AN ABSTRACT OF THE THESIS OF

<u>Karen Viste-Sparkman</u> for the degree of <u>Master of Science</u> in <u>Wildlife Science</u> presented on <u>December 13, 2005</u>.

Title: White-breasted Nuthatch Density and Nesting Ecology in Oak Woodlands of the Willamette Valley, Oregon.

Abstract approved:

Richard A. Schmitz

Habitat loss causes a reduction in available resources for wildlife, alters the configuration of remaining habitat, and may isolate wildlife populations. Whitebreasted nuthatches (Sitta carolinensis) are experiencing long-term population declines in the Willamette Valley of Oregon, where they are historically associated with oak woodlands. As secondary cavity-nesters, white-breasted nuthatches may be limited by the availability of existing cavities for nesting and roosting. Oak vegetation in the Willamette Valley has changed since European-American settlement times from vast areas of open oak savanna to isolated closed-canopy stands separated by agricultural fields. We examined nuthatch density, nest cavity selection, and nest success in relation to oak woodland structure and landscape context. We conducted point transect surveys in 3 strata: woodland interiors, large woodland edges, and small woodlands. We located and monitored nuthatch nests and sampled vegetation at nest locations and matching random locations around each nest. Woodland structure and edge density were measured at a 178-m radius (home range) scale, and landscape context was measured using vegetation cover within a 1-km radius around point

transects and nests. We used program DISTANCE to fit detection functions and calculate nuthatch densities. We used conditional logistic regression to compare nest locations with random locations, and analyzed nest success with Mayfield logistic regression. White-breasted nuthatch density was significantly higher in small woodlands than in edges of large woodlands, which had higher nuthatch density than woodland interiors. Density of nuthatches increased with a combination of oak cover within a 1-km radius of the point, edge density within a 178-m radius, and number of oak trees >50 cm diameter at breast height (dbh) within a 100-m radius. Nest cavities were situated in oak trees containing more cavities than random oak trees that had cavities, and oak trees used as nest trees had a larger dbh than oak trees within random plots. Local woodland structure at nest locations was characterized by larger trees, measured by greater mean dbh, canopy cover, and basal area of oaks than random locations within the home range. Nest success in natural cavities was 71% and was not predicted by attributes of nest cavities, nest trees, local woodland structure at nests, woodland structure at the home range scale, or landscape context. These results suggest that the most suitable habitat for white-breasted nuthatches in the Willamette Valley includes oak woodlands in close proximity to one another with a high proportion of edge and mature oak trees. Managers should preserve trees containing cavities and large oak trees whenever possible. Thinning of small oaks and removal of conifers in oak woodlands to create more open, savanna-like conditions may also promote the development of larger oaks with more spreading branches, providing more opportunities for cavities to form and more foraging surface area for nuthatches.

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White-breasted Nuthatch Density and Nesting Ecology in Oak Woodlands of the Willamette Valley, Oregon

by Karen Viste-Sparkman

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APPROVED:
Major Professor, representing Wildlife Science
Head of the Department of Fisheries and Wildlife
Dean of the Graduate School
I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.
Karen Viste-Sparkman, Author

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WHITE-BREASTED NUTHATCH DENSITY AND NESTING ECOLOGY IN OAK WOODLANDS OF THE WILLAMETTE VALLEY, OREGON

CHAPTER 1: GENERAL INTRODUCTION

The vegetation of the Willamette Valley of Oregon has undergone dramatic changes since the onset of European-American settlement in the early 1800s, with a loss of more than 80% of oak cover and 99% of oak savanna (Defenders of Wildlife 1998). Prior to 1848, natural fires and frequent burning by indigenous people maintained a landscape of expansive prairie and open Oregon white oak (*Quercus garryana*) savanna (Sprague and Hansen 1946, Habeck 1961, Thilenius 1968, Johannessen et al. 1971). In areas that were not cleared for agriculture by the arriving settlers, fire suppression promoted the succession of oak savannas and prairies into dense oak woodlands (Habeck 1961, Thilenius 1968, Towle 1982). In the prolonged absence of fire, succession of oak woodlands has continued to Douglas-fir (*Pseudotsuga menziesii*) forest (Franklin and Dyrness 1988).

Oak woodlands that remain in the Willamette Valley today hold little monetary value, and face ongoing clearing for agriculture, Douglas-fir plantations, Christmas tree farms, vineyards, and housing for the expanding human population. Today, most remaining oaks grow in dense, even-aged woodlands less than 150 years old, sometimes surrounding remnant savanna oaks (Habeck 1961, Thilenius 1968). Forest-grown oaks form tall trees with ascending branches and narrow crowns, rather than the wide, spreading branches and mushroom-shaped crowns of open-grown savanna trees. In summary, during the last 150 to 200 years, the Willamette Valley landscape has

changed in the amount and configuration of oak cover, from extensive areas of open savannas to discrete closed-canopy stands surrounded by farm fields. With the continued clearing of oak woodlands, oak-associated species experience both habitat loss and further isolation of remaining populations.

Because of its importance to wildlife, Oregon white oak habitat is considered a conservation priority by Partners in Flight (Altman 2000) and the Oregon Department of Fish and Wildlife (Campbell 2004). Recent interest by land management agencies and conservation organizations has resulted in increased efforts to preserve and restore remnant oak savanna and woodland, as well as to establish future oak savanna. However, little information exists on specific habitat associations of oak-associated wildlife in the Willamette Valley.

White-breasted nuthatches (*Sitta carolinensis*) are wide-spread throughout deciduous woodlands of North America (Pravosudov and Grubb 1993). Nuthatches are closely associated with oak woodlands in the Willamette Valley, where they maintain territories year-round (Anderson 1970a, 1972; Hagar and Stern 2001). The slender-billed white-breasted nuthatch (*S. c. aculeata*) is found west of the Cascade and Sierra Nevada Mountains (Gabrielson and Jewett 1940). According to Breeding Bird Survey trends, this subspecies has experienced an insignificant decline of -6.4% (CI, -20.1%, 7.4%) per year in the Willamette Valley between 1966 and 2004, although the sample size is small (n=8 routes, average count = 1.1)(Sauer et al. 2005). The slender-billed white-breasted nuthatch is thought to be extirpated from the Puget Sound area, and is a state candidate species and a federal species of concern in

Washington state (U.S. Fish and Wildlife Service 2005, Washington Department of Fish and Wildlife 2005). Partners in Flight has designated the white-breasted nuthatch a focal species for conservation in western Oregon and Washington, associated with large oak woodlands and large trees (Altman 2000).

The white-breasted nuthatch population decline indicates that a loss of habitat may be continuing. Bird species that have increased in Willamette Valley oak woodlands in recent decades are those more associated with closed-canopy conifer forest (Hagar and Stern 2001). Conifer forest is much more abundant than oak woodland in western Oregon, so oak obligates such as white-breasted nuthatches justify unique emphasis in forest management.

Densities of white-breasted nuthatches in 5 Oregon white oak stands in the Willamette Valley fluctuated between 1 and 4 birds/10 ha throughout the year (Anderson 1970a). Breeding densities from around North America range from 0.5 to 4.9 pairs/10 ha, and are mainly between 1 and 2 pairs/10 ha (Stallcup 1968, Brawn and Balda 1988, Welsh et al. 1992, Matthysen 1998). In previous studies, vegetation variables that were correlated with abundance of white-breasted nuthatches in Willamette Valley oak woodlands included average length of secondary branches, vegetation in the upper layer, and distance between trees (Anderson 1970b, 1980). A recent study of bird abundance in oak woodlands of the Willamette Valley found that frequency of occurrence of white-breasted nuthatches showed negative correlations with oak subcanopy cover and Douglas-fir canopy cover, and a positive correlation with average diameter of oak (Hagar and Stern 2001). In an oak woodland in

California, white-breasted nuthatches were generally associated with low tree density (<100 trees/ha) and large tree diameter (>50 cm dbh)(Wilson et al. 1991).

White-breasted nuthatches forage by gleaning arthropods from the bark of tree trunks and branches. In Willamette Valley oak woodlands, frequency of foraging was highest on primary branches, followed by tree trunks, then secondary branches (Anderson 1970b). In a mixed deciduous forest in Illinois, oaks were the preferred foraging species, and the most common foraging sites were live branches more than 7.5 cm in diameter (Willson 1970). In a California blue oak (*Q. douglasii*) and coast live oak (*Q. agrifolia*) woodland, foraging took place primarily in deciduous trees, on limbs more than 5 cm in diameter, and at heights greater than 6 m (Wagner 1981). Nuthatches in Oregon consume a variety of invertebrates, including Araneida, Forficulidae (Dermaptera), Pentatomidae (Hemiptera), Elateridae, Curculionidae and Chrysomelidae (Coleoptera), and Phalaenidae (Lepidoptera)(Anderson 1976). In winter, they may also forage on shrubs, and augment their diet with plant material such as sedge seeds (Anderson 1976).

White-breasted nuthatches are secondary cavity-nesters or weak cavity excavators, dependent on naturally-occurring cavities (Pravosudov and Grubb 1993). Because their densities are naturally lower than many other songbirds in similar habitats, white-breasted nuthatches are often represented in low numbers in multispecies studies. Published data on nesting ecology are scarce and usually involve small sample sizes. Nest cavities are located predominantly in natural cavities of living trees, but sometimes in woodpecker-excavated holes (Bent 1948, McEllin 1979,

Ritchison 1981). Nest cavity heights range between about 1 and 20 m (Bent 1948). Mean cavity height was 6.2 m with a range of 4 to 12 m (n = 5) in a study in a Minnesota mixed forest (Ritchison 1981). Of 7 nests in ponderosa pine (*Pinus ponderosa*) forest in Colorado, mean nest height was 9.0 m (CI, 7.8 to 10.2 m), with a range of 7.5 to 12.3 m, and mean nest tree dbh was 53.8 cm (CI, 50.7 to 56.8 cm)(McEllin 1979). In riparian woodlands of Iowa, mean height of 9 nests was 7.2 m (CI, 5.2 to 9.2 m), and diameter of the tree at nest height was 33.2 cm (CI, 24.6 to 41.8 cm)(Stauffer and Best 1982).

We undertook this study in an effort to understand what features of Willamette Valley oak woodlands are associated with white-breasted nuthatch density, nest cavity selection, and nest success.

In chapter 2, we examine the relationship between white-breasted nuthatch density and Willamette Valley oak woodland structure and landscape context.

Specifically, we make a comparison between white-breasted nuthatch density in large woodland interiors, edges of large woodlands, and small woodlands. We then look at the importance of tree size, edge density, and proportion of oak woodland at a homerange scale (178-m radius) and proportion of oak woodland and conifer forest within the landscape context (1-km radius) in predicting nuthatch density.

In chapter 3, we investigate white-breasted nuthatch nest cavity selection and nest success in Willamette Valley oak woodlands. We look at nuthatch selection of nest trees by comparing attributes of nest trees with those of random trees available to nuthatches. We then compare the local woodland structure around nests with

woodland structure at random locations within a home-range scale. In addition, we consider how attributes of nest cavities, nest trees, woodland structure surrounding nests, and landscape context influence nest success.

Finally, in chapter 4 we make general conclusions about what we have learned about the use of Willamette Valley oak woodlands by white-breasted nuthatches. We assess how the results of this research contribute to the conservation of white-breasted nuthatches in Willamette Valley oak woodlands, and make management recommendations based on our findings.

CHAPTER 2: RELATIONSHIP BETWEEN WHITE-BREASTED NUTHATCH DENSITY AND OAK WOODLAND STRUCTURE AND CONTEXT

Introduction

Habitat loss reduces the extent of resources available for wildlife, changes the configuration of remaining habitat, and may isolate wildlife populations. Loss of oak savanna and oak woodlands in the Willamette Valley of Oregon has resulted in many small fragments of oak woodland, possibly isolating populations of oak-associated species like the white-breasted nuthatch (*Sitta carolinensis*). In addition, the structure of remaining oak woodlands has changed due to fire suppression.

Since European-American settlement of the Willamette Valley began in the early 1800s, its vegetation has undergone extreme changes. Prior to 1848 and dating back to at least 1647, vast expanses of prairie and open Oregon white oak (*Quercus garryana*) savanna were maintained by frequent fires, naturally occurring or set by indigenous people (Sprague and Hansen 1946, Habeck 1961, Thilenius 1968, Johannessen et al. 1971). With settlement of the valley came the suppression of fire, and oak savannas and prairies that were not cleared for agriculture developed into dense oak woodlands (Habeck 1961, Thilenius 1968, Towle 1982), and oak woodland succeeded into Douglas-fir (*Pseudotsuga menziesii*) forest (Franklin and Dyrness 1988). More recently, Douglas-fir plantations, Christmas tree farms, vineyards, and housing developments have replaced oak woodlands. Thus, over the last 150 to 200 years, Willamette Valley oak vegetation has changed in its extent, configuration, and structure, from extensive areas of sparse trees to isolated small woodlots and large

woodlands consisting of closely-spaced trees. Continued clearing of oaks contributes to both habitat loss and further isolation of the remaining oak woodlands.

The white-breasted nuthatch is a weak cavity excavator that is closely associated with oak woodlands in the Willamette Valley (Hagar and Stern 2001). The west coast subspecies, the slender-billed white-breasted nuthatch (*S. c. aculeata*) (Gabrielson and Jewett 1940), has been extirpated from the Puget Sound area and is a state candidate species and a federal species of concern in Washington state (U.S. Fish and Wildlife Service 2005, Washington Department of Fish and Wildlife 2005). The white-breasted nuthatch was designated by Partners in Flight as a focal species for oak woodland conservation in western Oregon and Washington, highly associated with large patches of oak woodland with large trees (Altman 2000).

Although few studies have been conducted on birds of Willamette Valley oak woodlands, previous research has identified some of the associations between woodland structure and the white-breasted nuthatch in the Willamette Valley (Anderson 1970b, 1980; Hagar and Stern 2001). While vegetation structure associations of birds are important in determining occupation of habitat, fragmentation of the surrounding landscape may also affect bird populations. Woodland fragmentation results in smaller woodland size, higher edge-to-interior ratio, further isolation from other woodlands, and a lower proportion of woodland in the landscape (Saunders et al. 1991, Fahrig 2003), which may influence bird densities. Non-migratory birds such as the white-breasted nuthatch (Pravosudov and Grubb 1993) may be less likely to travel large distances to inhabit isolated woodland fragments

(Andrén 1994). Researchers have increased efforts to examine habitat associations at multiple spatial scales to determine the relationship of bird densities with vegetation features at both the home range and landscape scales (Wiens 1989, Knick and Rotenberry 1995, Mazerolle and Villard 1999, Saab 1999, Hagan and Meehan 2002, MacFaden and Capen 2002).

We undertook this study in an effort to understand what attributes of oak woodlands were associated with white-breasted nuthatch density. The first objective of our study was to determine differences in white-breasted nuthatch density between large woodland interiors, edges of large woodlands, and small woodlands. The second was to identify attributes of woodland structure and configuration at the home range scale (178-m radius) and landscape context (forest cover within a 1-km radius) that are associated with density of white-breasted nuthatches.

Study Area

We conducted this study in Oregon white oak woodlands within the Willamette Valley of northwestern Oregon, including parts of Yamhill, Polk, Benton, and Linn Counties. Oak woodlands used as study sites consisted of large, dense stands of oak mixed with Douglas-fir, stands in low areas mixed with Oregon ash (*Fraxinus latifolia*), and small woodlots. All woodlands used as study sites were composed of at least 50% oak. Oregon white oak was the only native oak occurring within the study area. Land use in the Willamette Valley was predominantly agricultural, urban, and residential, with over 95% of land in private ownership

(Defenders of Wildlife 1998). Agricultural lands, other open vegetation types, or rural residential areas surrounded oak woodlands.

Study sites were individual woodlands of varying sizes ranging from about 0.2 to 344 ha. Study sites were chosen based on access and woodland size, and included rural property owned by 18 private landowners, 3 parcels of state land owned by Oregon State University and Oregon Department of Fish and Wildlife, and 3 National Wildlife Refuge units. Because we were not able to pick study sites randomly, we will confine our inferences to the study area.

Methods

Distance Sampling

To determine densities of white-breasted nuthatches in oak woodlands, we used distance sampling with point transects (Buckland et al. 2001, Thomas et al. 2002). Distance sampling is a method of estimating densities of objects of interest even if not all objects are detected. In point transects, the radial distance from a survey point to each animal detected is used to calculate a detection function, based on the premise that detectability of an animal decreases as distance to the object increases (Buckland et al. 2001). The key assumptions of distance sampling are: survey points are located randomly with respect to the animals being detected; all animals at the point are detected with certainty; animals are detected prior to movement in response to the observer; and distances to animals are accurately measured (Buckland et al. 2001).

We placed point transects into 3 strata. Woodland interior points were located in woodlands >100 ha and more than 130 m from an oak woodland/herbaceous field edge. Large woodland edge points were located in woodlands >25 ha, within 65 m of a woodland/field edge in 1 direction and more than 100 m from an edge in the opposite direction. Small woodland points were located in woodlands <12 ha and within 65 m of an edge in each of 2 opposing directions. Previous bird studies have found ecological processes such as predation, parasitism, and resource acquisition associated with edges (edge effects) usually occur within 50 m of a forest edge (Paton 1994). We considered any opening in the tree canopy with a minimum diameter of 50 m to contribute to an edge. This approximated the recommendation of classifying a minimum opening diameter of 3 times the canopy height as an edge (Paton 1994). The number of points in each stratum was limited to 20 by availability and accessibility of oak woodland, and we visited each point 3 times, with the exception of 2 points that we visited only twice. Because of the distribution and accessibility of oak woodlands of varying sizes, 20 interior points were located within 5 large woodlands ranging from 103 to 230 ha, 20 edge points were located within 10 large woodlands between 25 and 344 ha, and 20 points were located in 19 small woodlands, which were 0.2 to 11.1 ha in size. We used ArcView 3.2 (Environmental Systems Research Institute 1992-1999) to randomly choose points within strata at least 225 meters apart to avoid double-counting birds.

We conducted sampling during the period when most white-breasted nuthatches were incubating eggs and feeding nestlings (Gabrielson and Jewett 1940,

Adamus et al. 2001). White-breasted nuthatches frequently vocalize while foraging and visiting nests, and were therefore easily detectable. Surveys took place during the first 4 hours after sunrise to maximize detection rates. Each survey lasted 10 minutes to allow maximum detection of birds (Ralph et al. 1993) after a 1-minute waiting period to allow birds to resume normal activity (Reynolds et al. 1980). To maximize bird detection, we did not conduct surveys during windy or rainy weather (Robbins 1981). A single observer experienced in identification of the region's birds by sight and sound conducted all sampling.

We recorded the species, number, and distance to location of first detection for all birds detected. Whenever possible we measured the distance to the nearest meter for each observation using a laser rangefinder (Bushnell Yardage Pro 500®, Bushnell Corp., Overland Park, Kansas). In dense forest and at distances less than 20 meters, we estimated the distance to the observation. Flyovers were not included in the analysis.

Vegetation Sampling

We sampled vegetation within 0.04-ha (11.3-m radius) circular plots centered on each point (James and Shugart 1970), and within 3 0.04-ha plots at random distances within 100 m of each point. All randomly placed plots were 120 degrees from each other, with the direction of the first plot picked at random. The location of each point was recorded with a Global Positioning System (GPS) receiver. The number of each tree species was recorded within 5 size classes based on dbh: 3-10 cm,

11-30 cm, 31-50 cm, 51-70 cm, and ≥71 cm. Canopy cover (%), canopy height (m), groundcover layer cover (%) and composition, and shrub layer cover (%) and composition were also recorded. Distance from the point to the nearest forest/non-forest edge was measured with a tape measure or laser rangefinder for distances less than 50 m, and using Digital Orthophoto Quadrangle (DOQ) aerial photos and ArcGIS software (Environmental Systems Research Institute 1999-2005) for distances greater than 50 m.

The proportion of oak woodland and edge density (km/km²) within a 314-ha area (1-km radius) and within a 10-ha area (178-m radius) around each point count station were determined using 1:24,000 Willamette Valley GIS vegetation data layers (Klock and Barrett 1998) and ArcGIS software (Environmental Systems Research Institute 1999-2005). The 10-ha area was used as an estimate of a typical home range size for the white-breasted nuthatch (Stallcup 1968, Anderson 1970a, Brawn and Balda 1988, Welsh et al. 1992, Matthysen 1998).

Statistical Analysis

We used program DISTANCE version 4.1 (Thomas et al. 2004) to estimate density of white-breasted nuthatches (Buckland et al. 2001, 2004). This program fitted detection functions using the key detection functions/adjustment terms: uniform/cosine, uniform/simple polynomial, half-normal/cosine, half-normal/hermite polynomial, hazard-rate/cosine, and hazard-rate simple polynomial (Buckland et al. 2001). We examined histograms of the data, detection probability plots, probability

density plots, and chi-square goodness-of-fit statistics to determine the best grouping intervals and truncation distance for the data and to assess the fit (Buckland et al. 2001). We then identified the best model among the detection functions as the one with the lowest Akaike's Information Criterion, adjusted for small sample size (AIC_c) (Hurvich and Tsai 1989, Burnham and Anderson 2002). The difference between each model and the best model was calculated as ΔAIC_c . All models within 2 ΔAIC_c of the top model were considered to be competing models (Burnham and Anderson 2002). Modeling the detection function produced an estimate of the proportion of individuals detected and an estimate of density weighted by survey effort.

For the first analysis, we compared density estimates between the 3 strata to determine if nuthatch density differed between them. Acoustic properties between forest vegetation features can vary because of scattering of sound caused by foliage and tree trunks and fluctuations in air currents (Richards 1981), which may differ with forest structure or terrain. Any differences in density estimates between the woodland types could have been caused by differences in detectability. To compare detectability between strata, we chose the black-capped chickadee (*Poecile atricapillus*) as a species expected to have similar detectability as the white-breasted nuthatch based on its vocal qualities and behavior, and fit a detection function to determine density estimates within the three strata. For both nuthatch and chickadee data, density estimates were the mean of stratum estimates weighted by effort in stratum. Program DISTANCE produced variance for the density estimates in the final model by bootstrapping 999 samples within strata. The 2.5% and 97.5% quantiles of bootstrap

covariance estimates were used as confidence intervals. Because not all strata contained adequate detections to fit separate detection functions for the nuthatch and chickadee data, we used the global detection function to estimate densities. Since density estimates were not independently derived, we used the delta method to calculate differences between density estimates derived independently of the global detection function, using the *Z*-statistic and variances based on sample size to construct confidence intervals for differences between the density estimates (Buckland et al. 2001).

We used multiple covariate distance sampling, with attributes of woodland structure and landscape context as covariates, to determine how they were associated with the estimated nuthatch density for each count. Covariates were modeled in the scale parameter of the detection function (Buckland et al. 2001). This enabled us to parse out in more detail particular attributes of woodland structure and landscape context that predicted density estimates. We chose covariates after examining Pearson correlation coefficients and histograms of data. To limit the number of variables, we modeled highly correlated variables (r > 0.7) individually and identified the one with the best model fit based on the AIC $_c$. We included in the analysis 7 variables that we thought were important in determining white-breasted nuthatch presence at a site, comprising 2 covariates for oak tree size classes, 2 covariates for vegetation cover at a 178-m radius (home range) scale, and 2 covariates for vegetation cover at the landscape context (1-km radius) scale, and a covariate for stratum. We included number of small oaks (3-10 cm) and number of large oaks (\geq 50 cm dbh) from all 4

0.04-ha plots because we hypothesized that tree size would be important in predicting nuthatch density. Previous research in the Willamette Valley found that nuthatch density was negatively associated with oak subcanopy cover and positively associated with mean oak diameter (Hagar and Stern 2001). A study of oak woodlands in California found that white-breasted nuthatches were generally associated with large tree diameter (>50 cm dbh)(Wilson et al. 1991). Edge density in km/km² between forest and non-forest vegetation types within 178 m of the survey point was included because we hypothesized that nuthatches were associated with oak woodland edges. In previous studies throughout its range, the white-breasted nuthatch has been classified as an edge species (Sisk and Margules 1993) and an interior species (Blake and Karr 1987). Because nuthatches are strongly associated with oaks (Anderson 1970b, Hagar and Stern 2001), we included variables for percent oak cover within 178 m and percent oak cover within 1 km of the point to test the hypotheses that a larger percentage of oak at the home range scale and landscape context scale affect nuthatch density. We also included percent conifer cover within 1 km because nuthatches were previously found to have a negative correlation with conifer cover (Hagar and Stern 2001). A variable for stratum was included to determine how the 3 strata were associated with nuthatch density relative to other attributes of woodland structure and landscape context.

We modeled all 2-variable combinations, with the exception of those that were highly correlated. In addition, 3-variable combinations that included 1 variable from each scale were modeled (with the exception of variables that were highly correlated),

as well as the null and global models. We identified the best model as the one with the lowest AIC_c. For each model, we calculated Akaike weights (w_i) using the formula

$$W_{i} = \frac{\exp(-0.5 * \Delta_{i})}{\sum_{r=1}^{R} \exp(-0.5 * \Delta_{r})},$$

given the set of R models, where Δ_i is the difference between the AIC_c of an individual model and the lowest AIC_c (Burnham and Anderson 2002). The Akaike weight is the probability for each model, with the sum of all Akaike weights equal to 1 (Burnham and Anderson 2002). We summed the Akaike weights for all models containing each covariate to calculate variable relative importance weights $[w_+(i)]$.

Results

We detected 2,950 birds of 79 species, including 85 white-breasted nuthatches and 100 black-capped chickadees, during point transect sampling between 12 April and 17 June 2004. We detected 901 birds of 53 species in woodland interiors, 983 birds of 65 species in large woodland edges, and 1,066 birds of 62 species in small woodlands. Six white-breasted nuthatch detections occurred in woodland interiors, 25 in large woodland edges, and 54 in small woodlands. After truncating the 5% of detections at the greatest distance (n = 4) and grouping into 6 distance intervals, a half-normal key detection function with hermite series expansion provided the best fit to the nuthatch data (P = 0.998), 0.27 AIC $_c$ units better than uniform key function with cosine series expansion.

Without covariates, the pooled density estimate of white-breasted nuthatches for the 3 strata combined was 0.14 nuthatches/ha (CI, 0.09 to 0.21), or about 7.1 ha per nuthatch. There were 0.03 nuthatches/ha in interior woodlands (CI, 0.01 to 0.07), 0.12 nuthatches/ha in large woodland edges (CI, 0.06 to 0.20), and 0.27 nuthatches/ha in small woodlands (CI, 0.17 to 0.42).

Stratification into the 3 types of oak woodland resulted in nuthatch density estimates that were significantly different between all strata. There were 0.14 more nuthatches/ha in small woodlands than large woodland edges (CI, 0.05 to 0.25), 0.09 more nuthatches/ha in large woodland edges than woodland interiors (CI, 0.02 to 0.15) and 0.23 more nuthatches/ha in small woodlands than woodland interiors (CI, 0.14 to 0.33).

Thirty-seven black-capped chickadee detections occurred in woodland interiors, 43 in large woodland edges, and 20 in small woodlands. After truncating the 5% of detections at the greatest distance (n = 5) and grouping into 6 intervals, we found the best fit to the chickadee data (P = 0.992) using the half-normal key detection function with hermite series expansion. Overall chickadee density was 0.25 chickadees/ha (CI, 0.17 to 0.36). Large woodland edges had the highest density, at 0.34 chickadees/ha (CI, 0.22 to 0.49), followed by interior woodlands with 0.29 chickadees/ha (CI, 0.16 to 0.46), and small woodlands with 0.14 chickadees/ha (CI, 0.08 to 0.23). When we used the delta method to calculate differences in density between strata and construct confidence intervals, there were 0.20 fewer chickadees/ha in small woodlands than in large edges (CI, -0.33 to -0.06), and 0.15 fewer

chickadees/ha (CI, -0.28 to -0.01) in small woodlands than in woodland interiors. There was essentially no difference in chickadee density between woodland interiors and large woodland edges (CI, -0.21 to 0.11). This trend was in contrast to differences in nuthatch densities between strata, suggesting that differences between strata were due to actual densities of birds rather than detectability differences between oak woodland types.

To model covariates, we compiled a suite of 32 candidate models using combinations of 7 attributes of oak woodlands, including stratum (Table 2.1). Percent oak cover within 178 m and percent oak cover within 1 km were highly correlated (r = 0.791), as were stratum and edge density (r = 0.738), stratum and percent oak cover within 178 m (r = 0.876), and stratum and percent oak cover within 1 km (r = 0.807), so these variables were not included together in models.

When we modeled covariates using the nuthatch data, the top model included the proportion of oak woodland within 1 km, edge density, and number of large oaks (Tables 2.2 and 2.3). Number of small oaks also appeared in competing models. The variable relative importance weights suggested that percent oak cover within 1 km $[w_+(i)=0.921]$ was the most important determinant of nuthatch density, followed by edge density $[w_+(i)=0.772]$, number of large oak trees $[w_+(i)=0.346]$, and number of small oak trees $[w_+(i)=0.327]$. Percent oak cover at both scales (1-km and 178-m radius), edge density, and number of large oak trees were all positively associated with estimates of nuthatch density, while number of small trees and percent conifer cover had negative associations with nuthatch density.

Table 2.1. Summary statistics for woodland attributes associated with 60 point transects in 3 strata of Willamette Valley, OR oak woodlands between 12 April and 17 June 2004.

	Woodland interior			Lar	ge wo	odland	edge	Small woodland			All points					
(n = 20)			(n = 20)			(n = 20)				(n = 60)						
Woodland attribute	$\overline{\overline{x}}$	SE	Min.	Max.	$\overline{\overline{x}}$	SE	Min.	Max.	$\overline{\overline{x}}$	SE	Min.	Max.	\overline{x}	SE	Min.	Max.
Percent oak cover within 1 km (%)	45.4	3.6	17.2	65.1	27.6	2.8	10.9	53.3	6.3	1.0	0.6	17.8	26.4	2.6	0.6	65.1
Edge density ^a (km/km ²)	0.9	0.3	0.0	3.9	7.4	0.6	3.8	13.0	7.9	0.6	2.9	13.5	5.4	0.5	0.0	13.5
Large oaks ^b (trees/0.16 ha)	2.4	0.4	0.0	6.0	2.8	0.6	0.0	12.0	2.9	0.7	0.0	10.0	2.7	0.3	0.0	12.0
Small oaks ^c (trees/0.16 ha)	33.0	9.8	0.0	136.0	23.8	8.7	0.0	166.0	1.4	0.7	0.0	12.0	19.4	4.6	0.0	166.0
Percent oak cover within 178 m (%)	94.8	2.6	59.8	100.0	53.5	3.7	21.3	83.4	27.0	3.8	5.5	62.4	58.5	4.1	5.5	100.0
Percent conifer cover within 1 km (%)	9.8	3.0	0.0	42.9	6.9	2.3	0.0	35.4	2.0	1.0	0.0	20.3	6.2	1.3	0.0	42.9

^aDensity of forest/field edge within 178 m of the survey point.

^bOak trees >50 cm diameter at breast height in 4 0.04-ha plots within 100 m of the survey point.

^cOak trees ≤10 cm diameter at breast height in 4 0.04-ha plots within 100 m of the survey point.

Table 2.2. Models of woodland attributes used in predicting white-breasted nuthatch density at 60 points in Willamette Valley, OR oak woodlands between 12 April and 17 June 2004.

Model	K ^a	$ln(\mathcal{L})^b$	$AIC_c^{\ c}$	$\Delta {\rm AIC}_c{}^{ m d}$	w_i^{e}
Percent oak cover within 1 km + Edge density ^f + Large oaks ^g	4	-129.114	266.754	0.000	0.286
Percent oak cover within 1 km + Edge density	3	-130.283	266.877	0.123	0.269
Percent oak cover within 1 km + Edge density + Small oaks	4	-129.717	267.960	1.206	0.157
Percent oak cover within 1 km + Small oaks ^h	3	-130.964	268.240	1.485	0.136
Percent oak cover within 1 km + Large oaks	3	-132.558	271.427	4.672	0.028
Edge density + Percent oak cover within 178 m	3	-132.743	271.797	5.043	0.023
Percent oak cover within 1 km	2	-133.898	271.950	5.195	0.021
Percent oak cover within 1 km + Edge density + Large oaks + Small oaks + Percent oak cover within 178 m + Percent conifer cover within 1 km + Stratum ⁱ	9	-126.223	272.982	6.227	0.013
Percent oak cover within 1 km + Percent conifer cover within 1 km	3	-133.453	273.218	6.464	0.011
Percent conifer cover within 1 km + Small oaks + Percent oak cover within 178 m	4	-132.482	273.490	6.735	0.010
Edge density	2	-134.929	274.011	7.257	0.008
Edge density + Large oaks	3	-133.945	274.202	7.448	0.007

Table 2.2 (continued).

Model	K	$ln(\mathcal{L})$	AIC_c	$\Delta { m AIC}_c$	w_i
Small oaks + Stratum	4	-133.497	275.520	8.766	0.004
Percent conifer cover within 1 km + Edge density	3	-134.655	275.621	8.866	0.003
Edge density + Large oaks + Percent conifer cover within 1 km	4	-133.558	275.643	8.888	0.003
Large oaks	2	-135.767	275.688	8.933	0.003
Null	1	-136.921	275.893	9.139	0.003
Edge density + Small oaks	3	-134.885	276.082	9.327	0.003
Large oaks + Percent oak cover within 178 m	3	-135.464	277.239	10.485	0.002
Large oaks + Percent conifer cover within 1 km	3	-135.535	277.381	10.626	0.001
Small oaks	2	-136.631	277.415	10.661	0.001
Large oaks + Small oaks	3	-135.634	277.580	10.825	0.001
Percent conifer cover within 1 km	2	-136.736	277.626	10.872	0.001
Percent oak cover within 178 m	2	-136.806	277.765	11.011	0.001
Edge density + Small oaks + Percent conifer cover within 1 km	4	-134.637	277.801	11.046	0.001

Table 2.2 (continued).

Model	K	$ln(\mathcal{L})$	AIC_c	$\Delta { m AIC}_c$	w_i
Large oaks + Stratum	4	-134.935	278.396	11.642	0.001
Small oaks + Percent oak cover within 178 m	3	-136.175	278.661	11.907	0.001
Small oaks + Percent conifer cover within 1 km	3	-136.369	279.049	12.294	0.001
Large oaks + Percent oak cover within 178 m + Percent conifer cover within 1 km	4	-135.339	279.205	12.451	0.001
Stratum	3	-136.515	279.342	12.588	0.001
Percent oak cover within 178 m + Percent conifer cover within 1 km	3	-136.677	279.666	12.912	0.000
Stratum + Percent conifer cover within 1 km	4	-136.254	281.034	14.280	0.000

^aNumber of parameters in model.

^eAkaike weight.
$$w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum\limits_{r=1}^{R} \exp(-0.5 * \Delta_r)}$$

^bNatural logarithm likelihood of model.

Akaike's information criterion, adjusted for small sample size. AIC_c=-2 $ln(\mathcal{L}(\hat{\theta}))$ +2K+2K $\frac{(K+1)}{(n-K-1)}$

^dDifference between AIC_c value for a model and the best model.

^fDensity of forest-field edge in km/km² within 178 m of survey point.

^gTotal number of oaks >50 cm dbh in 4 0.04-ha plots within 100 m of survey point.

^hTotal number of oaks ≤10 cm dbh in 4 0.04-ha plots within 100 m of survey point.

ⁱCategorical variable for woodland type at survey point: woodland interior, large woodland edge, or small woodland.

Table 2.3. Covariates for woodland attributes used to calculate the scale parameter in the top model for predicting white-breasted nuthatch density at 60 points in Willamette Valley, OR oak woodlands between 12 April and 17 June 2004.

Parameter	Estimate	SE
Intercept	14.290	2.303
Percent oak cover within 1 km (%)	0.016	0.008
Edge density (km/km ²)	0.094	0.048
Large oaks (No. trees >50 cm dbh per 0.16 ha)	0.053	0.042

Discussion

Percent Oak Cover within 1 km

The proportion of oak cover within a 1-km radius was present in all competing models, and was most predictive of increased white-breasted nuthatch densities. If we consider only proportion of oak cover, this seems to counter the finding that nuthatches were detected at lower densities in large woodlands, which had a higher proportion of oak cover within 1 km (Table 2.1) than small woodlands. However, the combination of oak cover and edge density found in the top three models indicates that given a constant edge density, woodlands with a large proportion of oak within 1 km had higher nuthatch densities than woodlands that were more isolated. In our study, small woodlands were <12 ha, usually large enough for occupancy by only one pair of nuthatches. Proximity to other woodlands may increase the likelihood of small woodland colonization when the occupants die. Some of the smaller woodlands may

not be large enough to support a breeding pair of white-breasted nuthatches. In these woodlands, landscape supplementation, or the use of similar resources in several neighboring woodlands (Dunning et al. 1992), is probably occurring. We observed some nuthatches using several small woodlands in their daily foraging, and nuthatches may move beyond the 10-ha scale because of irregular home range shapes. However, if small woodlands are not spaced closely enough, nuthatches may not be able to move efficiently enough between woodlands to justify the energy expenditure required in maintaining a home range encompassing several woodlands.

The proportion of suitable habitat in the landscape has been considered important in determining the effects of habitat fragmentation (Saunders et al. 1991, Andrén 1994). A review of vertebrate studies found a significant response in presence or abundance of species to landscape context in most studies (Mazerolle and Villard 1999). In addition, proportion of cover at a landscape scale contributed to a response in half of bird studies in forest/agricultural landscapes reviewed (Mazerolle and Villard 1999). Landscape-scale features may play a larger part in determining bird abundance in areas where the matrix habitat is completely unsuitable rather than merely less suitable, such as forests in an agricultural matrix versus forests in a matrix of differently aged stands (Hagan and Meehan 2002).

White-breasted nuthatches have high site fidelity and are believed to remain on their territory for life once breeding begins (Pravosudov and Grubb 1993). European nuthatches (*Sitta europaea*) have a similar life history and juveniles usually established territories within 1 or 2 km of their parents' territory (Verboom et al.

1991). Isolated woodlots were less likely to be colonized by European nuthatches (Verboom et al. 1991). European nuthatches dispersed greater distances in habitat that was more fragmented, but were also less likely to move to another territory once they had settled (Matthysen et al. 1995).

Woodland Size and Edge Density

White-breasted nuthatches were found at significantly higher densities in small woodlands than in large woodland edges or woodland interiors, and at higher densities along large woodland edges than woodland interiors. Small woodlands are characterized by a high edge-to-interior ratio compared to large woodlands. When covariates were modeled, edge density within the home range scale was the second most important woodland measure, and was present in the top 3 models along with proportion of oak cover within 1 km. Previous studies of bird habitat associations have shown conflicting responses of white-breasted nuthatches to forest edges. In woodlands in agricultural Illinois, the white-breasted nuthatch was considered to be an interior species with abundance positively correlated to woodland size (Blake and Karr 1987). A study in the middle Atlantic states found a positive correlation between nuthatch density and forest area, with peak probability of occurrence in forests of 300 ha, although nuthatches were detected in forests as small as 1.6 ha (Robbins et al. 1989). In California oak woodlands in a chaparral and grassland matrix, the nuthatch was considered an oak specialist edge exploiter (Sisk and Margules 1993), and was found at highest density in the zone near the edge of oak woodlands. In the Georgia

Piedmont, white-breasted nuthatches were not associated with either edge or interior. They were present in patches larger than 13.25 ha and in isolated patches between 10 and 13.25 ha, but not present in isolated woodlands less than 3.25 ha (McIntyre 1995).

Higher densities of some species near edges have long been known by biologists (Leopold 1933, Johnston 1947). However, recent studies have focused on the deleterious effects of edges, such as an increase in nest predators, nest predation, and nest parasitism (Gates and Gysel 1978, Kroodsma 1982, Paton 1994, Marzluff et al. 2004). Bird density has been determined to be either higher or lower at edges, depending on the study, and species richness is generally found to be higher at edges (Sisk and Margules 1993, Murcia 1995).

Generalizations on edge effects are difficult to make because of the variety of study designs, forest types, edge types, and climatic conditions involved in the research. Most studies have concentrated on artificial edges and fragmented woodlands created by forest clearing for agriculture and timber production in areas that were historically forest dominated (Gates and Gysel 1978, Lynch and Whigham 1984, Robbins et al. 1989, Paton 1994). However, birds that respond negatively to human-created edges may not exhibit the same response to naturally occurring edges in a naturally patchy landscape (Edenius and Sjöberg 1997). In contrast to studies where edge has been created recently, many of the remaining oak woodlands in our study area were formerly prairie or oak savanna (Habeck 1961, Thilenius 1968, Towle 1982). Trees along edges of these woodlands have often grown for decades with one side exposed to open agricultural fields so the tree structure at the edge is a response to

long-term presence of edges along open fields. The wildlife species present in the Willamette Valley have been exposed to edges and open conditions of oak savannas for centuries. Closed-canopy oak woodlands that are now present are a recent phenomenon in various stages of developing into the conifer forests that have replaced the majority of the semi-open woodlands and savannas that were historically present in the Willamette Valley (Thilenius 1968, Franklin and Dyrness 1988).

Several factors may explain bird habitat selection in relation to forest edge. These factors include species-specific resource and patch use, interspecific interactions such as predation and prey abundance, microclimate, and vegetation structure (Murcia 1995, McCollin 1998, Villard 1998). Forest-dependent species are often negatively affected by increased edge, while species that use resources in multiple habitat types are more abundant on the edges (Gates and Gysel 1978, Kroodsma 1982, Sisk and Margules 1993, McCollin 1998, Marzluff et al. 2004). The white-breasted nuthatch differs from other obligate edge species in that it is almost wholly dependent on oak trees for foraging and nesting, and does not use adjacent farm fields or other open areas much, if at all. Cavity-nesting species are not as prone to interspecific interactions such as nest predation and brood parasitism, although nuthatches may be negatively influenced by interactions with European starlings (Sturnus vulgaris), which occur at higher densities near edges. However, differences in microclimate, vegetation structure, and availability of arthropod prey near woodland edges may explain increased white-breasted nuthatch use of these areas.

Forest edges have different microclimates than forest interiors, such as higher light availability and radiant heat, more exposure to wind, and changes in humidity and water flow (Saunders et al. 1991, Murcia 1995, Foggo et al. 2001) that may indirectly affect food supplies of forest birds. Increased light may influence plant growth, and wind may cause damage to trees, other plants, and lichens (Esseen and Renhorn 1998). However, natural edges, rather than artificial ones created by activities such as clear-cutting, provide more shelter from wind and a less abrupt change in microclimate from edge to interior (Esseen and Renhorn 1998). Time elapsed since edge creation, orientation of the edge, type of surrounding habitat, and management history each may influence microclimate at the edge (Sisk and Margules 1993, Murcia 1995). Because the woodlands in this study were well established and had not had recent clearing around them, most edges consisted of spreading canopies of mature trees. All edges bordered open fields used for agricultural production, pasture, lawn, or native prairie, thus edge effects attributable to the recent removal of trees were not apparent.

The greater availability of light at woodland edges allows oak trees to grow more openly, with wide-spreading branches. The distribution of branches on a tree is associated with the openness of the habitat, with more lateral branches found where there is less competition for light, while trees in dense shade will lose more lower limbs at an early age (Jackson 1979). Several studies have documented differences in vegetative structure between forest edges and interiors. In the eastern U.S., forest edges exhibit greater production of adventitious limbs by canopy trees and more plant

species of open habitat compared to interiors (Matlack 1994). Growth and recruitment in many plant species was higher near edges (Matlack 1994, Murcia 1995). Canopy and subcanopy cover increased with distance from edge, while mortality and tree stem density decreased (Williams-Linera 1990, Chen et al. 1992, Murcia 1995). Interior trees spaced closely together compete for sunlight, so their branches grow more upright.

A greater variety of bark surfaces resulting from both horizontal and vertical branching of open-grown trees provides habitat for a higher diversity of invertebrates (Jackson 1979) and more foraging surface for nuthatches, which glean arthropods from the bark of tree trunks and branches. Trees at the edge may also grow larger in diameter because of the lack of competition for light, moisture, and nutrients.

Fissured bark, which is more prevalent on larger oak trees, provides more shading and has been found to host a greater diversity of arthropods than smooth bark, as well as a larger surface area for invertebrates (Jackson 1979, Nicolai 1986). Nuthatches forage most frequently on large primary branches in oak woodlands of the Willamette Valley (Anderson 1970b). In Illinois, they were found to forage in oak trees most frequently on live branches more than 7.5 cm in diameter (Willson 1970). In a California blue oak (*Q. douglasii*) and coast live oak (*Q. agrifolia*) woodland, nuthatch foraging took place primarily on deciduous limbs more than 5 cm in diameter (Wagner 1981). These large branches are more prevalent on large trees with spreading canopies.

White-breasted nuthatches in Oregon consume a diverse array of bark-dwelling invertebrates (Anderson 1976). Studies on the effect of edge on forest invertebrates

have yielded varying results, with some orders more abundant near edges but others more abundant in interiors. Abundance of invertebrates in a boreal forest in Finland was higher along edges than in forest interiors, and this difference was attributed to changes in vegetation from edge to interior (Jokimäki et al. 1998). Since so much of the Willamette Valley was formerly in oak savanna, it is likely that a wide variety of invertebrates have adapted to conditions on open-grown trees. These invertebrates may require warmer conditions than are available in shady woodland interiors (Jokimäki et al. 1998). Epiphytes growing on the bark provide a mosaic of habitats for a diversity of arthropods (André 1983). Some epiphytes are found more commonly on large, horizontal branches than small branches and vertical surfaces (Jackson 1979).

In addition to foraging resources, trees with many lateral branches typically contain more cavities, which are necessary for nesting and year-round roosting sites. White-breasted nuthatches are weak excavators and are dependent on natural cavities or pockets of decay. In a study of cavity resources in Oregon white oak and Douglas-fir stands in the Willamette Valley (Gumtow-Farrior 1991), the number of cavities per tree increased with diameter of oaks, and open-grown oaks contained more cavities than densely-spaced closed-canopy trees. Cavity nesters in British Columbia preferred nesting near edges, and re-use of cavities was higher on sites with more edge (Aitken et al. 2002). In a study of aspen woodland fragments, cavity nesters were found predominantly near meadows, possibly because of higher densities of a cavity

competitor and nest predator, the northern flying squirrel (*Glaucomys sabrinus*), in woodland interiors (Lawler and Edwards 2002).

Forest Structure

Tree size was also important in determining white-breasted nuthatch density, with more large oaks and fewer small oaks in locations with higher population densities. The importance of large, spreading oaks for cavities and foraging of white-breasted nuthatches is well supported (Anderson 1970b, 1980; Gumtow-Farrior 1991, Wilson et al. 1991, Hagar and Stern 2001). The results are also consistent with a previous Willamette Valley study (Hagar and Stern 2001), in which white-breasted nuthatch abundance was found to have a negative correlation with oak subcanopy cover and a positive correlation with average diameter of oak. In our study, small oaks were scarce in small woodlands compared to large woodlands (Table 2.1), which may have contributed to the higher density of nuthatches in small woodlands. In a Tennessee deciduous forest, white-breasted nuthatches were associated with areas of low understory biomass and smaller trees in the understory, resulting in a more sparse understory (Anderson and Shugart 1974).

Management Implications

Examination of woodland structure at different spatial scales has important management implications for white-breasted nuthatches. Since most of the Willamette Valley is in private ownership, managing woodland for white-breasted nuthatches

requires that wildlife management agencies cooperate with local landowners. In prioritizing sites for conservation, vegetation maps can be useful at the coarse scale for identifying oak woodlands and determining the landscape context of the woodlands. Woodlands in close proximity to other oaks should be given a higher conservation priority than isolated woodlands. Even woodlands smaller than a nuthatch home range will support a breeding pair provided there are other woodlands close enough for efficient travel between them. Woodlands that are at least 4 ha, the approximate home range size for a white-breasted nuthatch pair in small woodlands, may be able to support a pair of nuthatches throughout the year, but proximity to other oaks will ease in colonization of the woodland and dispersal of young nuthatches from the woodland.

Recommendations to preserve large oak woodlands with large oaks for white-breasted nuthatches (Altman 2000) should be reconsidered and refined in light of further evidence. While nuthatches do require areas of oak that are relatively large for a songbird (about 7 ha per pair in our study), nuthatches make little use of woodland interiors, so configuration of woodlands, and not only their size, should be considered in management decisions. Since nuthatches are associated with woodland edges and have a negative association with interiors, managing for nuthatches requires opening up large oak stands to provide suitable habitat. While large trees should be preserved because of their value as foraging and nesting trees, thinning small trees and removing conifers to creating openings could create a larger area of habitat for white-breasted nuthatches. Conifer removal is essential in preserving oaks, which are not shade tolerant. In some large woodlands, it may be possible to restore the savanna structure,

creating a large area of many large oaks and a mosaic of edge. In locations where few large oaks remain, thinning the young trees and removing conifers will release existing oaks, encouraging the development of lateral branches. A variety of tree ages will ensure the persistence of future generations of oaks. Where opportunity exists, prescribed fire could eventually be returned to the ecosystem to maintain semi-open woodlands with large-diameter trees, control conifer encroachment, and promote oak regeneration.

These recommendations for nuthatch conservation are consistent with the goal of returning remaining oak woodlands to a condition structurally similar to the oak savannas that were present in the valley at the time of its settlement by European-Americans. Oak savanna is a natural mosaic, providing conditions that should promote populations of oak-associated species such as the white-breasted nuthatch. Although we were not able to include oak savannas in our surveys because of the scarcity of this habitat, the woodland attributes that were associated with increased nuthatch densities are consistent with oak savanna attributes. We strongly suspect that oak savanna restoration in the Willamette Valley will benefit white-breasted nuthatches. We recommend that restoration efforts be accompanied by monitoring of bird populations.

Literature Cited

Adamus, P. R., K. Larsen, G. Gillson, and C. R. Miller. 2001. Oregon Breeding Bird Atlas [CD-ROM]. Oregon Field Ornithologists. Eugene, OR, USA.

- Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119:391-402.
- Altman, B. 2000. Conservation strategy for landbirds in lowland valleys of western Oregon and Washington. American Bird Conservancy and Oregon-Washington Partners in Flight.

 http://www.orwapif.org/pdf/western_lowlands.pdf. Accessed 2005

 November 8.
- Anderson, S. H. 1970a. The avifaunal composition of Oregon white oak stands. Condor 72:417-423.
- -----. 1970b. Ecological relationships of birds in forests of Western Oregon. Dissertation, Oregon State University, Corvallis, USA.
- ----- 1976. Comparative food habits of Oregon nuthatches. Northwest Science 50:213-221.
- ------. 1980. Habitat selection, succession, and bird community organization. Pages 13-25 *in* R. M. DeGraff and N. G. Tilghan, technical coordinators. Management of western forests and grasslands for nongame birds. Intermountain Forest and Rangeland Experiment Station General Technical Report INT-86.
- -----, and H. H. Shugart. 1974. Habitat selection of breeding birds in an East Tennessee deciduous forest. Ecology 55:828-837.
- André, H. M. 1983. Notes on the ecology of corticolous epiphyte dwellers. Pedobiologia 25:271-278.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724-1734.
- Brawn, J. D., and R. P. Balda. 1988. Population biology of cavity nesters in Northern Arizona: Do nest sites limit breeding densities? Condor 90:61-71.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, England, UK.

- ----- 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, England, UK.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications 2:387-396.
- Defenders of Wildlife. 1998. Oregon's Living Landscape. Defenders of Wildlife, Lake Oswego, Oregon, USA.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.
- Edenius, L., and K. Sjöberg. 1997. Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. Ecography 20:425-431.
- Environmental Systems Research Institute. 1992-1999. ArcView GIS: Release 3.2 [software]. Environmental Systems Research Institute. Redlands, California, USA.
- -----. 1999-2005. ArcGIS: Release 9.1 [software]. Environmental Systems Research Institute. Redlands, California, USA.
- Esseen, P.-A., and K.-E. Renhorn. 1998. Edge effects on an epiphytic lichen in fragmented forests. Conservation Biology 12:1307-1317.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.
- Foggo, A., C. M. P. Ozanne, M. R. Speight, and C. Hambler. 2001. Edge effects and tropical forest canopy invertebrates. Plant Ecology 153:347-359.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.
- Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis, USA.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in forest-field ecotones. Ecology 59:871-883.

- Gumtow-Farrior, D. L. 1991. Cavity resources in Oregon white oak and Douglas-fir stands in the mid-Willamette Valley, Oregon. Thesis, Oregon State University, Corvallis, USA.
- Habeck, J. R. 1961. The original vegetation of the mid-Willamette valley, Oregon. Northwest Science 35:65-77.
- Hagan, J. M., and A. L. Meehan. 2002. Landscape-level variables for explaining bird occurrence in an industrial forest. Forest Science 48:231-242.
- Hagar, J. C., and M. A. Stern. 2001. Avifauna in oak woodlands of the Willamette Valley, Oregon. Northwestern Naturalist 82:12-25.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69-93 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, Inc., New York, New York, USA
- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Association of American Geographers, Annals 61:286-302.
- Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. Condor 49:45-53.
- Jokimäki, J., E. Huhta, J. Itämies, and P. Rahko. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Canadian Journal of Forest Research 28:1068-1072.
- Klock, C., and C. Barrett. 1998. Willamette Valley land use/land cover map (wvveg24k.zip). Oregon Department of Fish and Wildlife and Northwest Habitat Institute. http://www.nwhi.org/>. Accessed 2003 February 15.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology 9:1059-1071.
- Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. Journal of Applied Ecology 19:361-370.

- Lawler, J. J., and T. C. Edwards, Jr. 2002. Composition of cavity-nesting bird communities in montane aspen woodland fragments: the roles of landscape context and forest structure. Condor 104:890-896.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York, New York, USA.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28:287-324.
- MacFaden, S. W., and D. E. Capen. 2002. Avian habitat relationships at multiple scales in a New England forest. Forest Science 48:243-253.
- Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411-1427.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. Journal of Ecology 82:113-123.
- Matthysen, E. 1998. The nuthatches. T & A D Poyser, London, England, UK.
- -----, F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. Oikos 72:375-381.
- Mazerolle, M. J., and M.-A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6:117-124.
- McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography 21:247-260.
- McIntyre, N. E. 1995. Effects of forest patch size on avian diversity. Landscape Ecology 10:85-99.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58-62.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia 69:148-160.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1993. White-breasted nuthatch. Number 54 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of

- Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service General Technical Report PSW-GTR-144. Albany, California, USA.
- Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309-313.
- Richards, D. G. 1981. Environmental acoustics and censuses of singing birds. Pages 297-300 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds: Studies in avian biology No. 6. Cooper Ornithological Society, Lawrence, Kansas, USA
- Robbins, C. S. 1981. Bird activity levels related to weather. Pages 301-310 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds: Studies in avian biology No. 6. Cooper Ornithological Society, Asilomar, California, USA
- -----, D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monographs 103:1-34.
- Saab, V. A. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135-151.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.
- Sisk, T. D., and C. R. Margules. 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. Pages 57-69 *in* D. A. Saunders, R. J. Hobbs, and P. R. Ehrlich, editors. Nature conservation 3: reconstruction of fragmented ecosystems. Surrey Beatty and Sons, Sydney, New South Wales, Australia
- Sprague, F. L., and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. Northwest Science 20:89-98.
- Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:831-843.
- Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49:1124-1133.

- Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, and S. Strindberg. 2002. Distance sampling. Pages 544-552 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of Environmetrics. John Wiley & Sons, Ltd., Chichester, England, UK
- -----, J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, Scotland, UK. http://www.ruwpa.stand.ac.uk/distance/
- Towle, J. C. 1982. Changing geography of Willamette Valley woodlands. Oregon Historical Quarterly 83:66-88.
- U.S. Fish and Wildlife Service. 2005. Endangered, threatened, proposed, and candidate species, critical habitat, and species of concern in western Washington. Western Washington Fish and Wildlife Office. http://www.fws.gov/pacific/westwafwo/se/splisttableMar05.pdf. Accessed 2005 September 14.
- Verboom, J., A. Schotman, P. Opdam, and J. A. J. Metz. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61:149-156.
- Villard, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk 115:801-805.
- Wagner, J. L. 1981. Seasonal change in guild structure: oak woodland insectivorous birds. Ecology 62:973-981.
- Washington Department of Fish and Wildlife. 2005. Species of Concern in Washington State. http://wdfw.wa.gov/wlm/diversty/soc/soc.htm. Accessed 2005 September 14.
- Welsh, C. J. E., W. M. Healy, and R. M. DeGraaf. 1992. Cavity-nesting bird abundance in thinned versus unthinned Massachusetts oak stands. Northern Journal of Applied Forestry 9:6-9.
- Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology 78:356-373.
- Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169-174.

Wilson, R. A., P. Manley, and B. R. Noon. 1991. Covariance patterns among birds and vegetation in a California oak woodland. Pages 126-135 *in* R. B. Standiford, technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management. U.S. Forest Service General Technical Report PSW-126.

CHAPTER 3: WHITE-BREASTED NUTHATCH NEST CAVITY SELECTION AND NEST SUCCESS IN WILLAMETTE VALLEY, OREGON OAK WOODLANDS

Introduction

For secondary cavity-nesting birds, ecological processes at several spatial scales may influence nest cavity selection and nest success. The physical characteristics of the cavity and nest tree may make some cavities more suitable for cavity-nesters than others (Conner et al. 1976, Hooge et al. 1999, Giese and Cuthbert 2003) and may influence nest success (Christman and Dhondt 1997). The local woodland structure around the cavity may determine whether it is selected for nesting and how vulnerable it is to predation (Finch 1989, Li and Martin 1991). Selection of nest cavities within the home range may be limited by availability of suitable cavities (von Haartman 1957, Brush 1983, Newton 1994, Pöysä and Pöysä 2002). Indications of habitat quality such as food availability or microclimate conditions in the home range may influence reproductive success (Martin 1987, Fort and Otter 2004). In addition, fragmentation of the surrounding woodland may have a detrimental effect on nest success by making an area more attractive to predators (Andrén 1994, Robinson et al. 1995, Tewksbury et al. 1998, Stephens et al. 2004). Interspecific competition for cavities may force cavity-nesting birds to use nest cavities that are more vulnerable to predation (Rendell and Robertson 1989, Hooge et al. 1999). Understanding how nest cavity selection relates to nest success provides important insight into management for cavity-nesters.

The white-breasted nuthatch (*Sitta carolinensis*) is a weak cavity excavator or secondary cavity- nester (Pravosudov and Grubb 1993). In the Willamette Valley, nuthatches are permanent residents closely associated with oak woodlands, maintaining territories year-round (Anderson 1970b, 1972; Pravosudov and Grubb 1993; Hagar and Stern 2001). The white-breasted nuthatch has been experiencing long-term declines in the Willamette Valley according to Breeding Bird Survey trends (Sauer et al. 2005). In Washington state the slender-billed white-breasted nuthatch (*S. c. aculeata*), found west of the Cascade and Sierra Nevada Mountains from Washington to Baja California (Gabrielson and Jewett 1940), is a state candidate species and a federal species of concern (U.S. Fish and Wildlife Service 2005, Washington Department of Fish and Wildlife 2005). The white-breasted nuthatch is a Partners in Flight focal species for conservation in western Oregon and Washington, as it is thought to be representative of ecosystem health in large patches of oak woodland with large trees (Altman 2000).

Oregon white oak (*Quercus garryana*) woodland has also suffered losses since settlement of the Willamette Valley began. Burning by indigenous people maintained a landscape dominated by prairie and open oak savanna until the early 1800s (Sprague and Hansen 1946, Habeck 1961, Thilenius 1968, Johannessen et al. 1971). As European-Americans settled the valley, interrupting the historical fire regime, oak savannas and prairies developed into dense oak woodlands or were cleared for agriculture (Habeck 1961, Thilenius 1968, Towle 1982). Clearing of remaining oak woodlands in the Willamette Valley continues for uses such as agriculture, Douglas-fir

(*Pseudotsuga menziesii*) plantations, Christmas tree farms, vineyards, and residential development. Today, most remaining oaks grow in closed-canopy stands dating back to 1860 or later, some containing remnant open-grown oaks (Thilenius 1968). In the absence of fire, succession of oak woodlands to Douglas-fir forest occurs (Franklin and Dyrness 1988). Recently, emphasis has been placed on protecting and restoring Oregon white oak habitat because of its importance to wildlife (Altman 2000, Campbell 2004).

We studied white-breasted nuthatches nesting in Willamette Valley oak woodlands. The first objective of our study was to identify attributes of nest trees and local woodland structure around nest trees that are associated with nest cavity selection by nuthatches. The second objective was to identify features of nest cavities, nest trees, local woodland structure around the nest tree, woodland structure at the home range scale, and the landscape context of the woodland associated with nest success, where successful nests fledged at least 1 young from the nest.

Study Area

We carried out this investigation in Yamhill, Polk, Benton, Marion, and Linn Counties in the Willamette Valley of northwestern Oregon. Oak woodlands used as study sites represented a range of stand conditions and sizes, including dense woodlands and oak savannas. Woodlands had a species composition of at least 50% Oregon white oak, but some stands also included large numbers of Douglas-fir or Oregon ash (*Fraxinus latifolia*) trees.

We chose 40 study sites to which landowners granted us access, ranging in size from about 2 to 180 ha. Study site boundaries were dictated by land ownership, and study sites consisted of individual woodlands, groups of small woodlands, or parts of large woodlands. Since over 95% of land in the Willamette Valley is in private ownership (Defenders of Wildlife 1998), study sites included rural property owned by 31 private landowners, as well as land owned by the U.S. Fish and Wildlife Service, the state of Oregon, Benton County, and the city of Corvallis. Because it was not possible to choose study sites randomly, we will confine our inferences to the study area.

Methods

Locating and Monitoring Nests

We searched for nests from March through June in 2003 and 2004. We visited all study sites early in the nesting season. If white-breasted nuthatches were detected, we made an effort to locate at least 1 nest at that study site. At study sites where we did not initially detect white-breasted nuthatches, we used periodic playback calls while traversing the area, attempting to elicit a response. We visited these study sites at least once again during the breeding season. Nuthatches were quickly discovered in most study sites, as they were typically quite vocal and active during the early nesting season.

Nests were located by following birds carrying nesting material or food to the nest (Martin and Geupel 1993). Males typically feed females during incubation, and

both adults feed nestlings, resulting in frequent nest visits by adults throughout the nesting cycle (Pravosudov and Grubb 1993). Males are frequently vocal while foraging and may be easy to follow to the nest (Ghalambor and Martin 2000). A description of the location of each nest was recorded and, if necessary, a flag was placed at least 10 m away from the nest to assist in relocating nests without attracting nest predators. We recorded the nest location using a Global Positioning System (GPS) receiver.

To determine nest outcome, we attempted to monitor nests once or twice a week until nest fledging or failure, although we checked some nests less frequently due to time constraints. When the age of a nest could be determined, it was also visited on transition days, from egg to nestling or from nestling to fledgling (Martin and Geupel 1993). When possible, we examined nest contents using an elevating pole-mounted micro-video camera probe with LCD monitor (Treetop PeeperTM2, Sandpiper Technologies, Inc., Manteca, CA). Cavity height, opening size and direction, and other cavity characteristics made it impossible to check some nests using this equipment, so we checked these nests for activity from a distance by observing the nest cavity and noting behavior such as food-carrying, removal of fecal sacs, or sounds of begging young (Dudley and Saab 2003). Visits were as brief as possible and no extra observers were present (Martin and Geupel 1993), although some nests were more efficiently checked using 2 people. When fledging was suspected, we made an attempt to locate fledglings by observing parents or listening for young calling (Martin and Geupel 1993). Each nest visit was recorded, including

date, time, number of eggs or nestlings observed, adults observed, and behavioral notes or other comments (Ralph et al. 1993). These monitoring methods helped meet the assumptions of the Mayfield method for estimating nest success. These assumptions are that the fate of all individuals is known at each visit, survival rates are constant over the nests sampled during the study, all visits are recorded accurately, observer visits do not influence success, and success probability is not related to the probability of a visit (Williams et al. 2001). White-breasted nuthatches are only known to raise 1 brood during a season, although they may sometimes replace a lost clutch (Pravosudov and Grubb 1993).

Fledging date was the last date that young were observed in the nest (Martin and Geupel 1993). We considered nests successful if they fledged at least 1 young. When possible, we determined causes of nest failure such as hatching failure, nest-cavity competition, predation, abandonment, weather, or starvation (Ricklefs 1969).

Vegetation Sampling

After nesting was completed, we sampled vegetation in 0.04-ha (11.3-m radius) circular plots centered on each nest. To represent the forest structure at the home range scale, the same sampling methods were used to sample vegetation in 8 random 0.04-ha plots within a 10-ha (178-m radius) circle around the nest, including at least 3 plots containing oak trees with diameter at breast height (dbh) at least 10 cm. A previous study in the Willamette Valley found densities of 1 to 4 white-breasted nuthatches per 10 ha (Anderson 1970a). Breeding densities from around North

America range from 0.5 to 4.9 pairs per 10 ha, and are mainly between 1 and 2 pairs per 10 ha (Stallcup 1968, Brawn and Balda 1988, Welsh et al. 1992, Matthysen 1998). We felt a 10-ha representation of a home range centered on the nest was a reasonable approximation to the area that was available to the nuthatch pair. Random Universal Transverse Mercator (UTM) coordinates were chosen within the 10-ha area around the nest. Random plots were centered on these coordinates and we located them using a GPS receiver. Within the plots, we recorded dbh (cm) and species of each tree ≥ 3 cm dbh and height ≥2 m. Percent canopy cover was determined by averaging 4 canopy cover measurements taken using a spherical densiometer while standing in the plot center, facing the 4 cardinal directions. We made ocular estimates of percent cover of shrub and herbaceous layers. The distance from the center of the plot to the nearest forest-field edge with a canopy opening at least 50 meters across was measured using a tape measure or range finder for distances less than 50 m, and using ArcGIS (Environmental Systems Research Institute 1999-2005) and Digital Orthophoto Quadrangle (DOQ) aerial photos for distances over 50 m. We counted visible cavities within the plot by walking around the plot and using binoculars to examine all trees.

We chose one of the 8 plots at random and then sampled a random tree ≥10 cm dbh within that plot by picking a random number and counting trees from the north in a clockwise direction, from the center of the plot to the outside. At both the nest tree and random tree we recorded the tree species, dbh (cm), tree height (m), spread across the widest part of the crown (m), number of visible cavities in the tree, distance to nearest tree (m), and condition (percent based on an estimate of the proportion of live

to dead limbs). Additional measurements taken at the nest tree included nest cavity height (m), diameter of the bole or branch at cavity height (cm), and compass direction of nest entrance.

Land-use cover within the landscape context was determined using 1:24,000 Willamette Valley GIS vegetation data layers (Klock and Barrett 1998) and DOQ aerial photos. The proportion of oak woodland, conifer forest, non-forest, and the forest-field edge density (km/km²) within 178 m and 1 km of each nest were calculated using ArcGIS software (Environmental Systems Research Institute 1999-2005).

Statistical Analysis

To compare nest trees with randomly sampled trees and local woodland structure at nests with woodland structure at random woodland locations, we used conditional logistic regression analysis with nest or random location as the response variables and habitat attributes as the independent variables. Conditional logistic regression (also known as matched, paired, or case-control logistic regression) allows the investigator to control for potentially confounding factors by stratifying on that variable (Kleinbaum et al. 1982, Kelsey et al. 1996, Hosmer and Lemeshow 2000). In this study, a 10-ha area around each nest was the stratifying variable, and nest (case) trees or plots were matched with random (control) trees or plots from within the 10-ha area centered on the nest. Stratifying on the area around the nest helped to control for factors within a nuthatch pair's home range that may have differed among study sites

and confounded results, such as current or past management practices, age of stand, or other habitat attributes that we did not measure. Matching within a home-range sized area around the nest also confined the controls to trees or plots that were available to each white-breasted nuthatch pair (Johnson 1980). We conducted conditional 1:*m* logistic regression using SAS® (SAS Institute, Inc., Cary, NC) software version 9.1 and the macro MCSTRAT (Vierkant et al. 2000), based on proportional hazards regression with time as a constant.

We assessed the global model adequacy and fit by examining plots of the fit diagnostic statistic, leverage, and overall influence statistic versus the estimated logistic probability from the fitted model (Hosmer and Lemeshow 2000). We identified potentially influential case-control sets and fitted the model excluding each of these sets. The differences in the parameter estimates from the model with and without each set were examined, and the data were examined to determine the reason each set was an outlier (Hosmer and Lemeshow 2000). Although elimination of each of the sets had some effect on the parameter estimates, the significance of variables did not change. We considered the data to be within a reasonable range of values, so we decided to retain all of the sets within the data.

For the nest tree analysis, we included only nests in oak trees because we wanted to determine how oak tree structure was associated with selection of natural nest cavities. Trees that contained nests both years were included only once, and matched with 1 random tree for each year, so each nest tree was matched with 1 or 2

random trees. We calculated Pearson correlation coefficients and did not include variables that were highly correlated in the same model ($r \ge 0.7$).

We modeled each individual variable separately, and modeled combinations of variables that we thought were important together. The underlying hypothesis was that nuthatches selected nest trees based on the quality of the cavity, and cavities in large, open-grown oaks that most represented forest structure in historical oak savannas would be superior. We hypothesized that trees with more cavities, larger size (dbh), a lower proportion of live branches, and a greater distance to the nearest tree were more likely to support a suitable nest cavity. In a study of cavities in Willamette Valley oaks, large, open-form oaks were found to have a higher abundance of cavities than small oaks (Gumtow-Farrior 1991). Trees with more dead branches may have more decay and greater opportunity for cavities to develop.

We compared models using Akaike's Information Criterion, with small sample bias adjustment (AIC_c)(Hurvich and Tsai 1989, Burnham and Anderson 2002). We identified the model with the lowest AIC_c as the best model and the difference between each model and the best model was calculated as Δ AIC_c. Models within 2 Δ AIC_c of the best model were considered competing models. We calculated Akaike weights (w_i) for each model to determine model probabilities using the formula

$$w_{i} = \frac{\exp(-0.5 * \Delta_{i})}{\sum_{r=1}^{R} \exp(-0.5 * \Delta_{r})},$$

given the set of R models, where Δ_i is the difference between the AIC_c of an individual model and the lowest AIC_c , and the Akaike weights of all models sum to 1 (Burnham

and Anderson 2002). Variable relative importance $[w_+(i)]$ for each variable was calculated by summing the Akaike weights for all models containing that variable (Burnham and Anderson 2002).

To compare dbh of nest trees to a larger sample of trees in random plots, we included all oaks with dbh ≥ 10 cm within random plots at all study sites as the sample of random trees, based on the minimum dbh of a tree in which we found a nest. This measure represented the overall forest structure by including trees of a range of sizes in the proportion at which they were found within the woodland. Because these samples had non-normal distributions and unequal variances and sample sizes, we used a Wilcoxon rank-sum test for this comparison (Ramsey and Schafer 2002).

To determine the association between local woodland structure and nest cavity selection, we conducted conditional logistic regression using attributes of 0.04-ha plots centered on nests. In this analysis, as with the nest tree analysis, only nests in oak trees were included. From the 10-ha area around the nest, each nest plot was matched with all random plots that contained at least 1 oak tree \geq 10 cm dbh. Nest trees that nuthatches used both years were included only once, and the plots containing these trees were matched with all random plots containing trees from both years.

After we examined correlation statistics, we fitted variables of interest individually. Among correlated variables ($r \ge 0.7$), we retained the variable with the lowest AIC_c for analysis. We narrowed down the data to five variables that we hypothesized were important and characterized nest locations in terms of number and size of trees and location within the stand. These variables were used to create a set of

candidate models for nest plot analysis. We included mean dbh of oaks ≥10 cm because previous research found nuthatches used larger trees for nesting than other cavity-nesters (Stauffer and Best 1982), and larger oaks contain more cavities (Gumtow-Farrior 1991). We included percent canopy cover and oak basal area (m²/ha.) as further measures of tree size, since previous research has found vegetation in the upper layer to be associated with nuthatch abundance and nuthatches have been found to be associated with large oaks (Anderson 1970b, Hagar and Stern 2001). Distance to edge (m) was included because previous studies have found secondary cavity-nesters make higher use of cavities near edges (Aitken et al. 2002, Lawler and Edwards 2002). Finally, the number of small trees (woody stems with 3- to 20-cm dbh and height ≥ 2 m within each 0.04-ha plot) was included in models to test the hypothesis that a more open understory around the nest may be preferred by nuthatches to allow easier detection of predators approaching the nest. Nest boxes surrounded by sparse understories were preferred by house wrens, which also experienced higher nest success in more open locations (Finch 1989). We fitted 21 models, including each of these variables alone, combinations of variables that we hypothesized were important together, and the null and global models.

Daily survival rate was calculated using Mayfield estimates (Mayfield 1961, 1975) with confidence intervals (Johnson 1979, Hensler and Nichols 1981). To determine what woodland attributes might be important to nest success, we used Mayfield logistic regression with a binary outcome (survival=0, failure=1) divided by number of days observed as the response and woodland attributes as explanatory

variables (Hazler 2004). For nests that fledged and nests with unknown fate, the date we last saw young in the nest was considered the last active date, and nests that failed were assumed to fail halfway between the last active date and the date of the last check (Hazler 2004). Analysis was carried out using proc logistic with SAS® (SAS Institute, Inc., Cary, NC) software version 9.1. We assessed fit of the global model using deviance, Pearson goodness-of-fit, and Hosmer and Lemeshow goodness-of-fit tests and examining outliers and influence statistics. We removed outliers and refitted the model without those nests to examine the influence of individual nests on the outcome.

We included 16 variables for cavity characteristics, nest tree and nest plot measurements, and proportion of vegetation cover measured at the home range (178-m radius) and landscape (1-km radius) scales. We chose variables and combinations of variables that were important in selection of nest cavities in this study to determine if nest cavity selection criteria were predictors of individual fitness. Because previous studies of cavity-nesters have found that higher cavities are less prone to predation (Rendell and Robertson 1989, Li and Martin 1991), we chose to include cavity height in some of the models. We included a variable for year to test for differences in success between years. Previous studies have found that predation is related to quality of the cavity (Christman and Dhondt 1997). Diameter of the tree at cavity height may affect the quality of the cavity by limiting the volume of the cavity or providing protection through insulation, so we included this variable. Distance to edge was included because many studies have suggested that predation on nests is

higher closer to edges (Gates and Gysel 1978, Rendell and Robertson 1990, Paton 1994, Lahti 2001, Knutson et al. 2004). The quality of the habitat within the home range may determine whether adequate food resources are available, so we included mean oak basal area, proportion of oak cover, and edge density as indicators of resources available at the 178-m radius scale. We included proportion of conifer and oak cover within a 1-km radius because proportion of forest cover in the landscape may influence predation on nests and reproductive success (Zanette and Jenkins 2000, Luck 2003). Nuthatch density was negatively correlated with conifer cover in a previous Willamette Valley study (Hagar and Stern 2001). Nine 2-variable models and the top models from the results of the nest cavity selection and nest plot selection were included.

Results

We located 36 nests in 2003 and 41 nests in 2004. Eleven nests were located in artificial structures such as nest boxes (n = 7), buildings (n = 3), and posts (n = 1). In 2004, nuthatches re-used 10 nest cavities and a different cavity in 1 nest tree, so we included these trees only once in the analyses of nest trees and local woodland structure around nests. Re-used nest trees were matched with 2 random trees, 1 from each year, and plots surrounding re-used nest trees were matched with all plots from both years, or up to 16 plots. We excluded 4 nests that were located in ash, pear, or apple trees from analyses of nest trees and nest plots, since all random trees were oaks and all random plots included oaks. One nest did not have any matching trees or plots

Acorn woodpeckers (*Melanerpes formicivoros*) are suspected to have excavated three of the nuthatch nest cavities. The remainder that were not in artificial structures (*n* = 63) were in natural cavities in broken limbs or other dead parts of trees. Only 1 nest was in a dead tree. Of 52 cavities in oak trees, mean cavity height was 6.1 m (CI, 4.9 to 7.3), mean diameter at cavity was 49 cm (CI, 43 to 55), mean distance to nearest tree from cavity opening was 64.1 m (CI, 40.7 to 87.5), and mean distance to nearest branch from cavity opening was 14.7 m (CI, 1.8 to 27.6).

Attributes of Nest Trees

After calculating Pearson correlation coefficients for the measures of nest tree attributes we found dbh and spread to be highly correlated (r = 0.87). Land managers use dbh more commonly and it is easier to measure accurately, so we included dbh but not spread in models. We created a set of thirteen candidate models for nest tree analysis using number of cavities, distance to nearest tree, dbh, and tree condition.

We used only oak tree nests (n = 50) and their matching random trees (n = 62) to examine attributes of trees that predicted selection of a tree for nesting (Table 3.1). Of all 76 randomly sampled oaks, 40 trees contained 179 cavities. Number of cavities in a tree was clearly the most important predictor of nest tree selection, included in all competing models (Table 3.2). However, many of the random trees did not contain any cavities, and the presence of a cavity, rather the number of cavities, could have been driving the results. Since we already knew that white-breasted nuthatches

Table 3.1. Attributes of 50 white-breasted nuthatch nest trees and 62 random oak trees in Willamette Valley, OR oak woodlands 2003-2004.

	Nest trees					Random trees				
Tree attribute	$\overline{\overline{x}}$	SE	Min.	Max.		\overline{x}	SE	Min.	Max.	
No. cavities	8.2	0.9	1.0	28.0		2.4	0.4	0.0	13.0	
Nearest tree (m)	5.4	0.5	0.1	16.9		5.9	0.8	0.3	32.0	
dbh ^a (cm)	70.7	4.0	10.0	137.0		46.1	3.4	10.0	118.0	
Condition ^b (%)	76.6	3.2	0.0	95.0		84.7	1.8	0.0	95.0	
Spread (m)	14.9	0.8	3.5	29.2		11.2	0.7	2.2	23.0	
Height (m)	18.0	0.7	5.5	29.0		14.5	0.8	3.7	27.4	

required a pre-existing cavity for nesting, this outcome was uninformative. To determine if the number of cavities in a tree was important in nest tree selection, we eliminated all random trees without cavities from the data set, along with their matching nest trees.

Using the remaining 29 matched nest-random tree sets, the top model included number of cavities and distance to nearest tree (Table 3.3). All 3 competing models included number of cavities, and all models containing number of cavities performed better than any models without it (Table 3.3).

Among oak trees containing cavities, the odds that a tree was used as a nest tree increased 1.52 times (CI, 1.10 to 2.08, parameter estimate = 0.415, SE = 0.162, P

^aDiameter at breast height.
^bPercent of branches that are alive.

Table 3.2. Models of white-breasted nuthatch nest tree predictors among 50 oak trees used for nesting and 62 random oak trees within 178 m of the nest tree in Willamette Valley, OR oak woodlands 2003-2004.

Model	K ^a	$ln(\mathcal{L})^b$	$AIC_c^{\ c}$	$\Delta \operatorname{AIC}_c^{d}$	w_i^{e}
No. cavities + Distance to nearest tree + dbh ^f	3	-14.937	36.395	0.000	0.345
No. cavities + Distance to nearest tree	2	-16.467	37.189	0.795	0.232
No. cavities	1	-17.892	37.867	1.473	0.165
No. cavities + Distance to nearest tree + dbh + Tree condition	4	-14.913	38.715	2.320	0.108
No. cavities + dbh	2	-17.711	39.676	3.282	0.067
No. cavities + Tree condition	2	-17.823	39.900	3.506	0.060
No. cavities + dbh + Tree condition	3	-17.612	41.746	5.351	0.024
Distance to nearest tree + dbh	2	-24.621	53.496	17.102	0.000
dbh + Tree condition	2	-25.894	56.043	19.649	0.000
dbh	1	-27.355	56.792	20.398	0.000
Tree condition	1	-37.428	76.938	40.544	0.000
Null	0	-39.523	79.046	42.651	0.000
Distance to nearest tree	1	-39.471	81.025	44.631	0.000

^aNumber of parameters in model.

AIC_c=-2
$$ln(\mathcal{L}(\hat{\theta}))$$
+2 K +2 $K\frac{(K+1)}{(n-K-1)}$

^dDifference between AIC_c value for a model and the best model.
^eAkaike weight.
$$w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum_{r=1}^{R} \exp(-0.5 * \Delta_r)}$$

^bNatural logarithm likelihood of model.

^cAkaike's information criterion, adjusted for small sample size.

^fDiameter at breast height.

Table 3.3. Models of white-breasted nuthatch nest tree predictors among 29 oak trees used for nesting and 34 matching random oak trees containing cavities within 178 m of the nest tree in Willamette Valley, OR oak woodlands 2003-2004.

Model	K ^a	$ln(\mathcal{L})^b$	$AIC_c^{\ c}$	$\Delta \operatorname{AIC}_c^{\operatorname{d}}$	w_i^{e}
No. cavities + Distance to nearest tree	2	-12.840	30.142	0.000	0.446
No. cavities + Distance to nearest tree $+ dbh^{\rm f}$	3	-12.477	31.914	1.772	0.184
No. cavities	1	-14.959	32.065	1.924	0.170
No. cavities + Distance to nearest tree + dbh + Tree condition	4	-12.144	33.955	3.813	0.066
No. cavities + dbh	2	-14.883	34.228	4.086	0.058
No. cavities + Tree condition	2	-14.916	34.293	4.151	0.056
No. cavities + dbh + Tree condition	3	-14.862	36.684	6.542	0.017
dbh + Distance to nearest tree	2	-18.736	41.933	11.791	0.001
Tree condition	1	-20.661	43.469	13.328	0.001
Distance to nearest tree	1	-21.020	44.187	14.046	0.000
Null	0	-22.129	44.257	14.115	0.000
Tree condition + dbh	2	-20.190	44.842	14.700	0.000
dbh	1	-21.467	45.081	14.940	0.000

^aNumber of parameters in model.

$$AIC_c = -2ln(\mathcal{L}(\hat{\theta})) + 2K + 2K \frac{(K+1)}{(n-K-1)}$$

^dDifference between AIC_c value for a model and the best model.
^eAkaike weight.
$$w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum_{r=1}^{R} \exp(-0.5 * \Delta_r)}$$

^bNatural logarithm likelihood of model.

^cAkaike's information criterion, adjusted for small sample size.

^fDiameter at breast height.

= 0.010) for every additional cavity when distance to nearest tree was constant (parameter estimate = -0.197, SE = 0.124, P = 0.113).

The Wilcoxon rank-sum test included a sample of 3,829 oak trees with dbh \geq 10 cm within the random plots and 51 oak trees that contained nests. Nest trees were 41 cm larger than random trees (Z = 9.66, P < 0.0001). Nest trees had a mean dbh of 70 cm, and random trees had a mean dbh of 29 cm.

Local Woodland Structure around Nests

We matched 50 0.04-ha plots around nests with 282 random plots within 178 m of each nest (Table 3.4). The number of random plots associated with each nest ranged from 3 to 8 for nest trees that were used only 1 year, and from 8 to 16 for nest trees used both years. The model most predictive of nuthatch nesting within a plot included.

Table 3.4. Attributes of local woodland structure at 50 white-breasted nuthatch nests and 282 matching random plots in Willamette Valley, OR oak woodlands 2003-2004.

Attributes of local	Nest plots $(n = 50)$				Ra	Random plots ($n = 282$)			
woodland structure	\overline{x}	SE	Min.	Max.	\overline{x}	SE	Min.	Max.	
Mean dbh ^a of oaks (cm)	55	3.3	22	125	41	1.4	10	111	
Canopy cover (%)	83	1.8	40	97	69	1.6	0	100	
Oak basal area (m²/ha)	38	2.6	6	107	24	1.0	0	85	
Small trees ^b	15	4.4	0	149	25	2.1	0	212	
Distance to edge (m)	26	8.1	0	348	35	3.4	0	316	

^aDiameter at breast height

^bNumber of trees 3-20 cm dbh and at least 2 m tall within a 0.04-ha plot.

mean dbh of oaks, canopy cover, oak basal area, and small trees (Tables 3.5 and 3.6). Three models were closely competing with the top model, including the global model. All 4 top models contained mean dbh of oaks ($w_+(i) = 0.995$), canopy cover ($w_+(i) = 0.994$), and oak basal area ($w_+(i) = 0.969$). The odds that a nest plot would contain a nest increased 1.03 times (CI, 1.01 to 1.05) for every additional cm in mean oak dbh when canopy cover, basal area, and number of small trees remained constant. Each additional percentage of canopy cover increased the odds of a plot containing a nest 1.04 times (CI, 1.01 to 1.07), given a constant mean oak dbh, basal area, and number of small trees (Table 3.5). The odds of a plot having a nest in it increased 1.03 times for each additional m^2 /ha of basal area (CI, 1.01 to 1.06) when mean oak dbh, canopy cover, and number of small oaks did not change. The odds of a plot containing a nest did not change with each additional tree less than 20 cm diameter within that plot (CI, 0.97 to 1.01)(Table 3.5).

Table 3.5. Measures of local woodland structure in top model predicting 50 white-breasted nuthatch nests in Willamette Valley, OR oak woodlands 2003-2004.

Measure of woodland structure	Coefficient	SE	Z^{a}	P > Z
Mean dbh of oaks	0.029	0.010	7.874	0.005
Canopy cover	0.042	0.014	8.608	0.003
Oak basal area	0.030	0.012	5.810	0.016
Small trees	-0.012	0.009	1.882	0.170

^aWald statistic

Table 3.6. Models for predicting local woodland structure around white-breasted nuthatch nests among 50 plots centered on oak trees used for nesting and 282 random woodland plots within 178 m of nests in Willamette Valley, OR oak woodlands 2003-2004.

Model	K ^a	$ln(\mathcal{L})^{b}$	$AIC_c^{\ c}$	$\Delta \operatorname{AIC_{\it c}}^{\operatorname{d}}$	w_i^{e}
Mean dbh ^f of oaks + Canopy cover + Oak basal area + Small trees	4	-68.331	144.884	0.000	0.270
Mean dbh of oaks + Canopy cover + Oak basal area	3	-69.431	145.036	0.152	0.250
Mean dbh of oaks + Canopy cover + Oak basal area + Small trees + Distance to edge	5	-67.423	145.119	0.235	0.240
Mean dbh of oaks + Canopy cover + Oak basal area + Distance to edge	4	-68.639	145.499	0.615	0.198
Mean dbh of oaks + Canopy cover + Distance to edge	3	-72.194	150.561	5.677	0.016
Mean dbh of oaks + Canopy cover	2	-73.238	150.604	5.719	0.015
Mean dbh of oaks + Oak basal area	2	-74.748	153.623	8.738	0.003
Canopy cover + Oak basal area + Distance to edge	3	-73.807	153.788	8.904	0.003
Mean dbh of oaks + Oak basal area + Distance to edge	3	-74.509	155.191	10.307	0.002
Canopy cover + Oak basal area	2	-75.659	155.446	10.561	0.001
Small trees + Oak basal area	2	-77.489	159.105	14.220	0.000
Canopy cover + Small trees	2	-77.605	159.337	14.452	0.000
Oak basal area	1	-78.799	159.680	14.796	0.000

Table 3.6 (continued).

Model	K	$ln(\mathcal{L})$	AIC_c	$\Delta \operatorname{AIC}_c$	w_i
Oak basal area + Distance to edge	2	-77.927	159.982	15.097	0.000
Canopy cover + Distance to edge	2	-80.639	165.406	20.521	0.000
Canopy cover	1	-82.629	167.340	22.456	0.000
Mean dbh of oaks	1	-84.172	170.426	25.542	0.000
Mean dbh of oaks + Small trees	2	-83.826	171.780	26.895	0.000
Mean dbh of oaks + Distance to edge	2	-84.089	172.306	27.421	0.000
Small trees	1	-90.293	182.669	37.785	0.000
null	0	-92.203	184.446	39.562	0.000
Distance to edge	1	-91.846	185.774	40.890	0.000

^aNumber of parameters in model.

AIC_c=-2ln(
$$\mathcal{L}(\hat{\theta})$$
)+2K+2K $\frac{(K+1)}{(n-K-1)}$

^eAkaike weight.
$$w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum_{r=1}^{R} \exp(-0.5 * \Delta_r)}$$

Nest Success

We monitored 25 nests in 2003 and 39 nests in 2004. Time and logistical constraints prevented us from monitoring all nests. Four of the monitored nests were in non-oak trees, and 10 were in artificial structures. We included nest outcome from

^bNatural logarithm likelihood of model.

^cAkaike's information criterion, adjusted for small sample size.

^dDifference between AIC_c value for a model and the best model.

^fDiameter at breast height.

both years for 11 re-used trees in our nest success analysis. We considered a nest active once it contained eggs. We found that some cavities at which we observed activity were abandoned early in the nesting season before eggs were documented, so these were not considered nests. Females frequently spent extended periods inside the nest cavity during nest construction, and males were observed feeding females at the nest prior to egg-laying (personal observation). A nest was not included in analysis if we were only able to monitor through observations and we only observed activity at the cavity on one visit early in the nesting season. If nests in which activity stopped early in the season were actually failed nest attempts, eliminating them may have biased results in favor of nests that survived. We did not locate additional nest attempts for these birds. Females were frequently reluctant to flush from the nest so we could not always determine nest contents. In 2003, 1 nest attempt that failed was replaced by another clutch in the same cavity, which also failed. Only one of these nest attempts was included in the analysis. In 2004 a pair whose nest failed less than 1 week after hatching re-nested in a tree within 10 m of the first nest, and the second attempt fledged young. Both of these nests were in non-oak trees. We conducted nest searching on many of the same study sites both years of the study, so although the birds were not marked, many were likely the same individuals, and some nest cavities were re-used the second year, so samples are not independent.

Of 13 nests that were known to fail, the primary cause of nest failure was predation (n = 11), with nest contents disappearing before the expected fledge date. The difficulty in examining cavities prevented us from gathering detailed information

on nest disturbance. In 1 case, we found dead nestlings on the ground below the nest.

The eggs failed to hatch after at least 19 days of incubation in 1 nest.

Incubation lasted 15 days for the 1 nest for which we knew the start of incubation and hatching dates. We were able to determine nestling period for 3 nests for which we knew hatching and fledging dates. Two of these fledged 27 days after hatching, and the other fledged 25 days after hatching. We used a 40-day nesting period in calculating Mayfield estimates of nest success.

The overall Mayfield nest success for monitored nests (n = 64) was 75% (CI, 64% to 88%). Using only nests in oak trees (n = 50), Mayfield success was 71% (CI, 58% to 86%). Nest success was 100% in artificial structures that were monitored (n = 10).

Fitting Mayfield logistic regression models, the top model was mean dbh of oaks in the nest plot. The null model was within 2 Δ AIC_c of the top model (Table 3.7). Using the Hosmer and Lemeshow goodness-of-fit test (X^2 = 3.99, 8 df, P = 0.86) and examining outliers and influence statistics, we found a good fit to the global model. Because we found no meaningful relationship between habitat attributes and nest success, we considered the lack of independence of the data between years irrelevant.

Discussion

At the home range scale, nuthatches were more likely to nest in an oak tree containing cavities as the number of cavities in the tree increased. A greater number

Table 3.7. Models for predicting nest success of 50 white-breasted nuthatch nests in oak trees in Willamette Valley, OR oak woodlands 2003-2004.

Model	K ^a	$ln(\mathcal{L})^b$	$AIC_c^{\ c}$	$\Delta \operatorname{AIC}_c^{d}$	w_i^{e}
Mean dbh ^f of oaks in nest plot	2	-67.58	139.42	0.00	0.13
Canopy cover in nest plot	2	-67.84	139.93	0.51	0.10
Null	1	-69.04	140.17	0.75	0.09
Proportion conifer cover within 1 km	2	-68.31	140.88	1.46	0.06
Distance to nearest tree from nest tree	2	-68.32	140.90	1.47	0.06
No. small trees in nest plot	2	-68.35	140.96	1.54	0.06
Mean oak basal area within 178 m	2	-68.61	141.48	2.06	0.04
No. cavities in nest tree	2	-68.82	141.89	2.46	0.04
Oak basal area in nest plot	2	-68.85	141.96	2.53	0.04
Diameter at nest height	2	-68.85	141.96	2.53	0.04
Proportion oak cover within 178 m	2	-68.88	142.01	2.59	0.03
Nest tree dbh	2	-68.89	142.04	2.62	0.03
Edge density within 178 m	2	-68.98	142.21	2.79	0.03
Canopy cover in nest plot + Distance to edge	3	-67.84	142.20	2.78	0.03
Proportion oak cover within 1 km	2	-69.01	142.27	2.85	0.03
Distance to edge	2	-69.03	142.32	2.90	0.03
Cavity height	2	-69.04	142.34	2.92	0.03
Year	2	-69.04	142.34	2.92	0.03

Table 3.7 (continued)

Model	K	$ln(\mathcal{L})$	AIC_c	$\Delta \operatorname{AIC}_c$	w_i
Distance to nearest tree from nest tree + No. cavities in nest tree	3	-68.29	143.09	3.67	0.02
No. cavities in nest tree + Proportion oak cover within 1 km	3	-68.70	143.92	4.50	0.01
No. cavities in nest tree+ Edge density within 178 m	3	-68.73	143.98	4.56	0.01
No. cavities in nest tree + Nest tree dbh	3	-68.78	144.08	4.66	0.01
No. cavities in nest tree + Cavity height	3	-68.80	144.12	4.70	0.01
Oak basal area in nest plot + Cavity height	3	-68.84	144.20	4.78	0.01
Nest tree dbh + Distance to edge	3	-68.87	144.26	4.84	0.01
Proportion oak cover within 1 km + Edge density within 178 m	3	-68.98	144.47	5.05	0.01
Mean dbh of oaks in nest plot + Canopy cover in nest plot + Oak basal area in nest plot + No. small trees in nest plot	5	-66.66	144.69	5.27	0.01
Global	17	-61.89	176.90	37.48	0.00

AIC_c=-2
$$ln(\mathcal{L}(\hat{\theta}))$$
+2 K +2 $K\frac{(K+1)}{(n-K-1)}$

^dDifference between AIC_c value for a model and the best model.

^eAkaike weight.
$$w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum\limits_{r=1}^{R} \exp(-0.5 * \Delta_r)}$$

^aNumber of parameters in model. ^bNatural logarithm likelihood of model. ^cAkaike's information criterion, adjusted for small sample size.

^fDiameter at breast height.

of cavities in a tree may increase the likelihood that the tree contains a suitable nest cavity. An abundance of potential nest cavities in an area may decrease the risk of predation, since predators must search more cavities to find a nest (Martin and Roper 1988, Li and Martin 1991). For cavity-nesting species, the availability of alternative cavities provides roosting locations for the adults and fledglings, and may increase survival of fledglings (Short 1979). Nearby cavities may provide re-nesting locations if the nest fails (Short 1979).

Another explanation for increased use of cavity-rich trees for nesting is that nuthatches are more likely to encounter cavities while foraging on the bark of large, decaying trees. Cavity use may be related to encounter frequency (Brawn 1988, Finch 1989), so cavities in trees that are used frequently for foraging by nuthatches may have a higher likelihood of being used for nesting. Mechanical injuries to trees result in more cavities and increase the suitability of the bark for arthropods (Jackson 1979), increasing the available food resources on the tree. Nuthatches may concentrate their foraging activity in decaying trees, increasing the likelihood of encountering a suitable nest cavity nearby. By selecting nest cavities near high-quality foraging locations, nuthatches may be able to spend more time foraging near the nest, expending less energy while feeding young, and providing increased vigilance against predators.

The comparison of dbh between nest trees and the large sample of trees in random plots found that nest trees are substantially larger than trees in randomly sampled plots. However, we did not search all trees within random plots for cavities, and many probably did not contain cavities. A previous study of Oregon white oak

trees (Gumtow-Farrior 1991) found that the number of cavities in oaks increased with diameter of the tree, and others have determined that the number of cavities increases with tree age (Newton 1994), so it is not surprising that larger diameter trees had a higher probability of containing a nest cavity.

Comparison of the nest plots with random plots found that measures of tree size (mean dbh of oaks, canopy cover, oak basal area, and number of small trees) were all important predictors of nuthatch nests. Nest trees were larger than trees in random plots, and there were likely to be fewer small trees growing under a large tree with a dense canopy. Although the odds increased only slightly for each variable, the additive effect of increasing the mean dbh, canopy cover, and oak basal area may amount to trees that are noticeably larger to a white-breasted nuthatch. Basal area and canopy cover may also increase in plots with many small trees, but including mean dbh and number of small trees (with a negative coefficient) in the model suggests that nest plots contained fewer trees of larger size than random plots. The measures of local woodland structure within nest plots may have been influenced by the presence of nest trees, which were larger than random trees. Trees with large diameter and high canopy cover may lose more large limbs (Jackson 1979, Jackson and Jackson 2004) and may be more likely to contain a suitable nest cavity.

When we examined nest success, the results did not support increased reproductive success in nest trees with characteristics for which nuthatches selected. It seems likely that nuthatches search potential cavities and choose a cavity based on its characteristics, rather than the attributes of the tree. Cavities vary in quality, with

some being more susceptible to predation or adverse weather (Li and Martin 1991, Radford et al. 2003). Even in cavity-rich forests, not all cavities are of suitable quality for nest cavities, and characteristics of cavities such as opening size and internal volume have been found to be more predictive of which species used them than attributes of the tree or surrounding vegetation were (Peterson and Gauthier 1985). Some cavities were not necessarily available to the nuthatches, because either other species occupied them or they were too small for nuthatches to enter. Internal features that we could not easily observe or measure, such as cavity depth, cavity volume, and softness of wood may play an important role in selection of a nest cavity and may also have an effect on nest outcome (Peterson and Gauthier 1985, Brawn 1988, Rendell and Robertson 1989, Christman and Dhondt 1997).

Competition from other secondary cavity-nesters may restrict cavity selection, forcing nuthatches to use cavities that are not optimal for protection against predators and the elements. At least 3 times, we observed nuthatches carrying nesting material into cavities early in the nesting season, only to find when we returned 1-2 weeks later that European starlings (*Sturnus vulgaris*) occupied these cavities. These nests were not included in nest success analysis because nuthatch eggs were never confirmed, and the cavities may have been abandoned rather than usurped by starlings. We did not locate new nests for these nuthatches, so it is unknown if they were forced to move from the territory, were prevented from nesting, or were able to re-nest elsewhere. If cavities were so scarce that starlings prevented these nuthatches from nesting, the results were not reflected in our calculation of nest success. Starlings have been

documented displacing cavity-nesting species when nest cavities are limited (Weitzel 1988). In our study, starlings were present at most study sites and were seen attempting to enter cavities with active nuthatch nests in them. Competition for cavities may force nuthatches to use cavities with smaller openings and deeper cavities that are inaccessible to starlings. Because of their early nest initiation (Pravosudov and Grubb 1993) and aggressive defense of nest cavities (Kilham 1968, Kilham 1981), nuthatches may be able to out-compete cavity-nesting birds of similar size, but may be displaced by larger and more aggressive starlings.

Since attributes of nest trees and local woodland structure for which the nuthatches selected did not appear to improve reproductive success, perhaps limitation of available cavities or inter-specific competition forced nuthatches to use sub-optimal cavities. However, 53% of random trees that we sampled contained at least one cavity, suggesting that cavities should be plentiful within a nuthatch home range.

Nuthatch nest success in oak trees was high at 71%, so the small number of nests that failed may have prevented any model from emerging as a clear top model, or cavity characteristics that we did not model may have contributed to nest failure. Most nests may have been in cavities of similar quality, and predation may have occurred due to random encounters by predators.

Management Implications

In locations where oak restoration efforts are underway, large or decaying trees should be retained to protect potential nest cavities. In addition, thinning small oaks

and removing conifers will release oaks and may allow them to develop more side branches (Devine and Harrington 2004) and grow larger in the absence of competition, providing more possible cavity locations. Girdling or topping conifers to create snags is being used to remove conifers and create potential for cavity excavation in oak woodland and savanna restoration sites (Campbell 2004). It is unknown to what extent these snags will be used by wildlife, and which species will use them. White-breasted nuthatches did not use conifers for nesting in this study, but conifer snags were rare or absent on study sites.

Where possible, the return of fire to the oak ecosystem through controlled burns will help to maintain sparse tree densities and prevent conifer encroachment. In addition, burning could result in damage to some trees that may cause more cavities to develop, creating potential nest cavities for white-breasted nuthatches and other cavity-nesting species. We recommend future research to monitor wildlife communities at oak restoration sites.

The importance of cavities to white-breasted nuthatches in selecting nest sites suggests that augmentation with nest boxes may provide more cavity options for nuthatches. However, nest box placement is only a short-term solution, requires maintenance, and may provide competitors with additional nest cavities. Density dependence may limit populations in spite of availability of cavities if other resources are limiting (Pöysä and Pöysä 2002, Lohmus and Remm 2005). Nest cavities are not always a limiting factor (Brawn and Balda 1988, Waters et al. 1990), and it is not clear whether they were limiting in this study. Nest box augmentation can have varying

success in increasing secondary cavity-nesters, depending on the habitat and availability of natural cavities (Brawn and Balda 1988). Nest boxes may also have unknown or detrimental effects such as limiting numbers of open-nesting species or altering the species composition of cavity-nesters (Bock et al. 1992, Purcell et al. 1997). Nest box monitoring should accompany placement of boxes to determine impacts on cavity-nesting birds.

Literature Cited

- Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119:391-402.
- Altman, B. 2000. Conservation strategy for landbirds in lowland valleys of western Oregon and Washington. American Bird Conservancy and Oregon-Washington Partners in Flight.

 http://www.orwapif.org/pdf/western_lowlands.pdf>. Accessed 2005

 November 8.
- Anderson, S. H. 1970a. The avifaunal composition of Oregon white oak stands. Condor 72:417-423.
- -----. 1970b. Ecological relationships of birds in forests of Western Oregon. Dissertation, Oregon State University, Corvallis, USA.
- ----- 1972. Seasonal variations in forest birds of western Oregon. Northwest Science 46:194-206.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.
- Bock, C. E., A. Cruz, Jr., M. C. Grant, C. S. Aid, and T. R. Strong. 1992. Field experimental evidence for diffuse competition among southwestern riparian birds. American Naturalist 140:815-828.
- Brawn, J. D. 1988. Selectivity and ecological consequences of cavity nesters using natural vs. artificial nest sites. Auk 105:789-791.

- -----, and R. P. Balda. 1988. Population biology of cavity nesters in Northern Arizona: Do nest sites limit breeding densities? Condor 90:61-71.
- Brush, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. Condor 85:461-466.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Campbell, B. H. 2004. Restoring rare native habitats in the Willamette Valley: a landowner's guide for restoring oak woodlands, wetlands, prairies, and bottomland hardwood and riparian forests. Defenders of Wildlife. West Linn, Oregon, USA.
- Christman, B. J., and A. A. Dhondt. 1997. Nest predation in black-capped chickadees: How safe are cavity nests? Auk 114:769-773.
- Conner, R. N., O. K. Miller, and C. S. Adkisson. 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bulletin 88:575-581.
- Defenders of Wildlife. 1998. Oregon's Living Landscape. Defenders of Wildlife, Lake Oswego, Oregon, USA.
- Devine, W., and C. Harrington. 2004. Garry oak woodland restoration in the Puget Sound region: releasing oaks from overtopping conifers and establishing oak seedlings. Pages 1-8. 16th International Conference, Society for Ecological Restoration.
- Dudley, J., and V. A. Saab. 2003. A Field protocol to monitor cavity-nesting birds. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Res. Pap. RMRS-RP-44. Fort Collins, Colorado, USA.
- Environmental Systems Research Institute. 1999-2005. ArcGIS: Release 9.1 [software]. Environmental Systems Research Institute. Redlands, California, USA.
- Finch, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in house wrens. Condor 91:848-859.
- Fort, K. T., and K. A. Otter. 2004. Effects of habitat disturbance on reproduction in black-capped chickadees (*Poecile atricapillus*) in northern British Columbia. Auk 121:1070-1080.

- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.
- Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis, USA.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in forest-field ecotones. Ecology 59:871-883.
- Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.
- Giese, C. L. A., and F. J. Cuthbert. 2003. Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the Upper Midwest, USA. Forest Ecology and Management 179:523-534.
- Gumtow-Farrior, D. L. 1991. Cavity resources in Oregon white oak and Douglas-fir stands in the mid-Willamette Valley, Oregon. Thesis, Oregon State University, Corvallis, USA.
- Habeck, J. R. 1961. The original vegetation of the mid-Willamette valley, Oregon. Northwest Science 35:65-77.
- Hagar, J. C., and M. A. Stern. 2001. Avifauna in oak woodlands of the Willamette Valley, Oregon. Northwestern Naturalist 82:12-25.
- Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707–716.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. Wilson Bulletin 93:42-53.
- Hooge, P. N., M. T. Stanback, and W. D. Koenig. 1999. Nest-site selection in the acorn woodpecker. Auk 116:45-54.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York, New York, USA.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69-93 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, Inc., New York, New York, USA

- -----, and B. J. Jackson. 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor 106:37-49.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Association of American Geographers, Annals 61:286-302.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.
- -----. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.
- Kelsey, J. L., A. S. Whittemore, A. S. Evans, and W. D. Thompson. 1996. Methods in observational epidemiology. Oxford University Press, New York, New York, USA.
- Kilham, L. 1968. Reproductive behavior of white-breasted nuthatches. I. Distraction display, bill-sweeping, and nest hole defense. Auk 85:477-492.
- -----. 1981. Agonistic behavior of the white-breasted nuthatch. Wilson Bulletin 93:271-274.
- Kleinbaum, D. G., L. L. Kupper, and H. Morgenstern. 1982. Epidemiologic research: principles and quantitative methods. Lifetime Learning Publications, Belmont, California, USA.
- Klock, C., and C. Barrett. 1998. Willamette Valley land use/land cover map (wvveg24k.zip). Oregon Department of Fish and Wildlife and Northwest Habitat Institute. http://www.nwhi.org/. Accessed 2003 February 15.
- Knutson, M. G., G. J. Niemi, W. E. Newton, and M. A. Friberg. 2004. Avian nest success in Midwestern forests fragmented by agriculture. Condor 106:116-130.
- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365-374.
- Lawler, J. J., and T. C. Edwards, Jr. 2002. Composition of cavity-nesting bird communities in montane aspen woodland fragments: the roles of landscape context and forest structure. Condor 104:890-896.
- Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405-418.
- Lohmus, A., and J. Remm. 2005. Nest quality limits the number of hole-nesting passerines in their natural cavity-rich habitat. Acta Oecologica 27:125-128.

- Luck, G. W. 2003. Differences in the reproductive success and survival of the rufous treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. Biological Conservation 109:1-14.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics 18:453-487.
- -----, and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.
- -----, and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51-57.
- Matthysen, E. 1998. The nuthatches. T & A D Poyser, London, England, UK.
- Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.
- -----. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265-276.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.
- Peterson, B., and G. Gauthier. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. Wilson Bulletin 97:319-331.
- Pöysä, H., and S. Pöysä. 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39:502-510.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1993. White-breasted nuthatch. Number 54 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Purcell, K. L., J. Verner, and L. W. Oring. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114:646-656.
- Radford, A. N., M. A. Du Plessis, R. AN, and D. p. MA. 2003. The importance of rainfall to a cavity-nesting species. Ibis 145:692-694.

- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service General Technical Report PSW-GTR-144. Albany, California, USA.
- Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth. Duxbury, Pacific Grove, California, USA.
- Rendell, W. B., and R. J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. Condor 91:875-885.
- -----. 1990. Influence of forest edge on nest-site selection by tree swallows. Wilson Bulletin 102:634-644.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966 2004. Version 2005.2. USGS Patuxent Wildlife Research Center. http://www.mbr-pwrc.usgs.gov/bbs/. Accessed 2005 September 14.
- Short, L. L. 1979. Burdens of the picid hole-excavating habit. Wilson Bulletin 91:16-28.
- Sprague, F. L., and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. Northwest Science 20:89-98.
- Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:831-843.
- Stauffer, D. F., and L. B. Best. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bulletin 94:329-337.
- Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Number 1. Biological Conservation, and.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation of a western landscape. Ecology 79:2890-2903.

- Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49:1124-1133.
- Towle, J. C. 1982. Changing geography of Willamette Valley woodlands. Oregon Historical Quarterly 83:66-88.
- U.S. Fish and Wildlife Service. 2005. Endangered, threatened, proposed, and candidate species, critical habitat, and species of concern in western Washington. Western Washington Fish and Wildlife Office. http://www.fws.gov/pacific/westwafwo/se/splisttableMar05.pdf. Accessed 2005 September 14.
- Vierkant, R. A., J. L. Kosanke, T. M. Therneau, and J. M. Naessens. 2000. MCSTRAT: A SAS macro to analyze data from a matched or finely stratified case-control design. Technical Report Series No. 65. Department of Health Science Research, Mayo Clinic. Rochester, Minnesota.
- von Haartman, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339-347.
- Washington Department of Fish and Wildlife. 2005. Species of Concern in Washington State. http://wdfw.wa.gov/wlm/diversty/soc/soc.htm. Accessed 2005 September 14.
- Waters, J. R., B. R. Noon, and J. Verner. 1990. Lack of nest site limitation in a cavity-nesting bird community. Journal of Wildlife Management 54:239-245.
- Weitzel, N. H. 1988. Nest-site competition between the European starling and native breeding birds in Northwestern Nevada. Condor 90:515-517.
- Welsh, C. J. E., W. M. Healy, and R. M. DeGraaf. 1992. Cavity-nesting bird abundance in thinned versus unthinned Massachusetts oak stands. Northern Journal of Applied Forestry 9:6-9.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Zanette, L., and B. Jenkins. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117:445-454.

CHAPTER 4: GENERAL CONCLUSION

In this study we investigated the relationship between oak woodlands and white-breasted nuthatches. We examined densities of nuthatches in 3 types of oak woodlands. We then looked in more detail at attributes of woodland structure at multiple spatial scales that were associated with nuthatch density. In addition, we compared nest cavity locations with random locations within the home range scale. Finally, we investigated the success of nuthatch nests in response to tree and woodland characteristics at multiple spatial scales.

Nuthatch Density

Among all woodland habitats surveyed, nuthatch density was about 0.14 birds/ha, and density in small woodlands was almost twice as high, at 0.27 nuthatches/ha. White-breasted nuthatch density was higher in small oak woodlands than near edges of large woodlands, which in turn had a higher density than woodland interiors. Increased density of nuthatches was associated with a combination of higher proportion of oak woodland within 1 km (the landscape context), higher edge density within 178 m (an approximate home range scale), and a greater number of large oak trees (>50 cm dbh) within 100 m. A high proportion of oak woodland within 1 km allows more opportunity for colonization of woodlands by nuthatches. Greater ease of movement means nuthatches may be able to sample more areas and select the best available home range. Nuthatches may not be able to colonize isolated woodlands easily, and may not be able to efficiently replace birds that die. Increased light along

woodland edges, which occur at a higher density in small or linear woodlands, may produce more foraging sites in the form of open-grown oaks with spreading crowns. Nuthatches forage primarily on large lateral branches (Anderson 1970, Willson 1970, Wagner 1981) and nest in natural cavities (Bent 1948, Ritchison 1981), both of which are more abundant in large, open-grown, spreading oaks.

Nuthatch Nest Cavity Selection and Nest Success

White-breasted nuthatches selected nest cavities situated in trees containing more cavities than random trees that had cavities, and nest trees had a greater dbh than random trees. Local woodland structure around nests consisted of a combination of higher canopy cover, greater mean dbh of oaks, larger basal area, and fewer small oaks than were found at random locations at the home range scale. Larger oaks contain more cavities than small oaks (Gumtow-Farrior 1991). A higher number of cavities in a tree may result in a greater likelihood that a tree contains a cavity suitable for nesting. Because decaying oaks may contain habitat for more bark-dwelling invertebrates (Jackson 1979), white-breasted nuthatches may spend more time foraging in cavity-rich trees, increasing the likelihood that they will encounter a potential nest cavity. The attributes of nest cavities and surrounding vegetation that we measured did not contribute significantly to models of nest success, suggesting that there was no difference in predation among nest cavities selected by nuthatches in this study. Nest success was 71% (CI, 58% to 86%) in natural cavities, and 100% in artificial structures.

Contributions to Nuthatch Biology

Surprisingly little published data exists on white-breasted nuthatch breeding biology, despite the wide range of the species. This is probably in part because nuthatches use natural tree cavities, making nests difficult to examine. In addition, nuthatches have relatively large home ranges compared to similar-sized songbirds, so multi-species studies of nesting ecology generally involve small numbers of nuthatches. Previously published nesting studies included sample sizes ranging from 5 to 9 nests (McEllin 1979, Ritchison 1981, Stauffer and Best 1982). By concentrating our efforts on this one species over a large area, we were able to present data for 52 natural nest cavities in oak trees and 50 oak trees used for nesting.

White-breasted nuthatches in our study area of the Willamette Valley nested primarily in natural cavities in oak trees, but occasionally used other hardwood species, and readily used nest boxes where they were present. Although natural cavities appeared to be plentiful in the study area, competition from European starlings and other secondary cavity-nesters may limit the number of cavities that are available to nuthatches in some locations.

Within the Willamette Valley, nuthatches appeared to be limited in their selection of home range by woodland size and condition, avoiding dense interior woodlands and isolated woodlands, while preferring woodlands with a high proportion of edge, high proportion of oak woodland within 1 km, and more large trees. It appears that if conditions are suitable for nuthatches to establish a home range and build a nest, they are usually successful in fledging young.

Management Implications

Remaining oak woodlands in the Willamette Valley are in various conditions on the continuum of succession from oak savanna to coniferous forest. Species that have increased in oak woodlands in recent decades are those associated with conifer habitat (Hagar and Stern 2001). Woodlands that white-breasted nuthatches currently occupy at low densities represent potential for restoration work. Thinning small trees and removing conifers and other competing species from dense woodlands will create conditions that are more open, allowing development of wider-spreading oak crowns. Release of Oregon white oaks from conifers has been shown to result in production of new side branches in oaks and increased growth of small oaks (Devine and Harrington 2004). These open-form trees may provide more foraging substrate for nuthatches, and increase the likelihood of potential nest cavity formation. Removing tall conifers will allow more light to reach shade-intolerant oaks and may provide a more favorable microclimate for bark-dwelling invertebrates that nuthatches consume (Jokimäki et al. 1998). Large oaks (>50 cm dbh) and decaying and cavity-rich trees should be preserved, and care should be taken during mechanical removal operations to minimize damage to oaks that are retained. Where feasible, prescribed fire or mechanical mowing should be implemented to preclude future development of conifer seedlings. We recommend monitoring bird and other wildlife populations to detect any responses to oak restoration and management treatments.

Many oak woodlands in the Willamette Valley are on private land so cooperation with landowners is essential in managing for white-breasted nuthatches

and other oak-associated species. State and federal programs are available to provide funding and technical support for oak restoration on private land. Harvest and sale of mature conifers for lumber and small oaks for firewood may provide landowners additional monetary compensation for restoration on their property. Land management agencies and organizations should continue to place a high priority on protecting remaining oak stands through land acquisition and easements. Particular emphasis should be placed on preservation and acquisition of oak woodlands in close proximity to other oaks to promote movement of oak-associated species between stands.

Installation of nest boxes with appropriately sized openings in suitable habitat may provide more nesting options for white-breasted nuthatches. However, nest cavities may not be a limiting factor for nuthatches, and the addition of nest boxes could have unintended consequences, such as favoring certain species of cavitynesting species or limiting populations of open-nesting birds through competition (Brawn and Balda 1988, Bock et al. 1992, Purcell et al. 1997). Nest boxes also have the disadvantage of requiring maintenance and monitoring.

Given the profound loss of oak habitat that has occurred in the Willamette Valley over the last 200 years, protection of remaining woodlands in any condition is crucial to the continued survival of white-breasted nuthatches and other oak-associated species. The slow growth of oak trees means much forethought needs to go into planning for future generations. As interest and effort in oak savanna restoration

continue to increase, we expect a commensurate benefit to the health of populations of oak-associated wildlife species such as the white-breasted nuthatch.

BIBLIOGRAPHY

- Adamus, P. R., K. Larsen, G. Gillson, and C. R. Miller. 2001. Oregon Breeding Bird Atlas [CD-ROM]. Oregon Field Ornithologists. Eugene, OR, USA.
- Aitken, K. E. H., K. L. Wiebe, and K. Martin. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119:391-402.
- Altman, B. 2000. Conservation strategy for landbirds in lowland valleys of western Oregon and Washington. American Bird Conservancy and Oregon-Washington Partners in Flight.

 http://www.orwapif.org/pdf/western_lowlands.pdf. Accessed 2005

 November 8.
- Anderson, S. H. 1970a. The avifaunal composition of Oregon white oak stands. Condor 72:417-423.
- ----- 1970b. Ecological relationships of birds in forests of Western Oregon. Dissertation, Oregon State University, Corvallis, USA.
- ----- 1972. Seasonal variations in forest birds of western Oregon. Northwest Science 46:194-206.
- ----- 1976. Comparative food habits of Oregon nuthatches. Northwest Science 50:213-221.
- ------. 1980. Habitat selection, succession, and bird community organization. Pages 13-25 *in* R. M. DeGraff and N. G. Tilghan, technical coordinators. Management of western forests and grasslands for nongame birds. Intermountain Forest and Rangeland Experiment Station General Technical Report INT-86.
- -----, and H. H. Shugart. 1974. Habitat selection of breeding birds in an East Tennessee deciduous forest. Ecology 55:828-837.
- André, H. M. 1983. Notes on the ecology of corticolous epiphyte dwellers. Pedobiologia 25:271-278.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.
- Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. National Museum Bulletin 195.

- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724-1734.
- Bock, C. E., A. Cruz, Jr., M. C. Grant, C. S. Aid, and T. R. Strong. 1992. Field experimental evidence for diffuse competition among southwestern riparian birds. American Naturalist 140:815-828.
- Brawn, J. D. 1988. Selectivity and ecological consequences of cavity nesters using natural vs. artificial nest sites. Auk 105:789-791.
- -----, and R. P. Balda. 1988. Population biology of cavity nesters in Northern Arizona: Do nest sites limit breeding densities? Condor 90:61-71.
- Brush, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. Condor 85:461-466.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, England, UK.
- ----- 2004. Advanced distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, England, UK.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Campbell, B. H. 2004. Restoring rare native habitats in the Willamette Valley: a landowner's guide for restoring oak woodlands, wetlands, prairies, and bottomland hardwood and riparian forests. Defenders of Wildlife. West Linn, Oregon, USA.
- Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications 2:387-396.
- Christman, B. J., and A. A. Dhondt. 1997. Nest predation in black-capped chickadees: How safe are cavity nests? Auk 114:769-773.
- Conner, R. N., O. K. Miller, and C. S. Adkisson. 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bulletin 88:575-581.
- Defenders of Wildlife. 1998. Oregon's Living Landscape. Defenders of Wildlife, Lake Oswego, Oregon, USA.

- Devine, W., and C. Harrington. 2004. Garry oak woodland restoration in the Puget Sound region: releasing oaks from overtopping conifers and establishing oak seedlings. Pages 1-8. 16th International Conference, Society for Ecological Restoration.
- Dudley, J., and V. A. Saab. 2003. A Field protocol to monitor cavity-nesting birds. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Res. Pap. RMRS-RP-44. Fort Collins, Colorado, USA.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.
- Edenius, L., and K. Sjöberg. 1997. Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. Ecography 20:425-431.
- Environmental Systems Research Institute. 1992-1999. ArcView GIS: Release 3.2 [software]. Environmental Systems Research Institute. Redlands, California, USA.
- -----. 1999-2005. ArcGIS: Release 9.1 [software]. Environmental Systems Research Institute. Redlands, California, USA.
- Esseen, P.-A., and K.-E. Renhorn. 1998. Edge effects on an epiphytic lichen in fragmented forests. Conservation Biology 12:1307-1317.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.
- Finch, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in house wrens. Condor 91:848-859.
- Foggo, A., C. M. P. Ozanne, M. R. Speight, and C. Hambler. 2001. Edge effects and tropical forest canopy invertebrates. Plant Ecology 153:347-359.
- Fort, K. T., and K. A. Otter. 2004. Effects of habitat disturbance on reproduction in black-capped chickadees (*Poecile atricapillus*) in northern British Columbia. Auk 121:1070-1080.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.
- Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis, USA.

- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in forest-field ecotones. Ecology 59:871-883.
- Ghalambor, C. K., and T. E. Martin. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. Animal Behaviour 60:263-267.
- Giese, C. L. A., and F. J. Cuthbert. 2003. Influence of surrounding vegetation on woodpecker nest tree selection in oak forests of the Upper Midwest, USA. Forest Ecology and Management 179:523-534.
- Gumtow-Farrior, D. L. 1991. Cavity resources in Oregon white oak and Douglas-fir stands in the mid-Willamette Valley, Oregon. Thesis, Oregon State University, Corvallis, USA.
- Habeck, J. R. 1961. The original vegetation of the mid-Willamette valley, Oregon. Northwest Science 35:65-77.
- Hagan, J. M., and A. L. Meehan. 2002. Landscape-level variables for explaining bird occurrence in an industrial forest. Forest Science 48:231-242.
- Hagar, J. C., and M. A. Stern. 2001. Avifauna in oak woodlands of the Willamette Valley, Oregon. Northwestern Naturalist 82:12-25.
- Hazler, K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. Auk 121:707–716.
- Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. Wilson Bulletin 93:42-53.
- Hooge, P. N., M. T. Stanback, and W. D. Koenig. 1999. Nest-site selection in the acorn woodpecker. Auk 116:45-54.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York, New York, USA.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.
- Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69-93 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, Inc., New York, New York, USA
- -----, and B. J. Jackson. 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor 106:37-49.

- James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. Association of American Geographers, Annals 61:286-302.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661.
- ----- 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.
- Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. Condor 49:45-53.
- Jokimäki, J., E. Huhta, J. Itämies, and P. Rahko. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Canadian Journal of Forest Research 28:1068-1072.
- Kelsey, J. L., A. S. Whittemore, A. S. Evans, and W. D. Thompson. 1996. Methods in observational epidemiology. Oxford University Press, New York, New York, USA.
- Kilham, L. 1968. Reproductive behavior of white-breasted nuthatches. I. Distraction display, bill-sweeping, and nest hole defense. Auk 85:477-492.
- -----. 1981. Agonistic behavior of the white-breasted nuthatch. Wilson Bulletin 93:271-274.
- Kleinbaum, D. G., L. L. Kupper, and H. Morgenstern. 1982. Epidemiologic research: principles and quantitative methods. Lifetime Learning Publications, Belmont, California, USA.
- Klock, C., and C. Barrett. 1998. Willamette Valley land use/land cover map (wvveg24k.zip). Oregon Department of Fish and Wildlife and Northwest Habitat Institute. http://www.nwhi.org/. Accessed 2003 February 15.
- Knick, S. T., and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology 9:1059-1071.
- Knutson, M. G., G. J. Niemi, W. E. Newton, and M. A. Friberg. 2004. Avian nest success in Midwestern forests fragmented by agriculture. Condor 106:116-130.
- Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. Journal of Applied Ecology 19:361-370.

- Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365-374.
- Lawler, J. J., and T. C. Edwards, Jr. 2002. Composition of cavity-nesting bird communities in montane aspen woodland fragments: the roles of landscape context and forest structure. Condor 104:890-896.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons, New York, New York, USA.
- Li, P., and T. E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405-418.
- Lohmus, A., and J. Remm. 2005. Nest quality limits the number of hole-nesting passerines in their natural cavity-rich habitat. Acta Oecologica 27:125-128.
- Luck, G. W. 2003. Differences in the reproductive success and survival of the rufous treecreeper (*Climacteris rufa*) between a fragmented and unfragmented landscape. Biological Conservation 109:1-14.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28:287-324.
- MacFaden, S. W., and D. E. Capen. 2002. Avian habitat relationships at multiple scales in a New England forest. Forest Science 48:243-253.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics 18:453-487.
- -----, and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507-519.
- -----, and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. Condor 90:51-57.
- Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology 85:1411-1427.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. Journal of Ecology 82:113-123.
- Matthysen, E. 1998. The nuthatches. T & A D Poyser, London, England, UK.
- -----, F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. Oikos 72:375-381.

- Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255-261.
- -----. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.
- Mazerolle, M. J., and M.-A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6:117-124.
- McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography 21:247-260.
- McEllin, S. M. 1979. Nest sites and population demographies of white-breasted and pigmy nuthatches in Colorado. Condor 81:348-352.
- McIntyre, N. E. 1995. Effects of forest patch size on avian diversity. Landscape Ecology 10:85-99.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58-62.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265-276.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia 69:148-160.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.
- Peterson, B., and G. Gauthier. 1985. Nest site use by cavity-nesting birds of the Cariboo Parkland, British Columbia. Wilson Bulletin 97:319-331.
- Pöysä, H., and S. Pöysä. 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39:502-510.
- Pravosudov, V. V., and T. C. Grubb, Jr. 1993. White-breasted nuthatch. Number 54 *in* A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.
- Purcell, K. L., J. Verner, and L. W. Oring. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk 114:646-656.

- Radford, A. N., M. A. Du Plessis, R. AN, and D. p. MA. 2003. The importance of rainfall to a cavity-nesting species. Ibis 145:692-694.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service General Technical Report PSW-GTR-144. Albany, California, USA.
- Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth. Duxbury, Pacific Grove, California, USA.
- Rendell, W. B., and R. J. Robertson. 1989. Nest-site characteristics, reproductive success and cavity availability for tree swallows breeding in natural cavities. Condor 91:875-885.
- -----. 1990. Influence of forest edge on nest-site selection by tree swallows. Wilson Bulletin 102:634-644.
- Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309-313.
- Richards, D. G. 1981. Environmental acoustics and censuses of singing birds. Pages 297-300 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds: Studies in avian biology No. 6. Cooper Ornithological Society, Lawrence, Kansas, USA
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.
- Ritchison, G. 1981. Breeding biology of the white-breasted nuthatch. Loon 53:184-187.
- Robbins, C. S. 1981. Bird activity levels related to weather. Pages 301-310 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds: Studies in avian biology No. 6. Cooper Ornithological Society, Asilomar, California, USA
- -----, D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monographs 103:1-34.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.
- Saab, V. A. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135-151.

- Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966 2004. Version 2005.2. USGS Patuxent Wildlife Research Center. http://www.mbr-pwrc.usgs.gov/bbs/. Accessed 2005 September 14.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.
- Short, L. L. 1979. Burdens of the picid hole-excavating habit. Wilson Bulletin 91:16-28.
- Sisk, T. D., and C. R. Margules. 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. Pages 57-69 *in* D. A. Saunders, R. J. Hobbs, and P. R. Ehrlich, editors. Nature conservation 3: reconstruction of fragmented ecosystems. Surrey Beatty and Sons, Sydney, New South Wales, Australia
- Sprague, F. L., and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. Northwest Science 20:89-98.
- Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:831-843.
- Stauffer, D. F., and L. B. Best. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bulletin 94:329-337.
- Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. Number 1. Biological Conservation, and.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation of a western landscape. Ecology 79:2890-2903.
- Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49:1124-1133.
- Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, and S. Strindberg. 2002. Distance sampling. Pages 544-552 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of Environmetrics. John Wiley & Sons, Ltd., Chichester, England, UK
- -----, J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population

- Assessment, University of St. Andrews, Scotland, UK. http://www.ruwpa.stand.ac.uk/distance/
- Towle, J. C. 1982. Changing geography of Willamette Valley woodlands. Oregon Historical Quarterly 83:66-88.
- U.S. Fish and Wildlife Service. 2005. Endangered, threatened, proposed, and candidate species, critical habitat, and species of concern in western Washington. Western Washington Fish and Wildlife Office. http://www.fws.gov/pacific/westwafwo/se/splisttableMar05.pdf. Accessed 2005 September 14.
- Verboom, J., A. Schotman, P. Opdam, and J. A. J. Metz. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61:149-156.
- Vierkant, R. A., J. L. Kosanke, T. M. Therneau, and J. M. Naessens. 2000. MCSTRAT: A SAS macro to analyze data from a matched or finely stratified case-control design. Technical Report Series No. 65. Department of Health Science Research, Mayo Clinic. Rochester, Minnesota.
- Villard, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk 115:801-805.
- von Haartman, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339-347.
- Wagner, J. L. 1981. Seasonal change in guild structure: oak woodland insectivorous birds. Ecology 62:973-981.
- Washington Department of Fish and Wildlife. 2005. Species of Concern in Washington State. http://wdfw.wa.gov/wlm/diversty/soc/soc.htm. Accessed 2005 September 14.
- Waters, J. R., B. R. Noon, and J. Verner. 1990. Lack of nest site limitation in a cavity-nesting bird community. Journal of Wildlife Management 54:239-245.
- Weitzel, N. H. 1988. Nest-site competition between the European starling and native breeding birds in Northwestern Nevada. Condor 90:515-517.
- Welsh, C. J. E., W. M. Healy, and R. M. DeGraaf. 1992. Cavity-nesting bird abundance in thinned versus unthinned Massachusetts oak stands. Northern Journal of Applied Forestry 9:6-9.
- Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology 78:356-373.
- Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169-174.
- Wilson, R. A., P. Manley, and B. R. Noon. 1991. Covariance patterns among birds and vegetation in a California oak woodland. Pages 126-135 *in* R. B. Standiford, technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management. U.S. Forest Service General Technical Report PSW-126.
- Zanette, L., and B. Jenkins. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. Auk 117:445-454.