-site

selection by hairy woodpeckers could reflect winter (non-breeding) habitat requirements in addition to breeding season requirements.

In addition to the caveats presented above, selection of nest-sites may be dictated by a variety of factors including microclimate of the nest cavity, avoidance of features associated with potential nest predators, availability of cover near the nest, and other factors (Short 1979, Hooge et al. 1999, Aitken et al. 2002). Despite other selection pressures, predation is likely the most important influence on the evolution of nest-site selection in primary cavity-nesting birds (Martin and Clobert 1996, Brightsmith 2005). Several aspects of nest-site selection may reflect predator avoidance. Woodpeckers often select cavity trees that are moderately to heavily decayed and have larger diameters than those available at random (Raphael and White 1984, Dobkin et al. 1995, Saab and Dudley 1998). This choice could represent a tradeoff between decayed trees that are easily excavated by woodpeckers, and trees so heavily decayed that they are vulnerable to windthrow and destruction by nest predators (e.g., corvids). When pre-existing cavities are used, nests of greater heights may be favored (Hooge et al. 1999, Saab et al. 2004). Higher nests may experience a reduced risk of nest predation (Albano 1992). Nesting sites are often characterized by higher snag and tree densities than random plots (Li and Martin 1991, Saab et al. 2002). Avoidance of areas with large amounts of downed wood could reduce risk of nest predation by small to mid-sized mammals because these predators often occur in areas with higher density of downed woody debris (Ream 1981, Smith and Maguire 2004).

Recent information on nest-site selection and nest survival of cavity-nesting birds in northwestern North America comes mainly from recently burned forests (Saab et al. 2004, Saab et al. 2007), forests dominated by aspen (Dobkin et al. 1995, Aitken et al. 2002), or mesic-westslope forests (Aubry and Raley 2002a, Blewett and Marzluff 2005). Ponderosa pine is one of the mostly widely distributed tree species in western North America and is very important to cavity-nesting birds because of the relatively thick sapwood (Bull et al. 1997). Disturbance regimes in ponderosa-pine dominated forests prior to European settlement varied greatly depending on local topography and moisture gradients (Arno et al. 1995, Schoennagel et al. 2004). Current forest structure likely differs from historic structure with regard to age-distribution within and among stands (Cooper 1960), presence of forest openings, size classes of trees present (Kaufman et al. 2000), presence of shade-tolerant species in the understory (Keane et al. 2002), and abundance of coarse woody debris (Agee 2002). These changes in forest structure may have implications for nest-site selection, nest survival, and the relationship between the two in contemporary ponderosa-pine dominated forests. Given the widespread distribution of ponderosa pine and anthropogenic changes to disturbance regimes in lower elevation coniferous forests (see Keane et al. 2002), information is needed to understand how alterations of ponderosa pine forests may have affected habitat selection and reproductive success of cavity-nesting birds.

Selection of nesting habitat has been demonstrated for woodpeckers at a variety of spatial scales (Schreiber and deCalesta 1992, Dobkin et al. 1995, Saab et al. 2002, Giese and Cuthbert 2003, Knutson 2004, Russell et al. 2007). Most selection has been reported

at the scale of the nest tree or immediately surrounding habitat (Raphael and White 1984, Li and Martin 1991). Instances in which several scales have been addressed simultaneously are rare, but recent work in burned ponderosa-pine forests points to fine scale habitat features (0.04 ha) as more important than coarse scale (>0.09 ha - 300 ha) features with regard to nest-site selection (Russell et al. 2007). In another study, presence of cavity-nesting birds was best explained by local scale (100 m radius) features compared to habitat features at larger spatial scales (Warren et al. 2005).

Despite the other life-history requirements that may guide nest-site selection (Hooge et al. 1999), we focused our investigation on habitat features measured at the scale of the nest tree and surrounding habitat. We assumed that avoidance of nest predation was likely the most important force guiding nest-site selection in these primary cavity-nesting birds (Martin and Clobert 1996, Brightsmith 2005). Several aspects of nest-site selection may reflect predator avoidance. Woodpeckers often select cavity trees that are moderately to heavily decayed and have larger diameters than those available at random (Raphael and White 1984, Dobkin et al. 1995, Saab and Dudley 1998). This choice could represent a tradeoff between decayed trees that are easily excavated by woodpeckers, and trees so heavily decayed that they are vulnerable to windthrow and destruction by nest predators (e.g., corvids). We predicted that nesting woodpeckers would choose snags over live trees with decay and that snags used would be of larger diameter than those available at random (which would likely prevent predators from easily accessing the nest cavity). When pre-existing cavities are used, nests of greater heights are typically favored (Hooge et al. 1999, Saab et al. 2004) though little

information exists for a height preference when nests are newly constructed. Nests that are higher may experience reduced risk of nest predation (Albano 1992). We predicted that nests that were higher would confer higher nest survival. Nesting sites are often characterized by higher snag and tree densities than random plots (Li and Martin 1991, Saab et al. 2002) We predicted that these two species would choose plots with higher snag densities, but that they would avoid areas with high tree density which may harbor arboreal small mammals such as red squirrels (*Tamiasciurus hudsonicus*). Avoidance of areas with large amounts of downed wood could also reduce the risk of nest predation by small to mid-sized mammals because these predators often occur in areas with higher density of downed woody debris (Ream 1981, Smith and Maguire 2004). We predicted that both species would avoid areas with higher volumes of coarse woody debris.

In addition to predictions about habitat selection, we formed predictions about the general relationship between nest-site selection and nest survival. Several theoretical relationships have been suggested to explain observed relationships between these two phenomena. Under the "nest-quality" hypothesis we would expect the same habitat covariates that explain the variation in nest-site selection to also explain the variation in nest survival; individuals should choose habitats that confer the highest survival (Martin 1998). Hypotheses for other possible relationships between nest-site selection and nest survival are: the "nest-concealment" hypothesis (nests that are more concealed are less likely to be depredated), the "needle in a haystack" hypothesis (nests placed in places in common substrates are less likely to be depredated because of the large number of potential nest locations a predator must search), and the "rare site" hypothesis which

predicts that nests in uncommon places will evade predation because predators will not expend time searching uncommon nest sites (Filliater et al. 1994).

One other hypothetical relationship is termed the “ecological trap”, and probably poses the worst alternative for populations. According to the “ecological trap” hypothesis, individuals may choose nest sites according to long-term evolutionary pressures which are decoupled from current constraints on successful nesting (such as recent changes in predator communities; Donovan and Thompson 2001, Battin 2004). We predicted that these two woodpeckers would choose nest sites that conformed to the “nest-quality” hypothesis, that is, that the same habitat features that best explained the variation in nest sites, would also best explain the variation in nest survival.

In this study we examine nest-site selection and nest survival of northern flickers and hairy woodpeckers in ponderosa pine forests at three locations within the interior Columbia River Basin. Our objectives were to determine the availability of nesting habitat within our study locations, evaluate nest-site selection, estimate nest survival, and finally to examine our prediction that woodpeckers should choose nest sites that confer the highest nest survival. Information from this study can be used to develop standards and guidelines for managing woodpecker habitats in low- to mid-elevation ponderosa pine forests of the interior Columbia River Basin. This study will also help to identify potential differences in vital rates among similar habitats using two species that represent an important forest guild.

## METHODS

### Study Area and Sampling Units

We used study locations and sampling units from a larger parent study, the Birds and Burns Network (<http://www.rmrs.nau.edu/lab/4251/birdsnburns>), the goal of which is to “understand the ecological trade-offs of different fire conditions for wildlife”. We selected three study locations (Washington, Idaho, and Oregon) on National Forest and Nature Conservancy land in the interior Columbia River basin (Figure 1) that were a subset of the larger parent study. Data collected for this study were prior to any prescribed fire treatments implemented for the Birds and Burns Network.

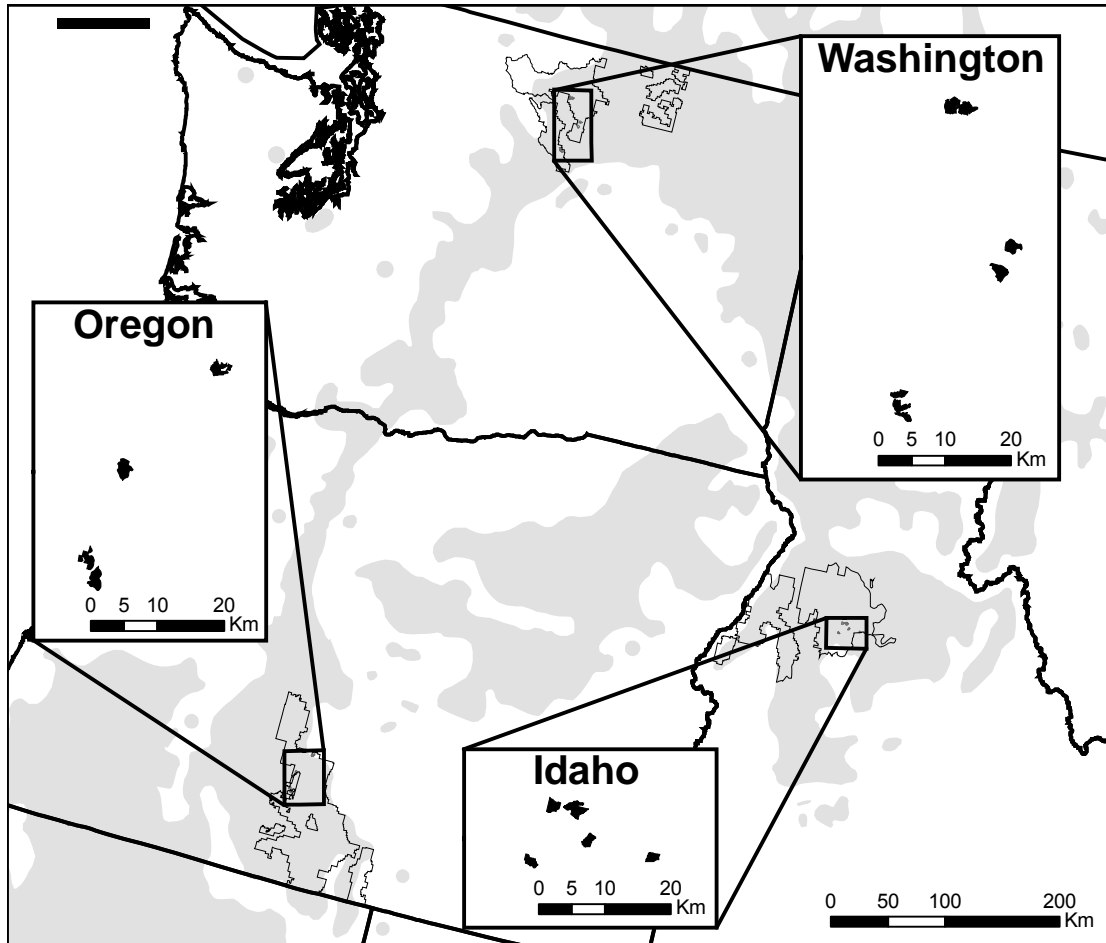
Participation in the study was limited to lands proposed by managers for “forest restoration” (i.e., prescribed fire and/or mechanical thinning operations), where NEPA (National Environmental Policy Act) requirements were complete or near completion for those treatments. Once participants were selected, polygons representing areas in need of forest restoration were selected using maps of vegetation cover types and GIS. These criteria were coupled with the need to feasibly survey areas daily on foot (with initial daily access being facilitated by roads and/or trails). From among the geographic areas meeting all these criteria we then selected paired sampling units (*unit-pairs*) that were approximately 500 ha in extent, each pair consisting of two *units* (approximately 250 ha in size). *Units* were selected based on similarities in topography, elevation, and vegetation characteristics. Our sampling frame was constrained by the requirements of the larger parent study and is not necessarily representative of all ponderosa-pine forests

in the interior Columbia River Basin. Our ability to draw inference is limited to the areas represented by the *Units* selected as part of the larger parent study. We controlled for some potential confounding effects that may have been introduced because of geographic location by including interactions terms for study *location* and/or *unit-pair* or by using stratification in our logistic regression models (see Statistical Methods below).

Study *locations* (hereafter referred to by state name: Washington, Idaho, and Oregon) were approximately 15 km<sup>2</sup> and located in the Okanogan National Forest, Okanogan County, Washington (48° 20' N, 120° 5' W), the Payette National Forest, Cascade County, Idaho (44° 58' N, 115° 39' W), and the Fremont National Forest and The Nature Conservancy-Sycan Marsh Property, Lake County, Oregon (42° 53' N, 121° 7' W, Figure 1). Elevations at the three locations ranged from 500-2100 meters. Topography in the Washington and Idaho locations consisted of steep slopes and incised drainages, while the Oregon location was relatively flat. Within the breeding season (May-Aug) minimum monthly average temperatures ranged from 4.6° C to 8.22° C, maximum monthly temperatures ranged from 22.8° C to 27.0° C, and average monthly precipitation during the breeding season ranged from 2.7 to 5.6 mm (USDC NOAA 2006).



Figure 1. Study locations used to compare nest-site selection and nest survival of two woodpecker species in dry mixed-conifer forests. Locations were selected based on the dominance of ponderosa pine in the overstory (range shown in gray) and prescribed fire opportunities. Sampling units within each location (4-6 per location) are in black. Sampling units were selected based on similarities in topography, elevation, and vegetation.



The study *locations* were dominated by ponderosa pine but contained a variety of tree species, including Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), limber pine (*Pinus flexilis*), grand fir (*A. grandis*), western larch (*Larix occidentalis*), and quaking aspen (*Populus tremuloides*). Dominant understory plant species included bluebunch wheatgrass (*Pseudoroegneria spicata*), pine grass (*Calamagrostis rubescens*), spirea (*Spirea spp.*), arctostaphylos (*Arctostaphylos spp.*), bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos spp.*), rose (*Rosa spp.*), ceanothus (*Ceanothus spp.*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and mountain mahogany (*Cercocarpus montanus*).

Past management activities varied among the three forest locations (USDA 1989a, USDA 1989b, USDA 2004). USDA Forest Service Forest Inventory and Analysis (USDA 2005) data based on 2004 surveys report higher basal area of live trees at Washington and Oregon locations than Idaho, the highest basal area of snags at the Washington location, and the highest gross biomass at the Oregon location. These data are consistent with the past management activities described for the three *locations*. Timber harvest and grazing pressure were higher historically in Oregon and Washington locations due to their increased accessibility and proximity to local economies as compared to the Idaho location. The remoteness and rugged terrain in the Idaho location is probably responsible for the larger trees diameters and lower live tree densities found there (Saab et al. 2006).

## Nest-Searching and Monitoring

### Nest Searching

We searched for nests of all primary-cavity nesting species from late April to late June in four breeding seasons (2002-2005), using methods by Dudley and Saab (2003). Units in Washington were not sampled during 2004 due to implementation of a prescribed-fire treatment on half of the units and in Oregon in 2005 due to budgetary constraints. The starting date for surveys varied slightly by location because commencement of nesting varies with latitude and elevation. Each unit was surveyed for nesting woodpeckers using 200-m-wide belt transects oriented on cardinal directions. Transects and observers were randomized to prevent bias in the detection of nests. Surveying was not conducted during periods of inclement weather.

We located nests using search images, behavioral cues, and by revisiting previously used nests. Our search effort was concentrated on snags and decayed portions of live trees because these are habitat features used for nesting. Behavioral cues (e.g., excavation, courtship, copulation, nest guarding, carrying food, carrying fecal sacs away from nest) were also used to identify nest locations and to determine the status of the nest (Martin and Guepel 1993). Locations of active nests were recorded for future visitation. A nest was considered active if at least one egg or nestling was viewed within the nest cavity or if parental behavior indicated that incubation or brooding had commenced.

### Nest Monitoring

Nests were revisited approximately every 3-4 days and the date, time of day, stage of the nest, behavioral observations of adults and young, and contents (if viewed with camera) of the nests were recorded. We attempted to view the contents of nests that were less than approximately 13 meters in height and did not have any obstructions with a camera mounted on a telescoping pole (Tree Top Peeper II; Sandpiper Technologies, Inc.). We viewed the contents of the nest using the camera at least once during the incubation stage and again during the nestling stage. We avoided viewing the nest with the camera when nestlings were close to fledging. Scheduled nest viewings were sometimes interrupted by inclement weather and logistics. When nest age could be determined, we estimated the fledging date, and visited nests within two days of that date.

Nests for which at least one fledgling left the cavity were considered successful. We confirmed nest success by noting the absence of nestlings in the cavity given that no signs of predation were evident and that sufficient time in the nestling stage had passed for fledging to occur as indicated by nestling development (Dudley and Saab 2003). Viewing or hearing fledglings in the immediate vicinity of the cavity tree established nest success. Nest failure was confirmed by obvious abandonment of eggs (i.e., multiple nest visits without any activity), obvious signs of predation (e.g., changes in the shape of the cavity, claw marks, presence of nest predator in cavity), broken eggs or dead nestlings in or near the cavity, and large numbers of insects in the cavity (e.g., ants). Nests for which fate could not be determined reliably were not included in analyses. Only two nests were excluded from the analysis for this reason, therefore, we did not feel that a bias had been

introduced by excluding fledged or failed nests in unequal amounts. Nests that fledged or failed on the day of the first visit were not included because an interval of observation could not be determined.

### Measurement of the Number of Young Fledged

We attempted to view every nest at some point during the nestling stage to estimate the brood size. We assumed that the number of nestlings viewed during the last visit prior to fledging represented the number of fledglings unless obvious signs of nestling removal were observed (e.g., dead nestling found on ground). For nests that could not be viewed with the camera, but for which fledging was confirmed by timing and or adult/young behavior at the cavity entrance, we assumed that the number of fledglings was at least one. Other clues were used to determine the number of nestlings (e.g., > 1 nestling seen at cavity entrance).

### Habitat Measurements

#### Habitat Scales

We measured habitat covariates at four spatial scales: the nest-cavity, the nest-tree, the microhabitat surrounding the nest tree, and landscape surrounding the nest tree (Figure 2). We measured habitat variables at random locations at these same scales with the exception of the nest-cavity scale (random plots were not necessarily centered on a tree or snag containing a cavity). For our purposes, microhabitat was defined as an area approximately 0.4 ha in size surrounding the nest tree. Microhabitat features were

measured using a plot that consisted of four 50-m transects radiating out from the plot center; these transects were oriented along each of the four cardinal directions (Figure 3). We determined from pilot work that rectangular plots of varying width centered on these transects were most appropriate for the detection of rare forest features such as snags (Bate et al. 1999). The width of the plot used for each habitat component was based on the abundance of that feature (features that were rarer on the landscape required plots that were wider; see Bate et al. 1999). The landscape scale was defined to be a circle around the nest-site with a 1-km radius (a circle of with area = 314 ha). We chose this area to represent landscape-level effects because it was sufficient to cover the described home range of both northern flickers and hairy woodpeckers (Royall and Bray 1980, Jackson et al. 2002, Covert 2003, Elchuk and Wiebe 2003). Different habitat variables were measured at the various habitat scales. Habitat covariates that were highly correlated ( $|r| > 0.70$ ) were not included in the same model.

#### Habitat Covariates and Measurement Techniques

We measured habitat features based on their hypothesized importance to both nest-site selection and nest survival (Table 1). For the nest-cavity scale, we included the height of the cavity (NESTHT) in nest survival models. This covariate was not included in nest-site selection models because non-nest random trees/snags did not necessarily contain cavities. For the nest-tree scale, we used a covariate that coded for the condition of the nesting substrate (SUBSTRATE). The SUBSTRATE covariate indicated whether the substrate was a snag or a live tree. Microhabitat scale covariates that were included in this analysis were: live tree density (TREEDEN; for live trees  $\geq 23$  cm DBH), snag

Figure 2. Habitat scales measured at nest sites and non-nest random sites. The scales measured, listed from the broadest to the finest scale, were: the landscape scale (1-km radius circle), the microhabitat scale (a cross-plot approximately 0.4 ha in size; see Figure 3 for more detail), the nest tree or snag (bottom right inset), and the nest-cavity (not measured at non-nest random sites; upper right inset).

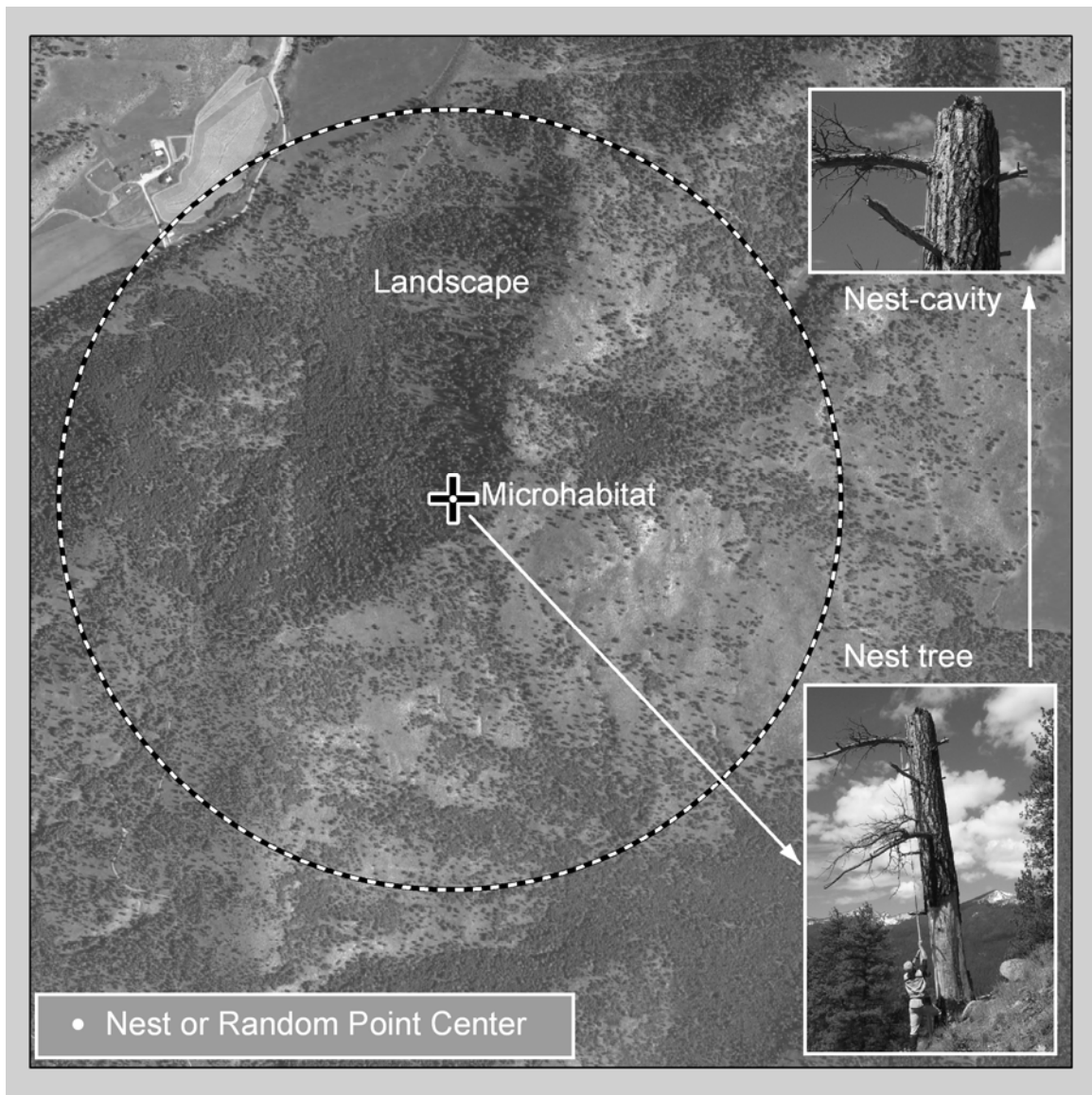


Figure 3. Plot configuration used to sample vegetation at nest and non-nest plots in ponderosa pine dominated forests. Plots are centered on a nest snag or random tree (dark circle). Each arm of the plot measures 50-m and arms are oriented at cardinal directions. East and west plot arms are offset from the center by 10-m to prevent double sampling immediately around the plot center. Total area of plot is approximately 0.4 ha (for snags).

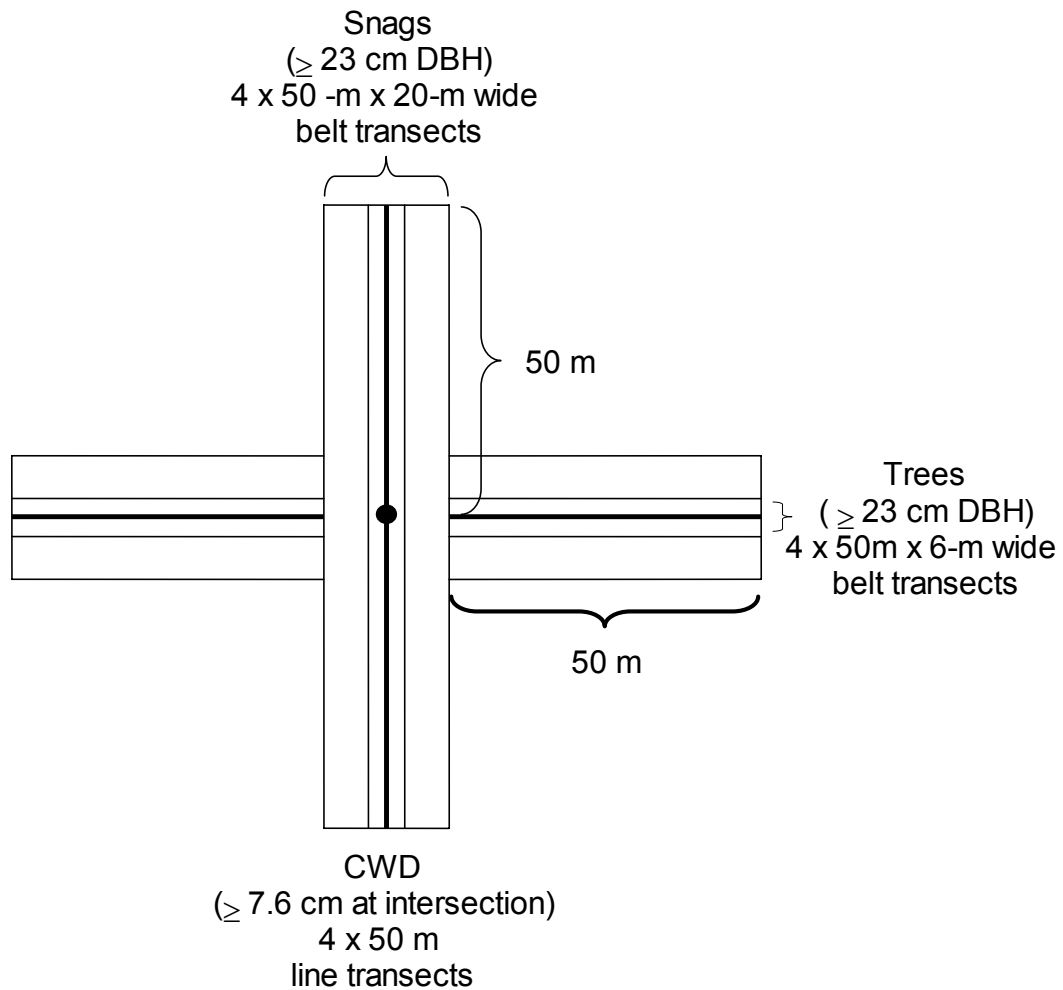




Table 1. Habitat variables used in nest-site selection and/or nest survival modeling efforts. Habitat scale is indicated in the column at left. Covariate names are indicated in parentheses.

Habitat Scale	Variable Measured	Used in Nest-site Selection Models	Used in Nest Survival Models
Nest-cavity	Cavity Height	No	Yes (NESTHT)
Nest tree or snag	Substrate (Snag or Tree)	Yes (SUBSTRATE)	Yes (SUBSTRATE)
	DBH	Yes (DBH)	Yes (DBH)
Microhabitat	Large Diameter ( $\geq 23$ cm DBH) Tree or Snag Count	Yes, densities calculated from counts for trees (TREEDEN) and snags (SNAGDEN)	Yes, densities calculated from counts for trees (TREEDEN) and snags (SNAGDEN)
	Coarse woody debris volume	Yes (CWDVOL)	Yes (CWDVOL)
Landscape	Proportion of high canopy closure	Yes (PROPHIGH)	Yes (PROPHIGH)

density (SNAGDEN; for snags  $\geq 23$  cm DBH), and coarse woody debris volume (CWDVOL; for all downed wood  $\geq 7.6$  cm at the point of intersection with a transect line). At the landscape scale we measured a single habitat feature, the proportion of high ( $\geq 70$  %) canopy closure within the 1-km radius landscape circle (PROPHIGH).

At the microhabitat scale, we measured features of all trees and snags  $\geq 23$  cm DBH, and all downed coarse woody debris  $\geq 7.6$  cm intersect diameter. We measured the height, species, and the decay class of all snags and trees. Heights were measured to the nearest half-meter using a clinometer. We calculated snag (SNAGDEN) and live tree (TREEDEN) densities for analysis by dividing the total number counted by the appropriate area (Figure 3). We measured the intersect diameter ( $d_i$ ) of all coarse woody debris ( $\geq 7.6$  cm intersect diameter) that intersected the four 50-m transects (Figure 3).

Intersect diameter is measured at the point of intersection with a line at an angle

perpendicular to the debris (as DBH would be measured on a standing tree or snag). We calculated the volume of coarse woody debris (CWDVOL) for each plot using an adaptation of equation 1 in DeVries (1974, p.129)

$$\text{Volume (m}^3/\text{ ha)} = \left( \frac{\pi^2}{8L} \right) \sum n d_i^2$$

where L = length of transect (m) and  $d_i$  = diameter (cm) of log<sub>*i*</sub> at the point of intersection.

We derived a single landscape covariate using a GIS and 2-meter resolution color aerial photographs. We used a heads-up digitizing procedure to derive the proportion of high canopy closure ( $\geq 70\%$  closure) within a 1-km radius buffer around each nest and non-nest random point (PROPHIGH). Canopy cover was initially classified into ten canopy closure categories broken into increments of 10% (i.e., 1-10%, >10-20%, ..., >90-100%) in addition to one category for < 1% canopy closure. We used the DigitalMylar CoverInterpreter v1.1 extension for ArcGIS to facilitate estimation of canopy closure. We later collapsed these categories into three classes commonly used by the USDA Forest Service (0-40%, >40-70%, and >70% canopy closure). We used a minimum mapping unit of approximately 1-ha because neither species has a reported home range smaller than this size (Royall and Bray 1980, Jackson et al. 2002, Covert 2003, Elchuk and Wiebe 2003). This minimum mapping unit also represented a realistic scale at which to classify each study location.

Twenty non-nest random plots were established in each sampling unit (except for one smaller unit in Idaho, where only ten plots were established) prior to nest searching.

Random plots were established using a GIS and a random point generator. Random points were  $\geq 250$  meters apart to maintain independence of points. In the field, a tree or snag located closest to the randomly generated coordinate was selected as the random plot center. We refer to these random plots as non-nest plots to highlight the fact that they may have been used for other life-history requirements (e.g., foraging or roosting) though they were not used for nesting. We randomly selected a suitable tree or snag ( $\geq 23$  cm DBH and either a snag or a tree with some sign of decay; hence a substrate that could be a suitable nest tree) from each non-nest plot as the random tree for comparison to actual nest trees.

### Statistical Analyses

We compared differences among forest study locations for the main habitat covariates of interest. We report means  $\pm$  one standard deviation (SD), effect sizes (differences between the means and their 95% CI) to compare differences in habitat among the three forest locations. We present effect sizes rather than significance tests because we did not form *a priori* hypotheses for differences among study locations. Because we chose to pool nests and non-nest random plots from three forest study locations, we were interested in potential inherent differences among locations that might affect nest-site selection and nest survival.

### Model Selection and Uncertainty

We used an information theoretic approach to evaluate hypotheses regarding nest-site selection and nest survival for northern flickers and hairy woodpeckers. The relative

support for each model was evaluated using Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002). We considered all models with  $\Delta AIC_c \leq 2$  to have received substantial support, while those with  $\Delta AIC_c$  from 4-7 had received considerably less support (Burnham and Anderson 2002). We report model averaged parameter estimates to account for model selection uncertainty (Burnham and Anderson 2002).

### Nest-Site Selection

We modeled nest-site selection using conditional logistic regression. Conditional logistic regression controls for potentially confounding factors by allowing for stratification on a variable (Agresti 1990). Our cases and controls were matched in an  $N:M$  case-control design where  $N$  represents greater than one case (nest) and  $M$  represents more than one control (non-nest) in a stratum (Hosmer and Lemeshow 2000). We conducted conditional logistic regression using PROC PHREG with the STRATA option (SAS Institute 2000). The PHREG procedure is typically used for survival time analysis based on proportional hazards regression, however, by setting time as a constant, it can also be used for more general matched case-control studies (Compton et al. 2002, Fortin et al. 2005).

We checked for correlation among model covariates by examining Pearson correlation coefficients (Neter et al. 1996). We considered covariates to be less than strongly correlated if the absolute value of the coefficient was  $< 0.7$  (Neter et al. 1996). No variables with strong correlation were used in the same model. To assess the degree of multicollinearity, we computed the variance inflation factor (VIF) by fitting the data to

a standard logistic regression model. We considered multicollinearity to be negligible if the VIF was  $< 2.5$  (Allison 1999).

We assessed model fit for nest-site selection models using a variety of techniques. To assess the goodness-of-fit (GOF) of the global model, we first examined plots of diagnostic statistics. We examined plots of the delta  $X^2$ , leverage, and overall influence diagnostic statistic using the macro MCSTRAT (Vierkant et al. 2000). We also examined plots of residual deviance and plots of the individual influence of each observation versus the estimated logistic probability from the fitted model (Hosmer and Lemeshow 2000). We omitted observations with residual deviance  $> |2|$  to determine the overall effect on parameter estimation. If parameter estimates were not greatly affected by the removal of observations, the observations were included. Finally, we fit a standard logistic regression model to our nest-site selection data and computed the Hosmer and Lemeshow GOF test to determine model fit (Hosmer and Lemeshow 2000).

For nest-site selection, we considered a suite of models that included single covariate models for each of the covariates of interest, a global model composed of all the possible covariates combined, and several multiple-covariate models for which we had reasonable *a priori* justification (Table 2). We constructed additive models only as we could not conceive of reasonable biological explanations for more complex models with interaction terms.

Interpretation of odds ratios rather than predicted probabilities for nest-site selection parameters was required due to our case-control design (Keating and Cherry 2004). Adjusted odds ratios describe the odds that an outcome will occur given an  $x$  unit

change in a covariate while the other covariate values remain constant (Hosmer and Lemeshow 2000). When reporting odds ratios, we report units of change when they differed from one (e.g., change in odds corresponding to a 10-unit change in habitat covariate). We used units of change greater than one when a one-unit change in a feature (e.g., tree density) would not be meaningful to managers.

Table 2. Nest-site selection models considered for northern flicker and hairy woodpecker. We evaluated this suite of models twice, once using stratification based on *location* and again using stratification based on *unit-pair*. The number of parameters (k) in each model is indicated.

Model Structure	Verbal hypothesis	k
SUBSTRATE	Snags are more easily excavated than live trees	1
DBH	Larger trees may offer more protection of cavity from weather and predators.	1
TREEDEN	High densities of live trees will be avoided because these plots are associated with nest predators.	1
SNAGDEN	Areas of high snag density will be selected because these areas offer increased options for cavity placement and potentially greater foraging opportunities.	1
CWDVOL	High coarse woody debris volume will be avoided due to potentially high predator densities.	1
PROPHIGH	Home ranges will not be selected in areas with high proportions of closed canopy. These areas will be avoided in an attempt to avoid higher nest predator (red squirrel) densities.	1
SUBSTRATE +DBH	Selection will be strongest at the scale of the nest tree.	
SUBSTRATE +TREEDEN	After initial snag selection, avoidance of high tree density at microhabitat scale (see reasoning above).	2
SUBSTRATE +SNAGDEN	After initial snag selection, selection of areas with high snag densities since these areas offer more cavity placement options. Selection of snags at two scales.	2
SUBSTRATE+CWDVOL	Initial snag selection coupled with avoidance of coarse woody debris as these areas may have higher predator densities.	2
SUBSTRATE+DBH+TREEDEN	Two strong nest-snag level factors will largely dictate nest sites, but surrounding live tree density will also have an effect (see reasoning above).	2
SUBSTRATE+DBH+SNAGDEN	Two strong nest-snag level factors will largely dictate nest sites, but surrounding live tree density will also have an effect (see reasoning above).	3
SUBSTRATE+DBH+CWDVOL	Two strong nest-snag level factors will largely dictate nest sites, but surrounding coarse woody debris volume will also have an effect (see reasoning above).	3
SUBSTRATE+TREEDEN+SNAGDEN	After initial snag selection, surrounding "stem" densities will also have an effect (see reasoning above).	3
SUBSTRATE+TREEDEN+CWDVOL	After initial snag selection, two microhabitat factors that may be tied to nest predator abundance will dictate nest-site selection (see reasoning above).	3

Table 2 (continued). Nest-site selection models considered for northern flicker and hairy woodpecker. We evaluated this suite of models twice, once using stratification based on *location* and again using stratification based on *unit-pair*. The number of parameters (k) in each model is indicated.

Model Structure	Verbal hypothesis	k
SUBSTRATE+SNAGDEN+CWDVOL	After initial snag selection, a tradeoff between availability of cavity abundance and avoidance of nest predator cover will dictate nest-site selection (see reasoning above).	3
TREEDEN+SNAGDEN+CWDVOL	Microhabitat characteristics will influence nest-site selection greater than any other scale, but all three factors will be important.	3
SUBSTRATE+DBH+TREEDEN+SNAGDEN+CWDVOL+PROPHIGH (GLOBAL MODEL)	The global model is always considered.	6



### Nest Survival

We modeled the daily survival rate (DSR) of nests as a function of habitat covariates using generalized linear models (Stephens 2003, Rotella et al. 2004) in PROC NLMIXED (SAS Institute 2000-2004). We considered the same covariates in nest survival models as were considered in our nest-site selection models. In addition, we considered the height of the nest cavity (NESTHT) in models of nest survival. We also included covariates that have recently been identified in the literature as having important effects on daily nest survival (Rotella et al. 2000, Grant et al. 2005).

Weather during the breeding season may influence nest survival (Ricklefs 1969, Conway and Martin 2000), therefore, we also considered the effect of minimum daily temperature (MINTEMP) on nest survival. This covariate was computed as the average minimum daily temperature between visits to a nest. Weather data were selected for the time periods of the study from the nearest possible National Weather Service COOP station (<http://www.weather.gov/om/coop>). We included a categorical covariate for year effects (YEAR) because it is reasonable to assume that there could be natural annual variation in nest survival. We also considered the effects of day in the nesting season (DIS) on nest survival. Recent modeling efforts show that nest survival can vary throughout the breeding season (Klett and Johnson 1982). DIS was computed as the Julian date within a given year (0-365 days). Because observers in nesting studies can influence nest survival (Rotella et al. 2000), we considered models with an added visit effect (VISIT). Visit effects were only considered for intervals during which a nest was observed using the TreeTop peeper camera. Visits to nests that did not include this

invasive viewing were not considered to be a great disturbance, as nests were generally not approached. The visit effect is recorded as the day in which the observer visited the nest and not for other days during the interval between nest visits. After considering our initial *a priori* model list, we added the VISIT covariate to all models to determine if model selection would be affected.

For nest survival models, we computed Pearson correlation coefficients for all variables prior to analysis and did not include covariates that were strongly correlated ( $|r| > 0.7$ ) in the same model. We examined variance inflation factors (VIF) by fitting the dependent variables to a multiple linear regression model to identify problems with multicollinearity ( $VIF > 2.5$ ). We evaluated the GOF of the global model using the USS Kernel-smoothed statistic (Sturdivant et al. 2007). We calculated GOF using the global model and determined if the observed statistic differed from the expected statistic using  $\alpha = 0.05$ .

We considered a total of 15 *a priori* models including a global model (Table 3). Most models were simple, single covariate models, but we also considered some additive models. We could not conceive of good biological explanations for more complex models (including those with interactions terms) and so we did not include these models in our *a priori* suite. We also kept our model list simple because our sample size was small and the ability of the software to converge on parameter values was limited by this constraint. We added a VISIT effect to the best model to evaluate if nest survival was affected by the collection of nest data (Rotella et al. 2000).

Table 3. Daily nest survival models considered for northern flickers and hairy woodpeckers including *a priori* verbal justifications. The number of parameters (k) for each model is reported.

Model Structure	Verbal Hypothesis and Justification (for <i>a priori</i> models)	k
CONSTANT DAILY SURVIVAL	Also referred to as the "null model".	1
DBH	Larger diameter trees may better insulate eggs and nestlings and reduce the risk of cavity destruction by predators.	2
NESTHT	Higher nests may prevent access by predators.	2
TREEDEN	Predators may be in higher densities where more cover/foraging opportunities exist at the microhabitat scale.	2
SNAGDEN	Increased snag densities result in more cavities to be searched by predators ("needle in haystack") and provide more cavities to chose from initially.	2
CWDVOL	Coarse woody debris provides cover and runways for potential nest predators.	2
PROPHIGH	Higher densities of potential nest predators may be associated with canopy cover at a larger scale than microhabitat around the nest.	2
MINTEMP	Nest may fail due to low temperature (low temps are expected to be limiting factor for sites at these elevations).	2
YEAR	Daily nest survival could vary from year to year due to fluctuating environmental conditions.	2
DIS	Emerging science shows that daily nest survival may vary depending on day in nesting season, which is probably tied to ultimate factors such as emerging predators, etc.	2
LOCATION	Given the disparate nature of the three study locations, we modeled nest survival as a function of <i>location</i> . A host of variables that were not measured could be explained by variation due to location (e.g. latitudinal differences in large-scale weather patterns)	3
TREEDEN + CWDVOL	Both of the microhabitat characteristics that we feel are linked to nest predator abundance may work in concert to determine daily nest survival.	3
DBH + TREEDEN + SNAGDEN	Selection for the nest tree is reportedly strong. An important covariate describing the nest tree is diameter. A combination of this covariate and a description of standing wood surrounding the nest may best explain nest survival.	3
TREEDEN + PROPHIGH	Two covariates, operating a different scales, and which are thought to be tied to nest predator densities will determine nest survival.	3

Table 3 (continued). Daily nest survival models considered for northern flickers and hairy woodpeckers including *a priori* verbal justifications. The number of parameters (k) for each model is reported.

Model Structure	Verbal Hypothesis and Justification (for <i>a priori</i> models)	k
VISIT	Visits to nests may influence nest survival, especially when visits are invasive (e.g. camera placed in cavity). We added a visit effect to all models in the suite to determine changes in model selection due to this effect. This covariate was not included in a single covariate model.	1
GLOBAL (DBH + NESTHT + TREEDEN + SNAGDEN + CWDVOL + PROPHIGH + MINTEMP + DIS)	The global model is always considered. We could not include all terms in the global model. Categorical variables were not included in the global model, nor was the VISIT effect.	9

## RESULTS

### Habitat Differences Among Study Locations

We measured vegetation at 310 random plots across the three study locations. We used a subset of these 310 plots, those that contained at least one snag or decayed live tree (n=276) for comparison of habitat covariates among locations and for comparison to used nest plots (Table 4). Overall, the Oregon and Washington locations were more similar to each other than the Idaho location (Table 5). The Idaho location had larger diameter trees than Washington and Oregon. The Idaho location also had lower live tree densities than the Washington and Oregon locations. Snag densities were similar for all locations and coarse woody debris volumes were highest in Oregon.

### Nest-Searching and Monitoring

The nesting season during the 4-year study ranged from an early initiation date of 17 April 2004 in Oregon to the latest fledging date of 2 August 2005 in Idaho. The average length of the nesting season was 99 days across the four field seasons (range = [90, 104]). On average, the nesting season started earliest in Washington (average estimated initiation date = 9 May) and latest in Idaho (average estimated initiation date = 17 May). We monitored nests from as early as 1 May to as late as 2 August.

We found 153 northern flicker nests and 72 hairy woodpecker nests from 2002-2005 (Table 6). Nest fate could not be determined for two northern flicker nests, and these nests were excluded from analysis. Of the remaining 151 Northern Flicker nests,

100 nests fledged at least one young. Of the 72 Hairy Woodpecker nests, 58 fledged at least one young.

Table 4. Area of each sampling *unit*, number of random points established initially, and number of random points that contained a suitable tree or snag for comparison with nest trees and snags in three study locations (ID=Idaho, OR=Oregon, WA=Washington). *unit-pair* groupings are indicated in column at left.

Unit-pair	Unit	Area (ha)	Percent of Total Survey Area	Random points established	Random points containing a "suitable" tree or snag
1	BH	220	4.3	20	20
1	FC	280	5.5	20	19
2	WM	216	4.2	10	5
2	DO	248	4.9	20	16
3	DM	224	4.4	20	15
3	PC	210	4.1	20	17
	ID Total	1398	27.5	110	92
4	TN	365	7.2	20	20
4	TS	350	6.9	20	19
5	CN	444	8.7	20	16
5	CS	429	7.4	20	16
	OR Total	1588	30.2	80	71
6	TD	369	7.2	20	19
6	RY	400	7.9	20	18
7	FY	392	7.7	20	19
7	LK	342	6.7	20	18
8	MT	253	5.0	20	19
8	HZ	351	6.9	20	20
	WA Total	2107	41.4	120	113
	Grand Total	5093	100.0	310	276

Table 5. Means  $\pm$  SD (range) for habitat covariates measured at random points in three ponderosa pine dominated study locations (WA = Washington, ID = Idaho, OR = Oregon). Effect sizes (differences between mean values) are reported for each of the primary habitat covariates (95% CI).

	Means			Effect Sizes		
	$\bar{X}_{WA}$ (n=113)	$\bar{X}_{ID}$ (n=92)	$\bar{X}_{OR}$ (n=71)	$\bar{X}_{WA}-\bar{X}_{ID}$	$\bar{X}_{WA}-\bar{X}_{OR}$	$\bar{X}_{ID}-\bar{X}_{OR}$
DBH (cm)	39.0 $\pm$ 13.6 (23-82)	53.8 $\pm$ 23.8 (23-124)	38.2 $\pm$ 13.7 (23-85)	-14.8 (-17.3, -12.2)	0.8 (-1.0, 2.6)	15.6 (13.0, 18.2)
TREEDEN (ha <sup>-1</sup> )	111.8 $\pm$ 50.8 (17-250)	82.8 $\pm$ 57.2 (0-335)	115.4 $\pm$ 48.5 (17-283)	29.0 (21.8, 36.2)	-3.6 (-10.2, 3.0)	-32.6 (-39.7, -25.6)
SNAGDEN (ha <sup>-1</sup> )	5.1 $\pm$ 7.8 (0-40)	6.5 $\pm$ 10.0 (0-58)	6.8 $\pm$ 17.0 (0-120)	-1.4 (-2.6, -0.2)	-1.7 (-3.5, -0.1)	-0.3 (-2.1, -1.6)
CWDVOL (m <sup>3</sup> ha <sup>-1</sup> )	31.7 $\pm$ 29.6 (0-137)	41.1 $\pm$ 41.2 (0-207)	51.8 $\pm$ 40.5 (0-189)	-9.5 (-14.2, -4.7)	-20.1 (-24.8, -15.4)	-10.7 (-16.1, -5.2)
PROPHIGH	0.45 $\pm$ 0.16 (0.19-0.90)	0.62 $\pm$ 0.22 (0.29-0.99)	0.38 $\pm$ 0.26 (0.06-0.86)	-0.17 (-0.23, -0.11)	0.07 (0.00, 0.15)	0.24 (0.15, 0.33)

Table 6. Sample sizes for northern flicker and hairy woodpecker nests used for analysis and numbers that fledged from 2002-2005. Two northern flicker nests could not be used for analysis, one that fledged on the first visit, and one for which the fate could not be determined. Fledged nests are those nests that produced at least one young.

Year	No. Nests	Northern Flicker				Hairy Woodpecker			
		OR	ID	WA	Total	OR	ID	WA	Total
2002	Used for analysis	14	13	11	38	9	12	10	31
	Fledged	8	8	9	25	9	8	10	27
2003	Used for analysis	18	24	24	66	9	9	11	29
	Fledged	13	16	18	47	7	6	9	22
2004	Used for analysis	6	19	-	25	1	5	-	6
	Fledged	4	8	-	12	1	3	-	4
2005	Used for analysis	-	13	9	22	-	4	2	6
	Fledged	-	9	7	16	-	3	2	5
Total	Used for analysis	38	69	44	151	19	30	23	72
	Fledged	25	41	34	100	17	20	21	58

### Nest-Site Selection

#### Northern Flicker

None of the covariates included in nest-site selection models for northern flicker were highly correlated (Table 7). Variance inflation factors for all covariates were below the threshold ( $< 2.5$ ) that would have indicated multicollinearity. Plots of diagnostic statistics indicated that some observations had greater influence on the model fit, but omission of these observations did not change the parameter estimates greatly; hence, we



Table 7. Pearson correlation coefficients ( $r$ ) for covariates used in nest-site selection models for northern flickers. Covariates with ( $|r| < 0.7$ ) were considered to be less than highly correlated.

Covariate	SUBSTRATE	DBH	TREEDEN	SNAGDEN	CWDVOL	PROPHIGH
SUBSTRATE	1.00	0.10	-0.15	0.34	0.24	0.09
DBH		1.00	-0.34	0.03	-0.08	0.15
TREEDEN			1.00	0.12	0.04	0.07
SNAGDEN				1.00	0.33	0.07
CWDVOL					1.00	-0.14
PROPHIGH						1.00

elected to include all observations. The goodness-of-fit test (Hosmer and Lemeshow 2002) did not indicate a lack of fit for the global model ( $X^2 = 10.4$ ,  $DF=8$ ,  $p=0.24$ ).

The best model for nest-site selection for northern flickers from our suite of models was the global model, regardless of the stratification specified (Table 8). No model was within two  $\Delta AIC_c$  units of this best model. Model averaged parameter estimates (Table 9) for the global model from both of these suites indicate that SUBSTRATE was the strongest predictor of a nest site indicating that snags were strongly favored for nest sites over live trees (including those with decay which could have harbored nest cavities). The odds ratio for Substrate was 3.45 (95% CI=[1.946, 6.108]). This ratio indicates an almost 3.5-fold increase in the odds that a nest would occur if the substrate was a snag rather than a live tree. Northern flickers favored nest trees of larger diameters compared to average conditions. The change in odds of use of a snag for nesting was 1.66 (1.659, 1.917) for every 10-cm increase in DBH, this corresponds to a 66% increase in the odds of use as tree diameter increases by 10-cm. There was not clear avoidance of higher live tree densities by northern flickers, the odds ratio (0.99) nearly overlapped one (95% CI=[0.988, 0.999]); this was true even with an odds ratio constructed for a 5 tree/ha change in live tree density. Northern flickers

avored nest sites where the microhabitat included a higher density of snags. The odds ratio for the SNAGDEN parameter was 1.22 (1.085, 1.375) when a change in 5 snags/ha was used to construct the odds ratio. Coarse woody debris volume did not appear to be important factor to nest-site selection by northern flickers; the odds ratio for that parameter overlapped one. Northern flickers did appear to avoid areas with a higher proportion of closed canopy as indicated by the odds ratio for the PROPHIGH parameter, which was considerably less than one (Table 9).

Table 8. Model selection results for nest site selection by northern flicker. Two sets of results are shown for nest-site selection models: the first group was based on *unit-pair* stratification while the second group featured *location* stratification. The number of parameters (k) is indicated for each model. Models were ranked using an information criterion, AIC. Models weights ( $w_i$ ) indicate support for a given model.

Model	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$
<u>Nest-site selection (<i>unit-pair</i>)</u>				
GLOBAL	6	387.524	0.000	0.999
SUBSTRATE + DBH + SNAGDEN	3	401.318	13.794	0.001
SUBSTRATE + DBH + CWDVOL	3	405.701	18.177	0.000
SUBSTRATE + DBH + TREEDEN	3	409.419	21.895	0.000
SUBSTRATE + DBH	2	409.666	22.142	0.000
DBH	1	445.300	57.776	0.000
SUBSTRATE + TREEDEN + SNAGDEN	3	445.486	57.962	0.000
SUBSTRATE + SNAGDEN	2	455.868	68.344	0.000
SUBSTRATE + TREEDEN + CWDVOL	3	457.683	70.159	0.000
SUBSTRATE + SNAGDEN + CWDVOL	3	457.690	70.166	0.000
SUBSTRATE + TREEDEN	2	457.801	70.277	0.000
SUBSTRATE + PROPHIGH	2	459.583	72.059	0.000
TREEDEN + SNAGDEN + CWDVOL	3	460.276	72.753	0.000
SUBSTRATE	1	462.320	74.796	0.000
SUBSTRATE + CWDVOL	2	462.704	75.180	0.000
SNAGDEN	1	475.538	88.014	0.000
TREEDEN	1	488.129	100.605	0.000
CWDVOL	1	491.623	104.099	0.000
PROPHIGH	1	494.503	106.979	0.000

Table 8 (continued). Model selection results for nest site selection by northern flicker. Two sets of results are shown for nest-site selection models: the first group was based on *unit-pair* stratification while the second group featured *location* stratification. The number of parameters (k) is indicated for each model. Models were ranked using an information criterion, AIC. Models weights ( $w_i$ ) indicate support for a given model.

Model	k	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$
<u>Nest-site selection (<i>location</i>)</u>				
GLOBAL	6	410.724	0.000	0.996
SUBSTRATE + DBH + SNAGDEN	3	421.970	11.246	0.004
SUBSTRATE + DBH + CWDVOL	3	426.041	15.317	0.000
SUBSTRATE + DBH + TREEDEN	3	429.255	18.532	0.000
SUBSTRATE + DBH	2	430.311	19.587	0.000
DBH	1	468.095	57.371	0.000
SUBSTRATE + TREEDEN + SNAGDEN	3	473.777	63.053	0.000
SUBSTRATE + PROPHIGH	2	484.556	73.832	0.000
SUBSTRATE + TREEDEN + CWDVOL	3	486.019	75.295	0.000
SUBSTRATE + TREEDEN	2	486.153	75.429	0.000
SUBSTRATE + SNAGDEN	2	489.890	79.167	0.000
TREEDEN + SNAGDEN + CWDVOL	3	490.236	79.512	0.000
SUBSTRATE + SNAGDEN + CWDVOL	3	491.757	81.033	0.000
SUBSTRATE	1	495.900	85.176	0.000
SUBSTRATE + CWDVOL	2	496.472	85.748	0.000
SNAGDEN	1	511.754	101.030	0.000
TREEDEN	1	517.701	106.977	0.000
PROPHIGH	1	523.269	112.546	0.000
CWDVOL	1	527.436	116.712	0.000

Table 9. Model averaged parameter estimates (SE) and odds ratios (95% CI) for northern flicker nest-site selection models. The units column indicates the theoretical change in units for a given parameter that was used to generate the odds ratio.

Parameter	Parameter Estimate	Units	Odds Ratio
<u>Stratification = <i>unit-pair</i></u>			
SUBSTRATE	1.24 (0.292)	1	3.45 (1.946, 6.108)
DBH	0.05 (0.007)	10	1.66 (1.659, 1.917)
TREEDEN	-0.01 (0.003)	5	0.99 (0.988, 0.999)
SNAGDEN	0.04 (0.012)	5	1.22 (1.085, 1.375)
CWDVOL	0.00 (0.003)	1	1.00 (0.996, 1.009)
PROPHIGH	-2.81 (0.866)	1	0.06 (0.011, 0.330)

Table 9 (continued). Model averaged parameter estimates (SE) and odds ratios (95% CI) for northern flicker nest-site selection models. The units column indicates the theoretical change in units for a given parameter that was used to generate the odds ratio.

Parameter	Parameter Estimate	Units	Odds Ratio
<u>Stratification = location</u>			
SUBSTRATE	1.28 (0.287)	1	3.59 (2.046, 6.305)
DBH	0.05 (0.007)	10	1.65 (1.430, 1.894)
TREEDEN	-0.01 (0.003)	5	0.97 (0.949, 1.001)
SNAGDEN	0.03 (0.011)	5	1.19 (1.062, 1.328)
CWDVOL	0.00 (0.003)	1	1.00 (0.997, 1.010)
PROPHIGH	-1.83 (0.667)	1	0.16 (0.043, 0.593)

#### Hairy Woodpecker

Nest-site selection models for hairy woodpecker did not include variables that were strongly correlated or those with multicollinearity (Table 10). Roughly eleven observations had residual deviance  $> 2$ , indicating that they could have been unduly affecting model fit. We dropped these observations one at a time, and re-fit the models to be sure that the general direction and magnitude of parameters did not change. The odds ratio for the parameter SUBSTRATE was affected by deletion of some observations with residual deviance greater than 2, but the change was not isolated to a single observation, nor was it in a consistent direction, so we chose not to remove any observations. The GOF test (Hosmer and Lemeshow 2002) did not indicate a lack of fit for the global model ( $X^2 = 4.88$ ,  $DF=8$ ,  $p=0.77$ ) when the data were fitted to a standard logistic model.

The most well supported nest-site selection models for hairy woodpeckers from both the suite of models stratified by *unit-pair* and those stratified by *location* were the

global models (Table 11), those containing all covariates. The next best models for hairy woodpeckers in both cases were  $> 2 \Delta AIC_c$  away from these global models.

Table 10. Pearson correlation coefficients ( $r$ ) for covariates used in nest-site selection models for hairy woodpecker. Covariates with ( $|r| > 0.7$ ) were considered to be highly correlated.

Covariate	SUBSTRATE	DBH	TREEDEN	SNAGDEN	CWDVOL	PROPHIGH
SUBSTRATE	1.00	0.09	-0.15	0.37	0.27	0.14
DBH		1.00	-0.27	0.04	-0.07	0.17
TREEDEN			1.00	0.07	0.01	0.09
SNAGDEN				1.00	0.31	0.07
CWDVOL					1.00	-0.14
PROPHIGH						1.00

Table 11. Model selection results for hairy woodpecker nest-site selection models. Two sets of results are shown for nest-site selection models, the first group uses *unit-pair* stratification while the second group featured *location* stratification. The number of parameters ( $k$ ) is indicated for each model. Models were ranked using the relative Akaike Information Criterion corrected for small sample size ( $\Delta AIC_c$ ). Models weights ( $w_i$ ) indicate support for a given model.

Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
<u>Nest-site selection (<i>unit-pair</i>)</u>				
GLOBAL	6	271.754	0.000	0.943
SUBSTRATE + TREEDEN + SNAGDEN	3	278.677	6.923	0.030
SUBSTRATE + DBH + SNAGDEN	3	279.726	7.972	0.018
TREEDEN + SNAGDEN + CWD	3	281.880	10.127	0.006
SUBSTRATE + DBH + TREEDEN	3	282.970	11.217	0.003
SUBSTRATE + DBH	2	288.894	17.141	0.000
SUBSTRATE + DBH + CWD	3	290.456	18.703	0.000
SUBSTRATE + TREEDEN	2	293.387	21.634	0.000
SUBSTRATE + SNAGDEN	2	293.741	21.987	0.000
SUBSTRATE + TREEDEN + CWD	3	295.277	23.523	0.000
SUBSTRATE + SNAGDEN + CWD	3	295.429	23.675	0.000
SNAGDEN	1	299.225	27.472	0.000
SUBSTRATE	1	301.689	29.935	0.000
SUBSTRATE + PROPHIGH	2	303.380	31.627	0.000
SUBSTRATE + CWD	2	303.628	31.875	0.000

Table 11 (continued). Model selection results for hairy woodpecker nest-site selection models. Two sets of results are shown for nest-site selection models, the first group uses *unit-pair* stratification while the second group featured *location* stratification. The number of parameters ( $k$ ) is indicated for each model. Models were ranked using the relative Akaike Information Criterion corrected for small sample size ( $\Delta AIC_c$ ). Models weights ( $w_i$ ) indicate support for a given model.

Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
DBH	1	305.005	33.251	0.000
TREEDEN	1	305.899	34.146	0.000
CWD	1	318.248	46.494	0.000
PROPHIGH	1	318.996	47.242	0.000
<u>Nest-site selection (location)</u>				
GLOBAL	6	290.587	0.000	0.949
SUBSTRATE + TREEDEN + SNAGDEN	3	297.903	7.316	0.024
SUBSTRATE + DBH + SNAGDEN	3	298.167	7.580	0.021
TREEDEN + SNAGDEN + CWD	3	301.830	11.243	0.003
SUBSTRATE + DBH + TREEDEN	3	303.076	12.489	0.002
SUBSTRATE + DBH	2	308.803	18.216	0.000
SUBSTRATE + DBH + CWD	3	310.187	19.600	0.000
SUBSTRATE + SNAGDEN	2	313.125	22.538	0.000
SUBSTRATE + TREEDEN	2	313.137	22.550	0.000
SUBSTRATE + SNAGDEN + CWD	3	314.806	24.219	0.000
SUBSTRATE + TREEDEN + CWD	3	314.908	24.321	0.000
SNAGDEN	1	318.673	28.086	0.000
SUBSTRATE	1	322.488	31.901	0.000
DBH	1	323.920	33.332	0.000
SUBSTRATE + CWD	2	324.379	33.792	0.000
SUBSTRATE + PROPHIGH	2	324.508	33.920	0.000
TREEDEN	1	325.772	35.185	0.000
CWD	1	338.538	47.951	0.000
PROPHIGH	1	339.932	49.345	0.000

Many of the same covariates that were important to northern flicker nest-site selection were also important to hairy woodpeckers. The SUBSTRATE covariate was estimated to be a positive value, highlighting that hairy woodpeckers largely used snags as opposed to live trees (Table 12). The 95% CI for the SUBSTRATE odds ratio

overlapped one, indicating weaker support for this covariate as a driver of hairy woodpecker nest-site selection than the same covariate for northern flickers. Diameter of a potential nest tree, and increasing snag density at the microhabitat scale also had positive effects on nest-site selection by hairy woodpeckers. Both of these covariates had corresponding odds ratios with confidence intervals that did not include one. There was a 30% increase in the chance that a stand would be used as a nest-site as snag densities were increased by 5 snags/ha. Conversely, an increase in live tree density of 5 live trees/ha led to a 6% decrease in the chances that a site was chosen for nesting. Coarse woody debris volumes at the macrohabitat scale and the proportion of high canopy closure at the landscape scale were not supported as important factors in nest-site selection for hairy woodpeckers.

Table 12. Model averaged parameter estimates (SE) and odds ratios (95% CI) for hairy woodpecker nest-site selection models. The unit's column indicates the theoretical change in units for a given parameter that was used to generate the odds ratio.

Parameter	Estimate (SE)	Units	Odds Ratio
<u>Stratification = unit-pair</u>			
SUBSTRATE	0.70 (0.363)	1	2.02 (0.993, 4.099)
DBH	0.03 (0.008)	10	1.30 (1.116, 1.509)
TREEDEN	-0.01 (0.004)	5	0.94 (0.902, 0.971)
SNAGDEN	0.05 (0.010)	5	1.28 (1.121, 1.463)
CWDVOL	-0.00 (0.004)	1	1.00 (0.990, 1.007)
PROPHIGH	-0.10 (1.020)	1	0.91 (0.121, 6.797)
<u>Stratification = location</u>			
SUBSTRATE	0.65 (0.354)	1	1.93 (0.967, 3.864)
DBH	0.02 (0.007)	10	1.28 (1.111, 1.481)
TREEDEN	-0.01 (0.004)	5	0.94 (0.905, 0.973)
SNAGDEN	0.05 (0.013)	5	1.28 (1.122, 1.456)
CWDVOL	-0.00 (0.004)	1	1.00 (0.992, 1.008)
PROPHIGH	0.71 (0.793)	1	2.04 (0.431, 9.643)

## Nest Survival

### Northern Flicker

None of the covariates included in our nest survival models for northern flicker were highly correlated (all  $|r| \leq 0.7$ ). Multicollinearity was not detected among the covariates at a level that would have been problematic ( $VIF < 2.5$ ). Examination of the USS kernel-smoothed statistic indicated that the global model sufficiently fit the data ( $\hat{S}_s = 45.89$ ,  $E[\hat{S}_s] = 45.04$ ,  $Var[\hat{S}_s] = 33.96$ ,  $p = 0.88$ ).

Model selection results from the suite of *a priori* models for northern flickers revealed that no one model was supported over the others (Table 13). The null model, which represents a constant daily survival rate, was equally supported for northern flickers as models that contained habitat or other covariates of interest. Eleven models had  $\Delta AIC_c$  scores  $< 2$ , indicating that support was spread among a variety of models.

The 95% CI for model averaged parameter estimates included zero for 9 out of 13 parameters included in these models (Table 14). Minimum temperature (averaged over the observation interval) had a positive effect on nest survival for northern flickers. Increases in coarse woody debris volume around the nest-site, increases in diameter of the nest tree, and increasing day in the nesting season all had negative effects on nest survival, but the confidence intervals surrounding the parameter estimates for these effects were very close to zero. Inclusion of a VISIT effect did not change the model selection results. None of the main habitat covariates of interest were important in the explanation of nest survival for northern flickers. From our suite of *a priori* models,



daily nest survival was explained equally well by a single covariate representing constant survival as by any habitat covariates.

Table 13. Model selection results for the suite of nest survival models for northern flickers. The number of parameters ( $k$ ), relative Akaike Information Criterion ( $\Delta AIC_c$ ) and model weight ( $w_i$ ) are provided.

Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
NULL	1	381.198	0.000	0.129
MINTEMP	2	381.478	0.280	0.112
YEAR	4	381.809	0.612	0.095
LOCATION	3	382.036	0.838	0.085
NESTHT	2	382.141	0.943	0.080
SNAG	2	382.216	1.018	0.077
TREEDEN	2	382.285	1.087	0.075
PROPHIGH	2	382.404	1.206	0.070
DBH	2	382.564	1.366	0.065
DIS	2	383.145	1.947	0.049
CWDVOL	2	383.156	1.958	0.048
DBH+SNAGDEN	3	383.359	2.161	0.044
TREEDEN+PROPHIGH	3	383.380	2.182	0.043
TREEDEN+CWDVOL	3	384.285	3.087	0.028
GLOBAL	10	392.576	11.378	0.000

Table 14. Model averaged parameter estimates (SE) and 95% CI (confidence intervals) for parameters included in northern flicker nest survival models. The categorical variables LOC and YEAR code for study *locations* and study years, respectively. Categorical variable coding is indicated in parentheses.

Parameter	Estimate	SE	95%CI
CWDVOL	-0.001	0.000	(-0.001, -0.001)
DBH	-0.006	0.000	(-0.005, -0.006)
DIS	-0.002	0.000	(-0.002, -0.002)
LOC1 (Washington)	0.654	0.387	(-0.105, 1.413)
LOC2 (Oregon)	0.263	0.340	(-0.404, 0.929)
MINTEMP	0.051	0.002	(0.046, 0.055)
NESTHT	-0.027	0.035	(-0.096, 0.042)
PROPHIGH	-0.615	-0.411	(0.192, -1.421)
SNAGDEN	-0.027	0.031	(-0.087, 0.034)
TREEDEN	-0.011	0.011	(-0.032, 0.010)
YEAR3 (2003)	0.436	0.371	(-0.292, 1.164)
YEAR4 (2004)	-0.457	0.396	(-1.234, 0.321)
YEAR5 (2005)	0.271	0.497	(-0.704, 1.246)

Hairy Woodpecker

None of the covariates included in our nest survival models for hairy woodpecker were highly correlated (all  $|r| \leq 0.7$ ). Multicollinearity was not detected among the covariates at a level that would have been problematic ( $VIF < 2.5$ ). Examination of the USS kernel-smoothed statistic indicated that the global model sufficiently fit the data ( $\hat{S}_s = 12.12$ ,  $E[\hat{S}_s] = 11.57$ ,  $Var[\hat{S}_s] = 8.76$ ,  $p = 0.85$ ).

Results from the *a priori* nest-survival models for hairy woodpecker were less ambiguous than those for northern flicker. Two nest survival models were equally well supported, one, which explained daily nest survival in terms of differences among study locations, and another, which included effects for, live tree density and coarse woody debris at the microhabitat scale (Table 15). The confidence intervals for other parameters included in hairy woodpecker nest survival models included zero (Table 16).

Table 15. Model selection results for the suite of nest survival models for hairy woodpecker. The number of parameters (k), relative Akaike Information Criterion ( $\Delta AIC_c$ ) and model weight ( $w_i$ ) are provided.

Model	k	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
LOCATION	3	113.803	0.000	0.398
TREEDEN+CWDVOL	3	115.212	1.408	0.197
TREEDEN	2	116.888	3.084	0.085
NULL	1	117.825	4.022	0.053
CWDVOL	2	117.826	4.022	0.053
TREEDEN+PROPHIGH	3	118.479	4.676	0.038
DIS	2	118.601	4.798	0.036
MINTEMP	2	118.966	5.162	0.030
SNAGDEN	2	119.038	5.234	0.029
PROPHIGH	2	119.511	5.707	0.023
DBH	2	119.817	6.014	0.020
NESTHT	2	119.831	6.027	0.020
DBH+SNAGDEN	3	121.005	7.201	0.011
YEAR	4	122.612	8.809	0.005
GLOBAL	9	124.395	10.592	0.002

Table 16. Model averaged parameter estimates with standard errors (SE) and 95% confidence intervals for parameters included in hairy woodpecker nest survival models. The categorical variables LOC and YEAR code for study *locations* and study years respectively. Categorical variable coding is indicated in parentheses.

Parameter	Estimate	SE	95%CI
CWDVOL	-0.013	0.007	(-0.026, 0.000)
DBH	-0.001	0.011	(-0.023, 0.021)
DIS	-0.026	0.024	(-0.072, 0.021)
LOC1 (Washington)	2.146	1.051	(0.081, 4.212)
LOC2 (Oregon)	1.197	0.777	(-0.331, 2.726)
MINTEMP	0.078	0.085	(-0.089, 0.244)
NESTHT	0.001	0.040	(-0.078, 0.080)
PROPHIGH	-0.889	1.403	(-3.639, 1.862)
SNAGDEN	-0.019	0.020	(-0.058, 0.021)
TREEDEN	0.013	0.007	(-0.001, 0.027)
YEAR3 (2003)	-0.164	0.648	(-1.439, 1.110)
YEAR4 (2004)	-1.017	0.873	(-2.734, 0.700)
YEAR5 (2005)	-0.004	1.122	(-2.210, 2.203)

The confidence intervals for the *location* covariate which coded for the Washington *location* was above one while the covariate for Oregon was not fully below one, indicating that at least one study *location* demonstrated differences in nest survival for hairy woodpeckers. Nest survival for hairy woodpeckers was highest at the Washington study location and lowest at the Idaho study location (Figure 4).

The second best nest survival model for hairy woodpeckers included two microhabitat covariates. The confidence interval for the coarse woody debris parameter was fully less than zero. The model averaged parameter estimate for live tree density indicated a positive effect of live tree density on nest survival so that live tree density and coarse woody debris volume worked to counter each in the second best model. The effects of coarse woody debris volume on nest survival were most apparent at the

extreme ends of the range of volumes encountered across the study (Figure 5). After first examining the *a priori* model suite we added a VISIT effect to the two best models.

Adding a VISIT effect to the best models in the *a priori* model suite did not change the results.

Figure 4. Overall nest survival (Daily nest survival<sup>Days in Nesting Cycle</sup>) and 95% confidence intervals for northern flickers and hairy woodpeckers at three separate study locations: Oregon (OR), Idaho (ID), and Washington (WA) and in the whole study area (All).

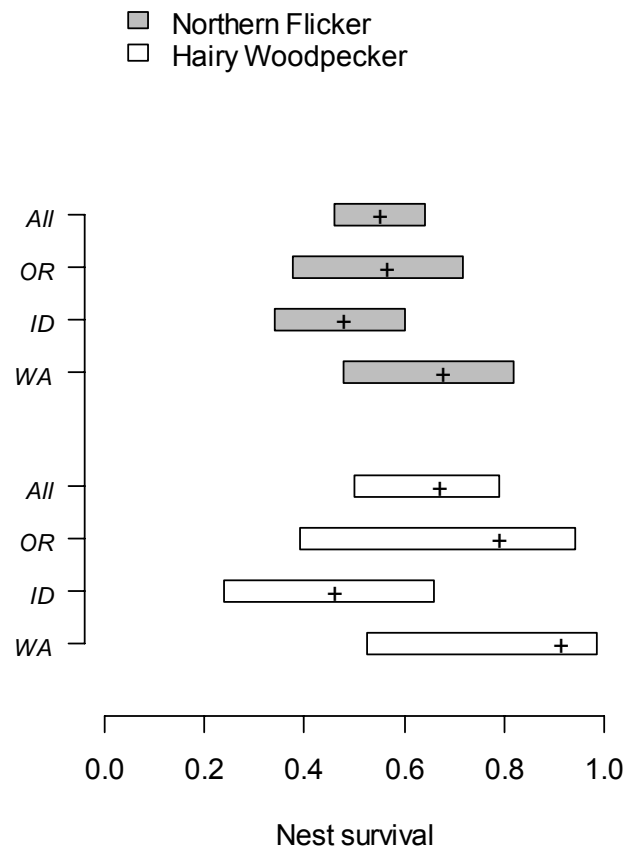
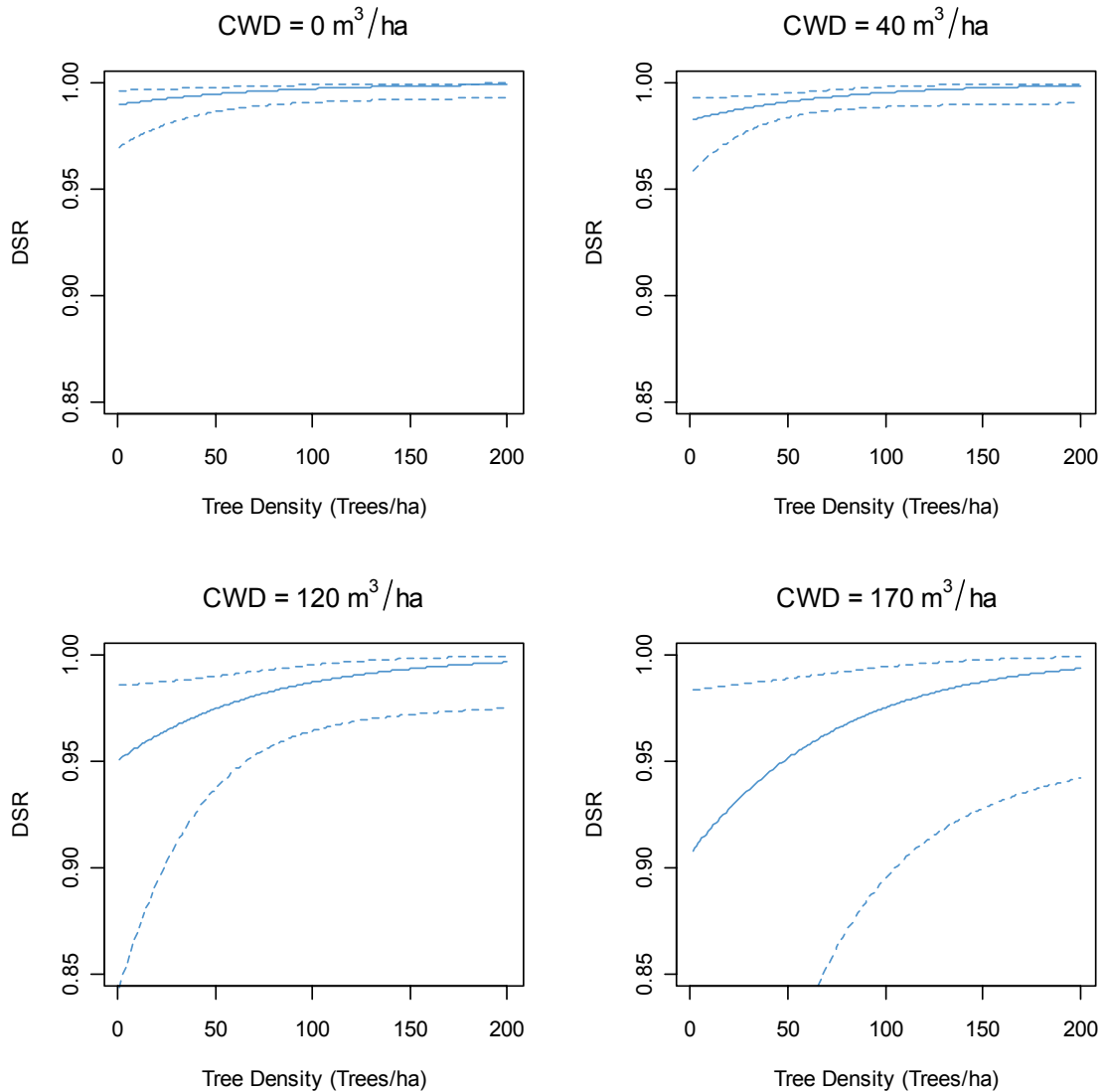


Figure 5. Daily survival rate (DSR) for hairy woodpecker nests as a function of live tree density and coarse woody debris volume (CWD). Dotted lines represent the 95% confidence interval. Corresponding nest survival can be calculated by  $DSR^{46}$  days. Overall nest survival ( $DSR^{\text{Days in Nesting Cycle}}$ ) for a 46 day nesting cycle drops from 0.63 for a DSR of 0.99 to less than 0.01 for a DSR of 0.90.



### Number of Young Fledged Per Nest

We could not use the nest camera on almost 50% of the nests for each species due to height limitations, obstructions in front of cavities (i.e. branches), or simply logistics and a limited number of cameras (e.g., nest fledged before camera was used on cavity). More nests were viewed with the fiber optic camera at the Oregon location than in Washington or Idaho. Differences in viewing rates were due to differences in nest cavity height (nests were lowest in Oregon) and difficulty of camera transport across rugged terrain in Idaho and Washington. When the fecundity of all nesting birds was considered, regardless of whether the cavity was viewed with a camera or not, Washington had the lowest mean number of nestlings produced for both species, while Oregon had the highest fledgling production for northern flickers.

### Range of Habitat Available to Nesting Woodpeckers

To further evaluate the degree to which nest-site selection and nest survival were affected by the range of habitat conditions available to northern flickers and hairy woodpeckers in our study, we produced density histograms for the main habitat covariates (Figure 6 and Figure 7). All non-nest random plots (n=308) were used to create the histograms, as opposed to only those random plots that contained a snag or decayed live tree suitable for nesting (n=276). The patterns observed were similar for both species and these results corroborate the results from nest-site selection and nest survival models.

Figure 6. Density histograms for main habitat covariates measured at northern flicker nest plots (n=151), plots used for nesting that fledged young (n=100), and non-nest random plots (n=308).

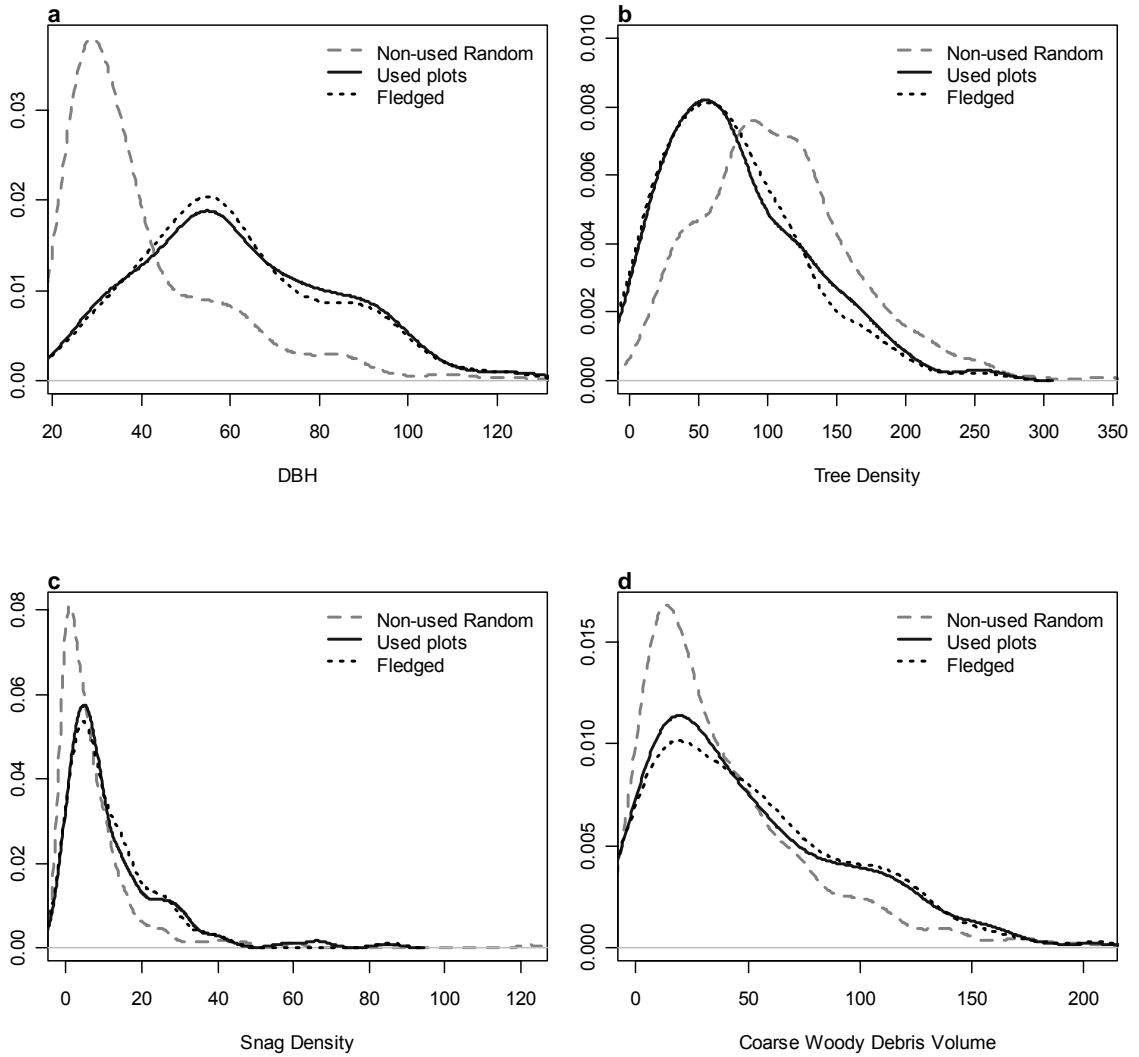
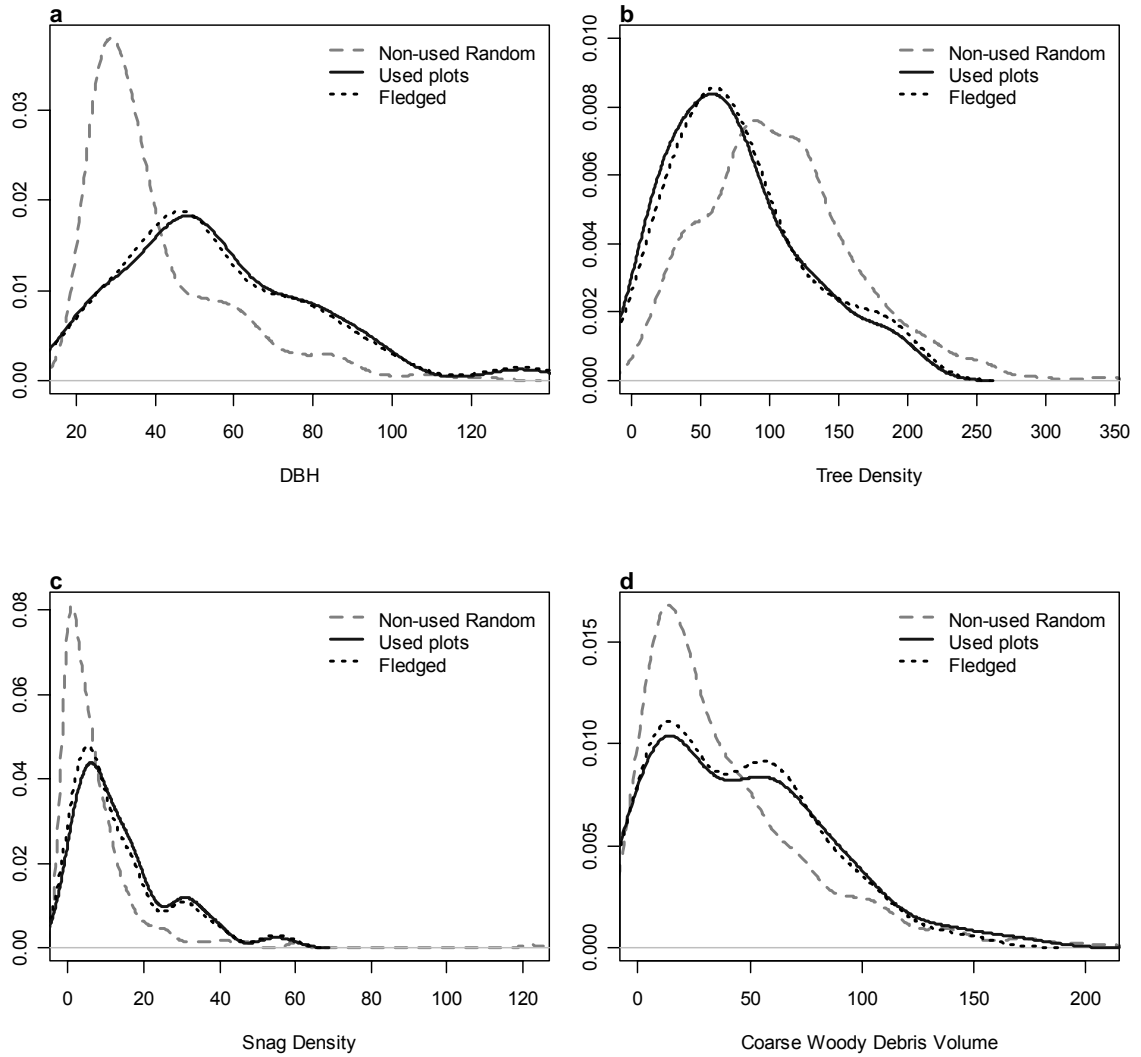


Figure 7. Density histograms for main habitat covariates measured at hairy woodpecker nest plots (n=72), plots used for nesting that fledged young (n=58), non-nest random plots (n=308).





## DISCUSSION

Characteristics of the nest-tree and the surrounding microhabitat were important in nest-site selection of northern flickers and hairy woodpeckers in our study. At the scale of the nest tree, hairy woodpeckers and northern flickers used snags more often than live trees. This result was not unexpected and merely emphasizes the importance of dead trees (snags) in forest ecosystems. Both woodpecker species used considerably larger diameter substrates (snags) for nest placement than those available at random. They also placed their nests in microhabitats with lower tree densities as we predicted, although this result was more marked for hairy woodpeckers. Both species used plots with higher densities of snags than expected at random. Landscape scale effects on habitat selection were evident only for northern flickers, who tended to use nest-sites with a lower proportion of high canopy closure than that measured at randomly selected plots.

Factors influencing nest survival were not always consistent with those affecting nest-site selection. Nest survival of northern flickers was not related to any of the covariates that we measured. Their nest survival was best represented by a constant daily survival rate. Nest survival for northern flickers in ponderosa pine forests that have not been recently disturbed may be a function of random predation, random weather events, or other events, which, when taken together over the whole nesting season, result in uniform daily nest survival that is unresponsive to habitat features around the nest-site or even in the surrounding landscape.

In contrast, hairy woodpecker nest survival was related to two habitat covariates, live tree density and coarse woody debris volume. Survival increased with increasing live

tree density, whereas it decreased with increasing coarse woody debris volume. The relationship between hairy woodpecker nest survival and live tree density was of particular interest because this species used nest plots with lower live tree densities. Hairy woodpecker nest survival also varied by study location; it was highest in Washington and lowest in Idaho, although the confidence intervals for nest survival estimates at each *location* overlapped.

Many of our predictions regarding nest-site selection were supported. Both hairy woodpeckers and northern flickers used snags as opposed to decayed live trees for nesting. Live trees were far more abundant in our study locations than snags, and though both hairy woodpeckers and northern flickers will use decayed portions of live trees (Raphael and White 1984) they clearly favor snags (Raphael and White 1984, Robertson 1993). The feature that best distinguished between nest sites and random sites was the presence of a snag (as opposed to live tree with decay). There are several reasons why woodpeckers may choose snags over live trees with decay, chief among them is the ease of excavation in snags (Short 1982). Additionally, we think that woodpeckers may choose snags because small mammals (squirrels and chipmunks; both potential nest predators) may avoid snags during diurnal feeding forays. Though squirrels and chipmunks use cavities in snags as nest sites and/or the base of snags for middens (Sutton 1992, Steel 1998), they also prefer foraging habitat with reasonable escape cover (e.g., downed wood or live branches with needles; Sutton 1992, Steel 1998). Snags potentially offer woodpeckers greater nest vigilance because nesting birds could more easily observe approaching predators while attending the nest.

Northern flickers and hairy woodpeckers used snags that were larger diameter than those measured at non-used random plots, as we expected. This result is consistent with other studies. The magnitude of the differences between used and unused trees/snags appears to vary depending upon the distribution of available tree/snag sizes (Raphael and White 1984, Gutzwiller and Anderson 1987, Hitchcox 1998, Saab et al. 2002, Martin et al. 2004). Several explanations for the selection of larger diameter snags are possible. Selection of larger diameter snags could simply be influenced by the superior insulative properties of these snags (Wiebe 2001). We also propose that because larger diameter snags usually persist longer and are therefore stronger than smaller snags (Russell et al. 2006), that large snags are less prone to physical destruction by nest predators such as bears (*Ursus* spp.) and bobcats (*Felis rufus*). We recommend that future studies include a measure of hardness of the snag near the cavity entrance, as this may be a factor in predation rates (Albano 1992).

Isolated snags were not as strongly favored as were those that were clumped with other snags. We hypothesized that increasing snag density would be indicative of woodpecker nesting and our data supported this supposition. Selection of high snag densities for nesting has been documented in recently disturbed habitats (Raphael and White 1984, Hejl and McFadzen 1999, Saab et al. 2002). Woodpeckers nesting in forests without recent disturbance may chose clumps over lone snags for the potentially protective nature of these clumps. The “swamping” of potential nest predators may occur when there are many potential nest sites to search (Martin and Roper 1988). Snags occurring in higher densities may also be used because they can persist longer than snags

occurring in lower densities (Russell et al. 2006) and nesting woodpeckers become familiarized with particular snag clumps over time. Cooper (1961) identified three distinct “scales of pattern” in ponderosa pine forests in Arizona, including the scale that he identified as “clumps or patches of trees similar in size and age, usually occupying 0.1 acre or more”. If ponderosa pine in more northerly, mesic conifer forests (where our study locations were found) exhibit similar clumping as was described by Cooper (1961), then snag clumps may be the rule rather than the exception for nesting woodpeckers in ponderosa pine forests.

We found support for our hypothesis that cavity-nesting birds would nest in areas of lower live tree densities because those areas might harbor lower densities of small mammalian nest predators. Red squirrels, occupants of ponderosa-pine dominated forests and documented nest predators, prefer interlocking tree canopies rather than open areas (Steele 1998, Bakker and Van Vuren 2004). Our results were stronger for hairy woodpeckers than for northern flickers. Results of other studies have been ambiguous about the influence of live tree densities on breeding cavity-nesting birds. In high-elevation forest drainages of the southwestern U.S., cavity-nesters as a group chose nest plots that had more trees than measured at random plots, presumably because higher live-tree densities offered greater foraging opportunities (Li and Martin 1991). However, in a multi-scale assessment of cavity-nesting bird habitat in streamside woodlands, nest plots and random plots were indistinguishable with regard to tree and snag density (Gutzwiller and Anderson 1987).

Northern flickers and hairy woodpeckers exhibited mixed responses in relation to nest placement and coarse woody debris volume. We hypothesized that avoidance of high coarse woody debris volume might reduce the risk of predation by small mammals, such as chipmunks (*Tamias spp.*) and tree squirrels (*Tamiasciurus spp.*) that use downed wood as runways, cover, or midden sites (Sutton 1992, Smith and Mannan 1994). Northern flickers used plots with higher volumes of coarse woody debris than those measured at non-nest random plots. It seems possible that northern flickers were trading off between foraging opportunities and avoidance of potential predation. Li and Martin (1991) surmised that nest-site selection is often a tradeoff between microhabitat, food availability, and avoidance of nest predation. Carpenter ants (*Camponotus spp.*) are the primary prey item of northern flickers (Moore 1995), and several ant species are associated with downed wood (Torgersen and Bull 1995, Lindgren and MacIsaac 2002), which may explain why flickers placed their nests in areas with high volumes of coarse woody debris. When we observed northern flickers foraging, however, they were primarily on ant mounds in open areas. Further investigation is required to determine if use of nest-sites with high volumes of coarse woody debris by northern flickers was driven by increased foraging opportunities. Hairy woodpecker nest-site selection was not influenced by coarse woody debris volume.

Cavity-nesting bird occurrence has been examined by some researchers as a function of landscape-level covariates (Lawler and Edwards 2002, Warren et al. 2005) and other work has linked predator density to landscape measures of canopy closure and nest predation rates (Tewksbury et al. 1998). Our single landscape covariate, proportion

of high canopy closure, played some role in nest-site selection of northern flickers. Northern flickers did not use nests that were in areas where the surrounding landscape included a high proportion of closed canopy. We found no evidence that canopy closure at a landscape scale affected nest use by hairy woodpeckers.

We expected that factors influencing nest-site selection would be consistent with those affecting nest survival (Nilsson 1984). Instead, daily nest survival was best explained by a constant rate for northern flickers and by a model that was in opposition to the best-supported nest-site selection model for hairy woodpeckers. Other studies report that habitat covariates were not an important influence on nest survival (or similar measures; Reynolds et al. 2001, Nur et al. 2004, Newlon 2005), whereas some studies provide evidence for a habitat influence on nest survival (Saab et al. 2007, Hitchcox 1998). Hitchcox (1998), while concluding that nest survival was higher in unlogged treatments, also reported that nest survival for northern flickers was not correlated with any microhabitat features.

Nest survival for northern flickers and hairy woodpeckers was not related to nest height or the diameter of the nesting substrate in our study. Several studies have documented positive relationships between nest height and nest survival (Li and Martin 1991, Burhans and Thompson 2006, Mahon and Martin 2006) yet others failed to find such a relationship (Nur et al. 2004, Burton and Mueller 2006). Nest height may not have been a factor in nest accessibility by predators in our study area. Avian predators (e.g. corvids) and small mammals are probably not as limited by heights as are larger predatory mammals. If small mammals and avian predators comprise the majority of

depredations in our study area then nest height may be less of a factor for nest survival. The girth of the nesting substrate has been implicated in measures of reproductive success in at least one study on cavity-nesting birds but diameter influenced clutch size rather than fledging success (Wiebe 2001). Cavity-nesting birds in our study tended to use larger diameter substrates for nesting and the variation in nesting substrate diameter was low relative to the range of available size classes. Such limited use of the available range of diameter size classes may have rendered our nest survival models insensitive to this covariate.

Live tree density at the microhabitat scale was not a factor in northern flicker nest survival in our study. Increasing live-tree density, in opposition to our prediction, positively influenced nest survival of hairy woodpeckers. This result was also in direct conflict with our hypothesis that woodpeckers would choose nests that conferred higher nest survival. Hairy woodpeckers, though considered opportunistic foragers (Sousa 1987), forage predominantly on standing snags or trees (Jackson et al. 2002). Hairy woodpeckers in our study may have been balancing between increased foraging opportunities in stands with high live-tree densities (a potential positive influence on nest survival) and increased predation risk that we assumed could be associated with these more dense stands (a potential negative influence on nest survival).

Nest survival for northern flickers and hairy woodpeckers was not tied to snag density in our study even though both species used nest sites with higher snag densities than that measured at random. The linkage between nest-site selection and nest survival was not evident. We predicted that higher snag density would confer higher nest survival

because potential predators might be "swamped" by more cavities to search in snag clumps. If nest predators use auditory (e.g., food begging by young) or olfactory cues to locate nests, then "swamping" will not be effective. The protective effect of any nest-site may also depend of the behavior of adult birds in response to the presence of predators, which varies by species (Bures and Pavel 2003). Quantification of nest cavities in snag clumps, the visibility of cavities from multiple angles, and an assessment of how adults approach the nest cavity when predators are nearby, could help elucidate whether nests in snag clumps are more protected than nests outside of clumps.

Hairy woodpecker nest survival was negatively influenced by coarse woody debris volume even though their nest site selection was apparently unaffected by this same covariate. We predicted that nest survival would be negatively influenced by coarse woody debris volumes due to higher occurrence of small mammalian predators in areas with runways and cover, but we also assumed that hairy woodpeckers would avoid nesting in areas with higher coarse woody debris volumes. Though the effect of coarse woody debris volume on nest survival was weak, at very high volumes (observed in our study) the effects on nest survival were marked. A volume threshold may exist, where there is a much greater chance of predation by small mammalian predators.

We expected to find lower nest-survival for nests surrounded by a higher proportion of closed forest canopy. Small mammals (potential nest predators) may be distributed unevenly across landscapes (Nupp and Swihart 2000) and some species are typically found in greater abundance where canopy closure is more complete (Tewksbury



et al. 1998, Nupp and Swihart 2000). Despite our expectations, nest-survival models including proportion of high canopy closure were not well supported.

Overall, our results do not support the "nest quality" hypothesis. Northern flickers seemed to choose nest locations without regard for the effects of habitat on nest survival. Nest survival of these woodpeckers may have been related to habitat covariates that we did not measure. Alternatively, we may have measured habitat covariates that affect nest survival, but not at the relevant spatial scale. For example, we measured the proportion of high canopy closure at a 1-km scale to capture the home range of the two woodpecker species in our study; however, nest survival may be more related to canopy closure immediately around the nest tree. Similarly, nest survival may be associated with coarse woody debris volume at the landscape scale as opposed to the microhabitat scale immediately surrounding the nest. Though hairy woodpecker nest-site selection was related to nest survival for at least two habitat covariates, those covariates did not appear to positively affect nest survival. Caution should be exercised in the interpretation of any relationship between nest-site selection and nest survival because habitat selection may be a result of long-term (multiple year) nesting success in the face of varying predation pressure (Forstmeier and Weiss 2004).

The lack of habitat effects on nest survival or other reproductive measures has been reported for many species (Filliater et al. 1994, Hitchcox 1998, Willson and Gende 2000). The relationship between habitat features and nest survival may also vary spatially (Chase 2002) or with predation pressure (De Santo et al. 2003). The abundance of predators (which may be linked to landscape-scale features) may also determine nesting

success as opposed to within-stand habitat features or nest-patch habitat (Rodewald and Yahner 2001). Manipulations of predator communities has led to the realization that "safe" nest sites may not be available in areas with diverse predator communities (Dion et al. 2000). Cavity-nesting birds, which require a specific substrate (dead and dying trees) to meet important life history requirements (nesting, roosting, and foraging), may be limited in choosing "safe" sites.

Nest survival estimates for both species in our study were low compared to recent estimates for primary cavity-nesting birds using similar methods. Nest survival for northern flickers has been reported to vary from a low of 49% to high of 100% (Li and Martin 1991) and nest survival for hairy woodpeckers is reported to vary from a low of 46% (this study) to a high of 91% (Li and Martin 1991, Saab et al. 2007). Our nest survival estimates across all locations for both species were on the lower end or in the middle of these ranges. Nest survival in Idaho was particularly low for both species compared to other studies (Hejl et al. unpublished, Li and Martin 1991, Saab and Dudley 1998, Saab et al. 2007). Preliminary analysis of tree squirrel (*Tamiasciurus hudsonicus* and *Tamiasciurus douglasii*) densities in our three study locations revealed that squirrel densities were highest in Idaho (0.62 squirrels/ha) followed by Washington (0.17 squirrels/ha), and Oregon (0.10 squirrels/ha; Saab, Russell and others unpublished data).

Our ability to detect a relationship between habitat features at used nest sites and subsequent nest survival may have been limited simply by the range of habitat conditions that were available and hence represented at used sites. In general, woodpeckers in our study were presented with a narrow spectrum of snag diameters and snag densities from

which to choose nest sites. Few relationships were observed between habitat features and nest survival. Relationships might have been observed for some habitat features if a broader range of habitat values existed. Comparison of our results to similar studies in forests representing a broader range of conditions will be useful for a better understanding of habitat influences on nest survival. We recommend replication of studies such as ours in areas where a large sample size can be achieved across a gradient of habitat conditions (possibly including recently disturbed areas where snag densities may be higher and live-tree densities may be lower). Investigation of recently disturbed areas immediately adjacent to areas that have not been disturbed will help elucidate the relative value of these forest conditions to woodpecker populations.

#### Management Implications

Northern flickers and hairy woodpeckers often create the majority of cavities used by other cavity-nesting birds (Saab et al. 2004). Northern flickers have been described as regionally abundant but locally rare in many parts of the United States and both species have probably declined (Moore 1995, Jackson et al. 2002). For the long-term persistence of these species (and dependent cavity-nesting vertebrates) habitat requirements should be identified in a variety of vegetation associations and conditions, and the relative contribution of these habitats to maintenance of their populations.

Our results show that large snags occurring in clumps are important to cavity-nesting birds. Processes that encourage the development of these snags clumps should be maintained (e.g., single-snag fires started by lightning). Larger scale forest processes that

maintain snag clumps within a matrix of live trees should also be considered. In ponderosa pine stands in Arizona bark beetle attacks (*Dendroctonus spp.* and *Ips spp.*) occurred in "scattered small infestations in groups of 1-10 trees" (Sanchez-Martinez and Wagner 2002). Bark beetle populations may be regulated by periodic disturbance by fire and their impact is likely regulated by ground fires (Santoro et al. 2001) hence maintenance of low to mixed-severity fires regimes may be crucial for woodpecker population persistence.

Nest survival for woodpeckers in our study was low compared to similar studies in recently disturbed sites (Hitchcox 1998, Saab et al. 2007). Forested areas subject to recent wildfire may provide woodpeckers and other cavity-nesting birds with ephemeral source habitats (abundant foraging, nesting and roosting sites) and reduced nest predation compared to sites with little recent disturbance (Saab and Vierling 2001, Saab et al. 2007).

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APPENDIX A

SUMMARY STATISTICS FOR HABITAT COVARIATES USED IN NEST-SITE SELECTION AND NEST SURVIVAL MODELS BY STATE: WASHINGTON (WA), IDAHO (ID), OREGON (OR), ALL THREE STATES COMBINED (ALL).



Appendix A: Summary statistics for habitat covariates used in nest-site selection and nest survival models by state: Washington (WA), Idaho (ID), Oregon (OR), all three states combined (ALL).

State	Species or Random		NESTHT	DBH	TREEDEN	SNAGDEN	CWD	PROPHIGH
WA	Random	mean		35.1	116.7	6.6	30.9	0.45
		SE		1.2	4.9	0.8	2.7	0.01
		N		119	119	119	119	119
	HAWO	mean	11.8	47.4	76.3	10.0	26.6	0.49
		SE	1.1	2.4	8.56	1.7	5.6	0.03
		n	23	23	23	23	23	23
	NOFL	mean	13.5	56.2	84.36	8.3	34.1	0.41
		SE	1.0	2.0	6.35	1.3	4.7	0.02
		n	44	44	44	44	44	44
ID	Random	mean		51.2	88.12	7.9	39.6	0.62
		SE		2.2	5.45	1.0	3.8	0.02
		N		109	109	109	109	109
	HAWO	mean	12.9	69.3	53.67	15.8	53.9	0.60
		SE	1.6	4.1	7.03	2.5	7.5	0.03
		n	30	30	30	30	30	30
	NOFL	mean	15.7	74.0	55.86	13.7	53.7	0.56
		SE	1.3	2.6	5.05	1.7	5.0	0.02
		n	69	69	69	69	69	69
OR	Random	mean		33.9	123.56	8.0	53.2	0.37
		SE		1.2	5.55	1.8	4.7	0.03
		n		80	80	80	80	80
	HAWO	mean	9.6	45.1	110.84	17.1	63.8	0.42
		SE	1.5	6.8	12.92	3.3	8.8	0.06
		n	19	19	19	19	19	19
	NOFL	mean	6.6	46.2	115.00	14.0	66.4	0.29
		SE	0.8	2.8	9.60	2.6	8.5	0.04
		n	38	38	38	38	38	38
ALL	Random	mean		40.5	108.5	7.4	39.8	0.491
		SE		1.0	3.2	0.7	2.1	0.013
		N		308	308	308	308	308
	Available	mean		43.8	103	6	40	0.49
		SE		1.1	3.3	0.7	2.3	0.014
		N		276	276	276	276	276
	HAWO	mean	11.7	55.9	76.0	14.3	47.7	0.517
		SE	0.9	2.9	5.9	1.5	4.6	0.024
		N	72	72	72	72	72	72
	NOFL	mean	12.8	61.8	79.0	12.2	51.2	0.447
		SE	0.7	1.8	4.3	1.1	3.5	0.017
		n	151	151	151	151	151	151