NEST SITE SELECTION, NEST SUCCESS, AND DENSITY OF SELECTED CAVITY-NESTING BIRDS IN NORTHEASTERN OREGON WITH A METHOD FOR IMPROVING THE ACCURACY OF DENSITY ESTIMATES

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AUTHORIZATION TO SUBMIT THESIS

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ABSTRACT

I studied the relationship between available habitat and density, nest site selection, and nest success in 5 species of cavity-nesting birds: the Pileated Woodpecker (*Dryocopus pileatus*), Black-backed Woodpecker (*Picoides arcticus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), Pygmy Nuthatch (*Sitta pygmaea*) and White-breasted Nuthatch (*Sitta caroliensis*) in the Upper Grande Ronde sub-basin of northeastern Oregon. Additionally, I investigated a method for estimating density of cavity-nesters by combining distance sampling and playback methods.

I compared nest site selection to available resources for 4 bird species. Habitat selected by 3 of these bird species was compared to selection observed in previous studies in northeastern Oregon to evaluate changes in patterns of selection. Although available resources in the current study differed greatly from those assessed in the 1970s in the same study area, Pileated Woodpeckers and Black-backed Woodpeckers exhibited no differences in patterns of nest site selection between sampling periods separated by 30 years. Williamson's Sapsuckers were less selective than the other woodpeckers and nested in the most abundant snags during both time periods. Logistic regression models to predict the use of a habitat plot as a nest location by each species are presented. In addition, I calculated nest success of Pileated Woodpeckers under current habitat conditions. Habitat variables at the nest site level generally were not explanatory in predicting nest success of Pileated Woodpeckers, but nest features such as the number of cavities, slope aspect, and cavity orientation were included in the best models.

I created multiple linear regression models describing the relationship between density and habitat to make predictions at the stand scale. The differences in the best models

to predict bird density among the 5 bird species represented the variation in forest conditions that are needed to sustain communities of cavity-nesting birds. Densities of Pileated Woodpeckers and Williamson's Sapsuckers were predicted by a combination of factors describing grand fir (*Abies grandis*) forest types with high densities of dead trees while White-breasted Nuthatches were predicted by lower densities of snags and live trees. Density of Pygmy Nuthatches was predicted by a combination of factors that represented ponderosa pine stands with large trees. Black-backed Woodpeckers were rare in all forest types and model predictions were weak.

In order to create reliable models, accurate estimates of density are needed. I estimated densities of several species of cavity-nesting birds using variable-width line transects. Immediately after concluding the line transect, I conducted playback surveys using tapes of calls and drumming of 4 of the species encountered. Counts of birds that responded to the tapes were tallied and compared to those counted using the distance sampling method. 61% of the total detections of Black-backed Woodpeckers and 48% of the Pileated Woodpecker detections were only acquired by eliciting a response using the playback method. Rare species such as these are therefore not accurately surveyed using passive methods alone. I combined these 2 survey methods by assuming the total number of birds detected (number from the transect and any additional birds from the playbacks) to be the true number of birds within an effective survey area (as calculated using only the distance data). I then estimated density based on the true number of birds within that effective survey area. I modeled the relationship between these 2 estimates by regressing the true density on the density of birds as estimated by the line transect method alone. The resulting model

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could be used to predict true density given estimates resulting from distance sampling and

provides a less biased estimate.

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INTRODUCTION

Habitat for terrestrial vertebrates in forested regions of the Interior Columbia River Basin has changed significantly since early European settlement (Wisdom et al. 2000).   Fire exclusion, timber harvest, overgrazing by livestock, and outbreaks of disease and insects have lead to changes in forest structure and composition (Hessburg et al. 1999). Within the Interior Columbia Basin, the severity of these changes are highly variable, but the effects are evident in the Blue Mountains in northeastern Oregon. Hessburg et al. (1999) found a significant decrease of remnant large trees, and both multi-story and single story old forest in the Blue Mountains. Historically, the fire regime in low elevation ponderosa pine (*Pinus ponderosa*) forest types included low intensity fires approximately every 20 years (Chappell et al. 2001). The exclusion of fire has allowed Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis)* to encroach upon open ponderosa pine forests over the past century (Wisdom et al. 2000).   Outbreaks of western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir tussock moth (*Orgyia pseudotsuga*) have spread through these replacement stands in the Blue Mountains, most severely in the 1980s and early 1990s (Swetnam et al. 1992, Wickman 1992). Evidence suggests that these outbreaks have become more severe as a result of prolonged fire exclusion (Swetnam et al. 1992). Additionally, intensive timber extraction methods result in late-seral forests being replaced with dense mid-seral forests, high road density and fragmented forest (Wisdom et al. 2000). Forest structure and composition has notably changed in this region in the past few decades.

The Interior Columbia Basin Ecosystem Management Project (ICBEMP) identifies wildlife "species of focus" that have been negatively affected by these changes

in wildlife habitat in this region (Wisdom et al. 2000). Many of these species are cavity-nesting birds.   Several species of cavity-nesters are uncommon and population trends are not well documented by census efforts such as the Breeding Bird Survey (Hejl 1994). Cavity-nesters are often associated with old-growth forests due to the high densities of snags for foraging and nesting (Mannan and Meslow 1984), and they are sensitive to management practices that result in snag removal (Zarnowitz and Manuwal 1985). Timber harvest, salvage logging of snags after forest fires, and high road densities, which expose snags to removal for firewood, have greatly decreased snag abundance throughout the Interior Columbia River Basin (Wisdom et al. 2000).

Habitat changes have had different effects on a variety of species of cavity-nesting birds. Pygmy Nuthatches (*Sitta pygmaea*), White-breasted Nuthatches (*Sitta carolinensis*), and White-headed Woodpeckers (*Picoides albolarvatus*) have been most affected by fire exclusion and timber harvest in historically open stands of large ponderosa pine (Dixon 1995, Wisdom et al. 2000). Both Three-toed Woodpeckers (*Picoides tridactylus*) and Black-backed Woodpeckers (*Picoides arcticus*) demonstrate irruptive population dynamics in stands with high levels of beetle infestation (Bull et al. 1986, Goggans et al. 1989) and are associated with recent stand-replacing fires (Hutto 1995, Murphy and Lenhausen 1998, Saab et al. 2004). Fire exclusion and salvage logging practices that remove snags after a fire have lessened the availability of foraging and nesting habitat for these birds. Pileated Woodpeckers (*Dryocopus pileatus*) and Williamson's Sapsuckers (*Sphyrapicus thyroideus*) are associated with late-succession conifer forests with high snag densities (Bull and Holthausen 1993, Conway and Martin 1993). Both of these birds depend on large-diameter trees for nesting (Bull and Meslow

1977, McClelland et al. 1979, Bull et al. 1986, Bull 1987). Many closed-canopy, mixed conifer forests that Pileated Woodpeckers and Williamson's Sapsuckers prefer have been greatly altered by outbreaks of forest insects. These defoliating insects convert green, continuous forest canopy to dead and opened forest (Wickman 1992). As a result of logging practices, large-diameter trees needed for nesting and roosting have been removed (Bull et al. 1992). The lengthening of the fire-return interval, the decline of late-succession ponderosa pine forest and the changes that have occurred in grand fir and mixed conifer stands are factors that affect the variety of cavity-nesting birds that use these forest types.

Many authors have recognized the importance of scale in wildlife studies and how both the spatial and temporal context of a study may influence predictions and inference (Morrison 2001, see Scott et al. 2002). Although several studies have identified important habitat attributes for cavity-nesting birds in the Blue Mountains (Bull and Meslow 1977, Bull et al. 1986, Bull 1987, Bull et al. 1992, Bull and Holthausen 1993), information that reflects present conditions of habitat and bird responses to habitat changes is lacking. A current perspective on nest selection and nest success in light of habitat changes is clearly necessary in order to understand cavity-nesting bird populations in this region. The benefit of framing current patterns of habitat selection in the context of historic studies is rarely achieved (Knick and Rotenberry 2000, Wiens 2002). Therefore, the availability of studies conducted in the same study area before severe outbreaks of western spruce budworm provides a unique opportunity to understand the temporal effects of these dramatic changes in forest structure and composition on cavity-nesting birds.

Just as the temporal scale under which we study a population must be addressed, the inferences made from data are highly dependent on the spatial scale at which studies are conducted. The models created under ICBEMP are intended for use at the broad scale (grain and extent). However, forest management decisions are often made at a finer scale. I present density-habitat relationship models to make predictions at the forest stand (4-65 ha) scale. In order to create reliable models, accurate estimates of density are needed. Distance sampling dramatically improves density estimates compared to fixed plot methods by estimating the effective area surveyed for each species. However, species such as woodpeckers and nuthatches are often undetected in population surveys (Hejl 1994). The playback method aids in detecting birds by broadcasting songs or calls in order to elicit a response. This method is used commonly for index counts in birds that are rare, elusive, or vocalize infrequently. Therefore, I also provide an improved method for estimating density by combining distance sampling and playback methods.

Over the past several decades, the scientific community has identified the need for measuring multiple aspects of population ecology to understand habitat quality (Van Horne 1983, Maurer 1986). Regardless of this recognition, rarely do studies incorporate survival and reproduction parameters due to the additional effort needed to collect these data (Bock and Jones 2004). Although density does provide useful information about populations and has been found to be correlated with breeding success in birds, Bock and Jones (2004) found that the disconnect between abundance and reproductive success is most probable in habitat that has undergone anthropogenic disturbance. I address this issue by providing estimates of density, habitat selection, and nest success of the Pileated Woodpecker in a post-disturbance forest.

This study focuses on 5 species of concern (as identified by the Interior Columbia Basin Ecosystem Management Project) found in the Upper Grande Ronde sub-basin of northeastern Oregon. These species are the Black-backed Woodpecker, Pileated Woodpecker, Pygmy Nuthatch, White-breasted Nuthatch and Williamson's Sapsucker. The objectives of this study will be addressed in 3 subsequent chapters.

Objectives

1. Compare current nest site attributes of 4 species of cavity-nesters to available habitat attributes.

2. Compare current nest selection to observations from the 1970s.

3. Calculate nest success of Pileated Woodpeckers.

4. Create density-habitat models for 5 species at the stand scale.

5. Evaluate a method for improving density estimates of cavity-nesting birds.

LITERATURE CITED

Brock, C.F. and Z.F. Jones. 2004. Avian habitat evaluation: should counting birds count? Froniers in Ecology and the Environment 2(8): 403-410.

Bull, E.L., and E.C Meslow. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. Journal of Forestry 77: 335-337.

_____, S.R. Peterson, and J.W. Thomas. 1986. Resource partitioning among woodpeckers in northeastern Oregon. PNW-444. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____. 1987. Ecology of the Pileated Woodpecker in northeastern Oregon. Journal of Wildlife Management 51: 472-481.

_____, R.S. Holthausen, and M.G. Henjum. 1992. Roost trees used by Pileated Woodpeckers in northeastern Oregon. Journal of Wildlife Management 56: 786- 793.

_____, and R.S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in northeastern Oregon. Journal of Wildlife Management 57: 335-345.

Chapell, C.B., R.C. Crawford, C. Barrett, J. Kagan, D.H. Johnson, M. O'Mealy, G.A. Green, H.L. Ferguson, W.D. Edge, and E.L. Greda, T.A. O'Neal. 2001. Wildlife habitats: descriptions, status, trends, and system dynamics. Pages 22-114 in D.H. Johnson and T.A. O'Neil, managing directors. Wildlife habitat relationships in Oregon and Washington. Oregon State University, Corvallis.

Conway, C.J. and T.E. Martin. 1993. Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests. Journal of Wildlife Management 57:322-328.

Dixon, R.D. 1995. Ecology of white-headed woodpeckers in the central Oregon Cascades. University of Idaho M.S. Thesis 148 p. Moscow, Idaho.

Goggans, R., R.D. Dixon, and L.C. Seminara. 1989. Habitat use by three-toed and Black-backed Woodpeckers Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. Technical Report 87-3-02.

Hejl, S.J. 1994. Human-induced changes in bird populations in coniferous forests in western North America during the past 100 years. Studies in Avian Biology 15:232-246.

Hessburg, P.F., B.G. Smith, S.D. Kreiter, C.A. Miller, R.B. Salter, C.H. McNicoll, and W.J. Hann. 1999. Historical and current forest and range landscapes in the Interior Columbia River Basin and portions of the Klamath and Great Basins. Part I: Linking vegetation patterns and landscape vulnerability to potential insect and pathogen

disturbances. General Technical Report PNW-GTR-485. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A) conifer forests. Conservation Biology 9(5): 1041-1058.

Knick, S.T. and J.T. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. Ecology 81(1): 220-227.

Mannan, R.W. and E. C. Meslow. 1984. Bird populations and vegetation characteristics in managed and old-growth forests, Northeast Oregon. Journal of Wildlife Management 48:1219-1238.

Maurer, B. A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. Journal of Wildlife Management 50(4): 556-566.

McClelland, B.R., S.S. Frissell, W.C. Fisher, and C.H. Halvorson. 1979. Habitat management for hole-nesting birds in forest of western larch and Douglas-fir. Journal of Forestry 77: 480-483.

Morrison, M.L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613-623.

Murphy, E.C., and W.A. Lenhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62(4): 1359-1372.

Saab, V.A., J.G. Dudley, and W.L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106: 20-36.

Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson. 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Swetnam, T.W., B.E. Wickman, H.G. Paul, and C.H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. Research paper PNW-RP-484. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4): 893- 901.

Wickman, B.E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. General technical report GTR-295. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wiens, J.A. 2002. Predicting species occurrences: progress, problems, and prospects. *In* Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Wisdom, M.J., R.S. Holthausen, B.C. Wales, C.D. Hargis, V.A. Saab, D.C. Lee, W.J. Hann, T.D. Rich, M.M. Rowland, W.J. Murphy, and M.R. Eames, 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. General technical report PNW-GTR-485. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Zarnowitz, J.E. and D.A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in the northwestern Washington. Journal of Wildlife Management 49 (1): 255-263.

CHAPTER 1. Nest selection and nest success of cavity-nesting birds in response to habitat changes in northeastern Oregon

ABSTRACT

Habitat changes in the Upper Grande Ronde sub-basin of northeastern Oregon due to timber harvest, fire exclusion, and recent insect outbreaks have altered the landscape. These changes have forced some cavity-nesting birds to adapt patterns of nest site selection and the resulting effects on nest success are unknown. In this study I compared nest site selection to available resources for 4 species of cavity-nesting birds: the Pileated Woodpecker (*Dryocopus pileatus*), Black-backed Woodpecker (*Picoides arcticus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), and Pygmy Nuthatch (*Sitta pygmaea*). Data for 3 of these bird species were compared to previous studies in the same study area to identify changes in patterns of selection. The ability to compare to studies conducted before severe outbreaks of western spruce budworm (*Choristoneura occidentalis*) provided a rare opportunity to understand the importance of the temporal context of habitat selection. In addition, I calculated nest success of Pileated Woodpeckers under current habitat conditions. Although available resources in the current study differed greatly from the 1970s, Pileated Woodpeckers and Black-backed Woodpeckers exhibited no differences in patterns of nest site selection between sampling periods separated by 30 years. Both species still select ponderosa pine snags preferentially for nesting. Williamson's Sapsuckers were less selective than other woodpeckers and nested in the most abundant snag species during both time periods. A variety of habitat components are needed to sustain populations of cavity-nesting birds. Habitat variables at the nest site level were generally not explanatory in predicting nest

success of Pileated Woodpeckers, but nest features such as the number of cavities, slope aspect, and cavity orientation were included in the best models.

INTRODUCTION

Many authors have recognized the importance of scale in wildlife studies and how both the spatial and temporal context of a study may influence predictions and inference (Morrison 2001, see Scott et al. 2002). Widespread disturbances, such as fire, intensive logging activity, or outbreaks of insects can greatly alter forest conditions. After a disturbance, the availability of forest conditions in terms of structure and composition may change patterns of habitat selection by wildlife. Forested habitat in the Interior Columbia River Basin has changed significantly since early European settlement (Wisdom et al. 2000). Historically, the fire regime in low elevation ponderosa pine (*Pinus ponderosa*) forest types was characterized by low intensity fires approximately every 20 years (Chappell et al. 2001). The exclusion of fire has allowed Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis)* to encroach upon open ponderosa pine forests over the past century (Wisdom et al. 2000). This pattern of prolonged fire exclusion has led to outbreaks of western spruce budworm and Douglas-fir tussock moth (*Orgyia pseudtsuga*) in these replacement stands in the Blue Mountains of northeastern Oregon, most severely in the 1980's and early 1990's (Swetnam et al. 1992, Wickman 1992).

These widespread habitat changes have invoked concern over species of cavity-nesting birds (Wisdom et al. 2000). Although several studies have identified important habitat attributes for cavity-nesting birds in the Blue Mountains (Bull and Meslow 1977, Bull et al. 1986, Bull 1987, Bull et al. 1992, Bull and Holthausen 1993), information that reflects present conditions of available habitat and bird responses to these changes is

lacking. In addition to understanding how cavity-nesting birds have adapted nest selection, it is important to also understand how habitat conditions affect productivity. A current perspective on nest selection and nest success in light of habitat changes is clearly necessary in order to understand cavity-nesting bird populations in this region.

Although authors have recognized the importance of the temporal scale of study, the benefit of framing current patterns of habitat selection in the context of historic studies is rarely achieved (Knick and Rotenberry 2000, Wiens 2002). Therefore, the availability of studies conducted in the same study area before severe outbreaks of western spruce budworm provides a unique opportunity to understand the temporal effects of these dramatic changes in forest structure and composition on cavity-nesting birds.

This study focuses on 4 species of concern (as identified by the Interior Columbia Basin Ecosystem Management Project) found in the Blue Mountains of northeastern Oregon. These species are the Black-backed Woodpecker, Pileated Woodpecker, Pygmy Nuthatch and Williamson's Sapsucker. The objectives of this study are: 1) compare current nest site attributes of 4 species of cavity-nesters to available habitat attributes. 2) compare current nest selection to data collected in the 1970s. 3) calculate nest success of Pileated Woodpeckers.

METHODS

Study Area

The study area consists of 2 areas located in the Upper Grande Ronde sub-basin (618,000 hectares) and within the Wallowa-Whitman National Forest. In order to apply my results to the variety of forest types and conditions available to cavity-nesting birds in

the Blue Mountains of Oregon and Washington, these two areas were chosen to capture

the ecological variability that results from a gradient of elevation, moisture, and slope

aspects typical in this region.

The first area, The Starkey Experimental Forest, is located 35 km south of La

Grande, Oregon and comprised 11,400 ha. Starkey ranges between 1070 and 1525 m in

elevation and the average precipitation is 50 cm per year (Bull et al. 1986). The area is

covered by coniferous forest stands and open grasslands that consist of ponderosa pine,

Douglas-fir, western larch (*Larix occidentalis*), grand fir, lodgepole pine (*Pinus

contorta*), and subalpine fir (*Abies lasiocarpa*) (Bull and Holthausen 1993). Evidence of

outbreaks of budworm is extensive, and intensive timber harvest has created a mosaic of

stand types.

The Spring Creek area is 17 km west of La Grande and at 930-1140 m, is lower

in elevation than Starkey. Due to past selective forest management, this area is

characterized by open stands of live ponderosa pine and grasslands, and contains many

large trees (> 50 cm diameter at breast height (dbh)) (Bull et al. 1988). The occurrence of

grand fir and Douglas-fir stands is less common, making this area less subject to

outbreaks of western spruce budworm. Consequently, there are fewer dead trees and

downed logs.

Nest Searching

Nest searching took place between 30 March and 15 July in both 2003 and 2004.

Following morning bird surveys, I located nests both opportunistically and systematically

by playing tapes of both drumming and calls of woodpeckers to elicit responses. Upon

detection of the birds, observers located a nest by looking for the presence of fresh wood

chips to indicate a newly excavated cavity, following the bird to observe nesting behavior

such as excavating a cavity, entering or exiting a cavity, or by observing the young.

Observers confirmed suspected nests found during the excavation period as active nests

by revisiting them during the incubation period and scratching on the trunk in order to

observe an adult (Bull et al. 1990).

Nest Survival

      I monitored nest survival of Pileated Woodpeckers in both 2003 and 2004. After

confirming a nest as active, I observed nest contents with a monitor attached to a small,

electronic camera mounted to a telescoping pole and inserted into the cavity when it was

possible (nests height < 15 m) or by observing nest activity from the ground to determine

nesting status (Dudley and Saab 2003). I revisited each active nest at least once a week

to monitor survival through fledging or failure.

Habitat Measurements

      During the summers of 2003 and 2004, habitat attributes were measured at nest

trees and at points systematically placed throughout the study area. Systematic plots

were established in 117 stands in 3 forest cover types (grand fir, Douglas-fir/ponderosa

pine, and ponderosa pine). Plots were located along bird survey transects and were

spaced at least 250-m apart and at an adequate distance from a forest edge (50 m) so as to

not sample non-forest or grassland cover types.

      I measured habitat variables based on information from previous studies that have

identified important attributes for these cavity-nesting birds (Table 1.1). I used variable-

width crossed plots with 50-m arms (Figure 1.1) centered on either nest trees or at

systematic points (Saab 2003). Only live trees $\geq$ 23 cm dbh and snags at least 1.4 m in

height and ≥ 23 cm dbh were measured. For each live tree within 5 m (.2-ha plot) of the

transect line (arm of the cross), I recorded species and diameter at breast height (cm). For

each snag within 10 m (.4-ha plot) of the transect line, I recorded species, diameter at

breast height, decay class (1 –3; Bull et al. 1997), and height class on a scale of 1 to 3 (<

10m, 10 – 19 m, or > 20 m). Downed logs with a large end diameter (led) ≥ 23 cm were

measured if their large end was within 2 m (.08-ha plot) on either side of the transect line.

For each log I recorded species, decay class (1-3; Bull et al. 1997), and led (cm). In

addition to taking exact measurements, I categorized live trees, snags, and logs as small

(23 – 37 cm led), medium (38-49 cm), or large (≥ 50 cm) based on categories described

by O'Neil et al. (2001). All plot measurements are described further in Table1.1.

In addition to variables measured in both nest and available plots, more specific

information was collected to describe nest trees. These variables were: tree height, cavity

height, cavity orientation, diameter at breast height, tree species, decay class (live or 1-3;

Bull et al. 1997), percentage of bark remaining, percentage of branches remaining, top

condition (broken or intact), number of fungal conks, and position on slope (bottom,

middle, or top).

Data Analysis

Nest tree analysis.

To test for differences between trees used as nests and available trees (both snags

and live) in the study area, I analyzed categorical variables (height class, decay class, and

tree species) in a Pearson's chi-square analysis for each bird species. In these analyses, I

defined the expected use of a resource as the proportion available of each type in the

study area and compared this to the proportion of each type used as a nest tree by each

bird species. I applied 95% Bonferroni confidence intervals to detect significant differences between resources used and those available (Neu et al. 1974, Manly et al. 2002).

In addition to comparing the nest tree to all available trees and snags within the study area, I assessed nest site selection within the nest plots. The only continuous variable measured on nest trees and on all other trees (snags and live) in the plot was diameter at breast height. In order to detect differences in the size of the nest trees and trees available within nest plots I performed a one-way analysis of variance with the nest tree treated as a block (Zar 1999). All analyses were performed in the SAS statistical program (SAS Institute 1999).

Nest plot analysis.

I assessed habitat selection at the plot level using logistic regression to model the probability that a given plot was a nest for each bird species. Variables were first screened for correlations in a correlation matrix in order to choose which variables should be used in the models and to eliminate problems with colinearity. A global model, including all variables that were retained from the correlation matrix, was evaluated using the Hosmer-Lemeshow goodness-of-fit test to ensure that the model adequately fit the data (Hosmer-Lemeshow 2000). In addition to a global model, 5 candidate models based on ecologically plausible relationships were considered for each bird species. Models were assessed using Akaike's Information Criterion (AIC) by comparing ΔAICc and choosing the model with the lowest AICc value (Burnham and Anderson 2002). In the case where competing models had a ΔAICc value less than 3, I performed model averaging in order to obtain parameter estimates (Burnham and Anderson 2002).

Nest success.

I modeled nest success (fledging of at least 1 young) in a logistic-exposure model proposed by Shaffer (2004). This general linear model allowed me to consider the influence of nest tree covariates on nest success and allowed the time of nest exposure to vary. Using an approach similar to the nest plot analysis, I ran a global model and a suite of 7 candidate models. These models included combinations of variables that described nest trees and surrounding habitat in addition to a constant survival model (intercept only). Models were compared using AICc and ranked by ΔAICc (Burnham and Anderson 2002).

RESULTS

Black-backed Woodpeckers

Nest tree characteristics.

In 2003 and 2004, I located a total of 14 Black-backed Woodpecker nests (Table 1.2). Smaller diameter stems, holes that were low to the ground, utilization of both live and dead trees, and a preference for ponderosa pine, characterized these nests (Table 1.2). Average dbh of all Black-backed nest trees (Table 1.2) was smaller than that of the other 3 cavity-nesting species and was significantly smaller than the average dbh of all other stems within Black-backed Woodpecker nest plots ($F = 6.47$; $P = .0114$). Black-backed Woodpeckers most commonly chose nest trees of less decay than the other 3 species of cavity nesting birds examined in this study (Figure 1.2). Half of the total nests were in live trees and 29% of the remaining nests were in decay class I snags. They avoided snags classified as decay class II (proportion used = 0.14 proportion available = 0.40, 95% Bonferroni confidence intervals = -0.092 – 0.372, Figure 1.2). Of the 7 nest trees

that were snags, Black-backed Woodpeckers significantly preferred ponderosa pine snags (proportion used = 0.57, available = 0.04, 95% Bonferroni confidence intervals = 0.102 – 1.04) and avoided Douglas-fir snags (proportion used = 0.14, available = 0.48, 95% Bonferroni confidence intervals = -0.188- 0.468) and grand fir (never used) (Figure 1.3). I also tested whether the height of Black-backed Woodpecker nest trees that were in snags differed from the height classes of available snags. Black-backed woodpeckers avoided snags less than 10 m tall (height class I) (proportion used = 0.14 proportion available = 0.52, 95% Bonferroni confidence intervals = -0.188 – 0.468) and preferred snags between 10 and 20 m tall (proportion used = 0.86 proportion available = 0.28, 95% Bonferroni confidence intervals = 0.53213 – 1.18787, Figure 1.5).

Nest plot characteristics.

Most Black-backed Woodpecker nests were found in the Douglas-fir/ ponderosa pine forest type (57%, Table 1.3). The average diameter of the stems surrounding the nest was smaller than the stems surrounding the nests of the other three cavity nesters (Table 1.3). The best model for predicting use of a plot as a Black-backed Woodpecker nest included a positive relationship with Douglas-fir forest type and the number of small live trees/ha and a negative relationship with slope and the number of logs per/ha. This model was the best model by a delta AICc of 3.4 and had an Akaike weight of .64 (Table 1.4, Appendix 1.1).

Pileated Woodpecker

Nest tree characteristics.

The 32 Pileated Woodpecker nests were in tall snags ($\bar{x}$ = 28.6 m) and larger in diameter ($\bar{x}$ = 79.2) than the nests of the other cavity-nesters (Table 1.2). The average

dbh of their nest trees was significantly larger than that of the surrounding stems (F = 128.7; P < .001). All nests were in snags, 91% of which were in decay class II (proportion used = 0.91, available = 0.40, 95% Bonferroni confidence intervals = 0.784 – 1.036, Figure. 1.2). These woodpeckers selected ponderosa pine (proportion used = 0.59, available = 0.04, 95% Bonferroni confidence intervals =0.373- 0.807) and larch snags (proportion used = 0.31, available = 0.08, 95% Bonferroni confidence intervals = 0.106- 0.514) and avoided grand fir (proportion used = 0.09, available = 0.40, 95% Bonferroni confidence intervals = -0.036 - 0.216) and Douglas-fir (never used) (Figure 1.3). Pileated woodpeckers selected snags classified as height class III (proportion used = 0.75, available = 0.19, 95% Bonferroni confidence intervals = 0.559 - 0.941) and avoided those in height class I (proportion used = 0.03, available = 0.52, 95% Bonferroni confidence intervals = -0.045 - 0.105, Figure 1.5).

Nest plot characteristics.

Most nests were located in the grand fir forest type (63.5%, Table 1.3). There was no single best model for predicting use of plots as a Pileated Woodpecker nest (Table 1.4, Appendix 1.1). Model averaging of the three top competing models produced parameter estimates. The resulting averaged model is: -2.7386 - 0.4161 (grand fir forest type) + 0.0494 (large snags/ ha) + 0.01105 (large live trees/ ha) + 0.0009 (logs/ ha). The number of large snags/ ha appeared in all of the top models.

Pygmy Nuthatch

Nest tree characteristics.

The 29 Pygmy Nuthatch nests that I located in 2003 and 2004 were in trees that averaged 54.6 cm dbh, but varied widely (range = 18-93 cm, Table 1.2). The mean

diameter of their nest trees was significantly greater than the diameter of other stems surrounding their nests (F = 15.18; P = .0001). Pygmy Nuthatches preferred snags classified as decay class II (proportion used = 0.79, available = 0.40, 95% Bonferroni confidence intervals = 0.601- 0.979, Figure 1.2) and chose snags in a wide range of heights (Figure 1.5). Although Pygmy Nuthatches used a variety of tree species to nest in, selection of ponderosa pine snags was significant (proportion used = 0.59, available = 0.04, 95% Bonferroni confidence intervals = 0.353 - 0.837, Figure 1.3).

Nest plot characteristics.

Most Pygmy Nuthatch nests were found in either ponderosa pine or Douglas-fir/ ponderosa pine forest types (86%, Table 1.3). The areas surrounding their nests were characterized by open forest consisting of large stems ($\bar{x}$ = 46.7 cm, Table 1.3) and few logs per ha ($\bar{x}$ = 4.6, Table 1.3). The best model for predicting use of a plot as a Pygmy Nuthatch nest site included a positive association with the ponderosa pine forest type and a negative association with the number of large live trees/ ha, small live trees/ ha, slope, and logs/ha (Table 1.4). This model was chosen with a delta AICc of 5.07 of the next best model and an Akaike weight of .92 offers strong evidence for being the best model (Appendix 1.1).

Williamson's Sapsucker

Nest tree characteristics.

In 2003 and 2004 I located more Williamson's Sapsucker nests than nests of the other cavity-nesters (n = 65, Table 1.2). Sapsucker nests differed from the other three cavity nesters in their use of the most abundant snag species for nesting, Douglas-fir and grand fir (80%, Figure 1.3). Williamson's sapsuckers preferred snags in decay class II

(proportion used = 0.89, available = 0.40, 95% Bonferroni confidence intervals = 0.793 -

0.987, Figure 1.2) and in height class II (proportion used = 0.69, available = 0.28, 95%

Bonferroni confidence intervals = 0.542 - 0.838, Figure 1.5). Like Pileated Woodpeckers

and Pygmy Nuthatches, sapsuckers chose large diameter stems for nesting ($\bar{x}$ = 60.9 cm,

Table 1.2) and the mean dbh of these stems was significantly larger than those

surrounding the nest (F = 88.8; $P < .0001$).

 Nest plot characteristics.

In addition to using both Douglas-fir and grand fir as nest trees, all nest trees were

found in those two forest types (Table 1.3). These areas also exhibited high densities of

snags. The best model for predicting use of a plot for a nest by Williamson's Sapsucker

indicated a positive association with the number of large snags/ha and a negative one

with large live trees/ha, slope, and logs/ha (Table 1.4). This model was chosen over the

next best model by a delta AICc of 5.48 and had an Akaike weight of .87 (Appendix 1.1).

Nest Success: Pileated Woodpeckers

Of the 32 Pileated Woodpecker nests found in 2003 and 2004, 23 (72%) of them

produced at least 1 fledgling ($\bar{x}$ = 1.96 SD = .56) and 9 failed (3 to predation, 6 with

cause unknown). At 1 of the 3 predated nests, remains of an adult were located near the

nest tree and attributed to predation by an *Accipter*. I could not differentiate between the

3 top models as the best model (Table 1.5, Appendix 1.2) for predicting nest survival in

Pileated Woodpeckers. The top model included the effects of cavity orientation and

slope aspect. The model including only the number of pileated cavities as an explanatory

variable and the constant survival model both had a ΔAICc less than 2. In order to

provide an estimate of nest success, I calculated a predicted daily survival rate (DSR)

using the logistic function in terms of each of the top 3 models (Shaffer 2004). I then determined an average survival rate by multiplying each of 3 DSR's by their model weight and taking the sum. This DSR raised to the power of the mean number of days in the nesting cycle (47 days) as observed for birds in this study, yields an overall estimated percentage nest success. For Pileated Woodpeckers in this study area in 2003 and 2004, the overall percentage of nest success was calculated as 70% (DSR = 0.9924, 95% CI: 0.9873, 0.9955).

DISCUSSION

Nest tree selection

All 4 species exhibited some degree of habitat selection at the nest tree level. Only Black-backed Woodpeckers chose nest trees smaller than the average of those available surrounding the nest. Pileated Woodpeckers, Pygmy Nuthatches and Williamson's Sapsuckers all chose larger trees to nest in than the average of those available surrounding their nest trees. These patterns are similar to those found by other authors. Martin et al. (2004) recorded an average dbh of 30.9 cm for trees with Black-backed Woodpecker nests, while Goggans et al. (1989) found nests in trees averaging 28 cm. Saab and Dudley (1998) and Raphael and White (1984) found that Black-backed Woodpeckers nested in smaller trees than all other cavity nesters in their studies.

Contrary to the Black-backed Woodpecker, many cavity nesters prefer large-diameter trees for nesting (Mannan and Meslow 1984). Several authors have reported that Pileated Woodpeckers nest in large-diameter trees (> 50 cm) (Bull and Meslow 1977, Bull 1987, McClelland et al. 1979, McClelland and McClelland 1999, Aubry and Raley 2002). Pygmy Nuthatches nested in large-diameter trees ($\bar{x}$ = 57.93) in Colorado

(McEllein 1979) and have been associated with mature forests (Szaro and Balda 1979). Williamson's Sapsuckers nest in a variety of tree sizes throughout their range. For instance, Conway and Martin (1993) recorded average dbh of nests much smaller than those in this study (30-50.8 cm in live trees, 25-63.5 cm in snags). Due to their large body size, Pileated Woodpeckers have a physical need for large-diameter snags, but Pygmy Nuthatches and Williamson's Sapsuckers do not share this morphological constraint. Snags found in old-growth forests are more likely to provide these 2 weak excavators with the advanced decay necessary for cavity excavation (Bull et al. 1986, Mannan and Meslow 1984, Kingery and Ghalambor 2001).

Snags taller than 10 m in height and in decay class II were preferred by several of the species in this study. By contrast, Black-backed Woodpeckers stood out amongst the other 3 species in choosing trees with the least amount of decay. In southwestern Idaho, Black-backed Woodpeckers nested in trees with less decay than other cavity nesters encountered (Saab and Dudley 1998), and Rapheal and White (1984) classified them as a "hard snag user". Pileated Woodpeckers most often chose taller snags for nesting. In coastal Washington, Aubry and Raley (2002) also found pileated nests in tall trees ($\bar{x} =$ 39.3 m), as did McClelland and McClelland (1999) in Montana ($\bar{x} =$30.7 m).

The strongest evidence for selection at the nest tree level was apparent in the choice of nest tree species. Pygmy Nuthatches, Black-backed Woodpeckers, and Pileated Woodpeckers all showed preference for ponderosa pine, with the latter 2 also preferring western larch. This was particularly interesting due to the overwhelming scarcity of these 2 snag species in the study area. Except for Pygmy Nuthatches, the cavity-nesting species in this study are known to select a variety of tree species throughout their range.

Pileated Woodpeckers chose Pacific silver fir disproportionately to its availability in coastal Washington (Aubry and Raley 2002) and exclusively used quaking aspen in interior British Columbia (Martin et al. 2004). Williamson's Sapsuckers nested in aspen snags preferentially and never used conifer snags in Arizona (Conway and Martin 1993). In the Sierra Nevada, Williamson's Sapsuckers nested in a wide variety of both live and dead tree species and were one of the least selective cavity nesters in the study (Raphael and White 1984).

Nest site selection

Nest site selection among the 4 cavity nesters was specific to each species. The best model for Black-backed Woodpeckers describes areas that have more small (23-37 cm dbh) live trees/ ha, fewer logs, shallow slope and are in the Douglas-fir forest type. Goggans et al. (1989) found that trees surrounding Black-backed Woodpecker nests in central Oregon averaged only 20 cm dbh and nests were in flat or gently sloping lodgepole pine stands. Black-backed Woodpeckers are most commonly associated with recent burns (Hutto 1995), and occupy areas structurally similar to those described by my best model for nest site selection (Saab and Dudley 1998). Portions of this study area were recently treated for fuels reduction through forest thinning and prescribed burning. Although Black-backed Woodpeckers used these areas, I was not able to quantify use of these areas in terms of burned or not burned, nor could I determine if these prescribed burns mimic ecological patterns favorable to Black-backed Woodpeckers in naturally occurring burns. The live ponderosa pine stands and the recently logged and burned fir stands in which these nests were found were relatively open and similar in structural conditions.

The late-succession, open ponderosa pine forest surrounding Pygmy Nuthatch nests is characteristic of this species. Some authors consider this cavity nester to be a long-needled pine forest obligate (Kingery and Ghalambor 2001). In the absence of ponderosa pine in the Sierra Nevada, Raphael and White (1984) found this species nesting in burned Jeffery pine/fir forest types. Due to their usual preference for old forest conditions (Kingery and Ghalambor 2001), the negative relationship with large live trees/ha in the habitat selection model was unexpected. However, Pygmy Nuthatch nests were in open areas with fewer stems/ha than other species (Table 1.3) and a negative association with the density of live trees or snags is explainable. Few studies have quantified nest selection of this species and their use of grand fir and Douglas-fir as nest trees and establishment of nest sites in both of these forest types, as found in this study, is less documented elsewhere. Although half of the Pygmy Nuthatch nests I found were located in ponderosa pine forest types, the overwhelming availability of large snags in grand fir and Douglas-fir forest types may explain their use of these areas.

Both Pileated Woodpeckers and Williamson's Sapsucker nests were found exclusively in grand fir and Douglas-fir forest types, associated with higher densities of large snags and logs. Throughout their range, both species are found in a variety of forest types (Raphael and White 1984, Bull 1987, Conway and Martin 1993, McClelland and McClelland 1999, Aubry and Raley 2002). The grand fir and Douglas-fir forest types in this study area had an abundance of logs and snags of these 2 conifer species. These areas were ideal for an unselective nester such as Williamson's Sapsucker. However, selection of large ponderosa pine by Pileated Woodpeckers in these forest types, where this snag species was rare, emphasizes this highly selective behavior. Although not

abundant, western larch snags were also available in both grand fir and Douglas-fir forest types. The positive relationship with log density in the best model for Pileated Woodpecker nests is likely explained by the importance of logs as hosts to ants, their main prey item (Bull and Holthausen 1993).

Nest Success: Pileated Woodpeckers

Nest success is assumed to be higher in primary cavity nesting birds, such as Pileated Woodpeckers, than in open cup or secondary cavity-nesting birds (Martin and Li 1992). Over a 10-year period between 1973 and 1983, Bull and Meslow (1988) reported a mean apparent nest success of 83% (n= 81 nests). Apparent nest success rates for Pileated Woodpeckers in 2003 and 2004 are only slightly less than those recorded during the 1970s in this study area. Nests that fail early have a higher probability of not being located by an observer as opposed to those that survive a longer period of exposure (Mayfield 1975, Johnson 1979, Shaffer 2004). Therefore, these apparent nest success rates may over estimate nest survival. Based on weekly visits, the modeled nest success rates account for the nests not found due to early failure. I report the modeled rates of nest success of Pileated Woodpeckers in this study area during the 2003 and 2004 nesting seasons (Table 1.4). I am therefore unable to directly assess whether the fitness of Pileated Woodpeckers has changed over the past 30 years as a function of habitat differences. I am, however, able to address the influences of habitat variables measured at the nests monitored in 2003 and 2004 on nest survival.

Given that 2 of the top 3 models were not distinguishable from the constant survival model in their ability to fit the data, habitat attributes at the nest tree level were probably not a strong influence on survival. Additionally, the 2 models other than the

constant survival model contained covariates that described the nest tree (number of cavities, aspect, and cavity orientation), but were not directly related to forest structural conditions. The number of cavities in the nest tree is likely an indicator of a tree or location that has been successful in the past for Pileated Woodpeckers. This may act as an indicator of an important resource not only to the Pileated Woodpecker, but to a land manager as well. Pileated Woodpecker nests that faced east or south were more likely to fledge at least 1 young than those that faced north or west. Due to the fact that several of the nest failures were at the beginning of the nesting cycle, nests that faced east or south may have benefited from additional thermal aid during incubation on these warmer sides of the tree (Weibe 2001). McEllin (1979) and Saab et al. (2004) found a similar pattern of selection of cavity orientation in a variety of cavity-nesting birds. Bull (1987) found cavity orientation selection related to the lean of the tree and attributed this as a protective feature from predation and weather as well.

Measures of fitness are important in assessing habitat quality (Van Horne 1983), but the scale at which this is evaluated can influence conclusions (Maurer 1986). Though I did not find a strong correlation between nest success and habitat attributes surrounding nest trees of Pileated Woodpeckers, further study on effects of habitat attributes in the larger landscape and continued monitoring of nest success may reveal different results. In particular, effects of habitat changes in the Blue Mountains may have had an influence on forage quality and availability, territory size, and vulnerability to predators. All of these are essential components of fitness of Pileated Woodpeckers at a broader scale.

Comparison with pre-budworm disturbance

Comparing studies in the same area separated by a time period of 30 years has contributed to the understanding of habitat selection in cavity-nesting birds and accounted for the influence of the temporal scale. Few studies have examined the effects of habitat change and disturbance on selection patterns in the same study area (but see Knick and Rotenberry 2000). Wiens (2002) demonstrated that habitat association models developed on data from one time period may be inadequate when applied to dynamic habitat conditions. Although the availability of habitat components in northeastern Oregon has changed in the past 30 years (Figure 1.6), my results indicate that habitat relationships for cavity-nesting birds remained similar. Ponderosa pine snags were used by all 3 species in the previous study, but have become increasingly rare relative to the abundance of grand fir and Douglas-fir snags due to mortality caused by the western spruce budworm. Williamson's sapsuckers rarely used ponderosa pine snags in the current study and exploited the most available snag species in both time periods. The continued selection of ponderosa pine snags by Black-backed Woodpeckers and Pileated Woodpeckers in the current study accentuates the selectivity of these 2 species.

Given the association of Black-backed woodpeckers with recent stand-replacing fires and the enigmatic behavior that characterizes this species, the ability to compare habitat selection between 2 time periods where stand-replacing fire has been relatively absent is a rare opportunity. During both time periods few nests of this species were located relative to other cavity-nesting species. Nest trees continue to be small-diameter, with little decay, and nest cavities are low to the ground (Table 1.2, 1.3, Figure 1.2, 1.3,

1.4).   Measures of the nest tree as well as the areas surrounding nests suggest that Black-backed Woodpeckers exhibit little variation over the two time periods.

Pileated Woodpeckers show a preference for tall, large-diameter ponderosa pine and larch snags in the grand fir forest type during both time periods (Table 1.2, 1.3, Figure 1.3, 1.4). Considering that other authors have shown Pileated Woodpeckers to use a variety of nest tree species and forest types throughout their range, their continual selection of ponderosa and larch snags in northeastern Oregon over the past 30 years is even more notable given the increasing rarity of these resources. The importance of retention of large snags of these species under any management condition cannot be over-emphasized. In addition to differences in species composition of available snags in this study area, the percentage of canopy cover has decreased due to the large proportion of dead grand fir and Douglas-fir. Except for this change in canopy cover, characteristics of Pileated Woodpecker nests of the 1970s and today are identical (Tables 1.2 and 1.3). Canopy cover was found to be significantly greater at Pileated Woodpecker nests sites than at available sites in the previous study with a mean of 70% (Bull 1987). Due to defoliation by spruce budworm, not a single nest in my study had a canopy cover greater than 68% with a mean of only 31%. Under these conditions, currently canopy cover at nests as compared to canopy cover in the study area is not different and not an explanatory variable for a nest location.

Williamson's Sapsuckers exhibited the largest difference in nesting habitat from data collected in the previous studies in the same area (Bull et al. 1986, Bull 1980) and were least selective among the species in the current study. In both studies, Williamson's Sapsuckers chose the most abundant snag species as nest trees most of the time (Figure

1.3, 1.4). In light of the variety of tree species used by these birds across their range, evidence suggests that advanced decay rather than snag species or size is more important to Williamson's Sapsuckers. In both studies, all nests were found in grand fir and Douglas-fir forest types. The increase in the abundance of snags in these two forest types under current conditions has likely improved nesting habitat for this abundant cavity-nester in the Blue Mountains.

Western spruce budworm and other forces of habitat change in the Blue Mountains have had varying impacts on habitat selection amongst cavity-nesting species. Due to the high percentage of dead trees, these conditions could be favorable in the short-term for these birds in terms of both nest availability and foraging. However, the longer-term impacts on cavity-nesting species of the lack of snag recruitment in addition to the effects on other forest vertebrates reliant on a higher proportion of live trees and denser canopy are unknown.   Further research on nest success and fitness is important for understanding these changes. In addition, reintroduction of fire and maintenance of open understory in old-growth stands of ponderosa pine discourages encroachment by Douglas-fir and grand fir. This forest type is still essential for a variety of species dependent on these conditions.   Considering the range of nesting habitat requirements for the 4 cavity-nesting bird species in my study, a variety of forest conditions and snag types are needed to accommodate cavity-nesters as a whole.

Table 1.1. Habitat characteristics measured in each plot in the Upper Grande Ronde sub-basin, 2003 and 2004.

Variables	Method
Dominant forest cover type	Johnson and Hall 1990
Number of canopy layers	visual count
Live trees/ha and snags/ha in 3 size classes:	O'Neil et al. 2001
DBH (23-37 cm, 38-49 cm, 50 cm and >)	
Percent Canopy Cover (%)	Densiometer
Percent slope	Clinometer
Azimuth(°)	Compass
Trees, snags, and log $\geq$ 23 cm:	
Species	
Decay class	Bull et al. 1997
Tree height (snags only) in 3 classes	visual assessment
($\leq$ 10 m, > 10-20m, > 20m)	
Diameter at breast height (DBH)	DBH tape
or large end diameter (LED)	

Table1.2 Frequency and mean (standard deviation) of measurements of nest tree characteristics of 4 cavity-nesting species and available snags in the Upper Grande Ronde sub-basin, 2003 and 2004. Data collected in the 1970s (Bull et al. 1986, Bull 1987) are included for comparison.

Characteristic	Black-backed Woodpecker		Pileated Woodpecker		Williamson's Sapsucker		Pygmy Nuthatch		Available Snags	
	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004
% PICO[1]	27	7	0	0	0	0	---	0	24	3
% PIPO	67	50	73	59.4	40	6.2	---	55.2	48	4.2
% LAOC	6	36	25	31.2	41	16.9	---	3.4	9	7.9
% PSME	0	7	0	0	1	38.5	---	31	16	47.7
% ABGR	0	0	2	9.4	9	36.9	---	10.3	3	39.5
Nest DBH (cm)	37 (21.1)	30.4 (7.9)	84 (59.2)	79.2 (23.1)	70 (26.4)	60.9 (17.9)	---	54.6 (21.0)	27 (16.9)	38.3 (8.5)
Tree Height (m)	19 (9.9)	15.4 (8.4)	28 (8.3)	28.6 (10.8)	24 (10.1)	17.2 (9.6)	---	15.3 (8.8)	14 (6.8)	---
Nest Height (m)	5 (6.2)	6.1 (5.1)	15 (4.9)	15.1 (5.4)	15 (7.1)	12.6 (5.7)	---	10.0 (5.7)	---	---
# of Holes	---	1.1 (0.5)	---	2.7 (2.0)	---	6.1 (8.9)	---	8.1 (9)	---	---
% in Snags	60%	50%	99 %	%100	51%	94%	---	93%	---	---
% Bark	97 (6.7)	92 (26.5)	43 (33.2)	31.5 (32.0)	87 (21.0)	92 (21.0)	---	76 (34.9)	91 (23.7)	---
% Branches	85 (27.9)	75 (28.3)	34 (32.4)	31 (30.6)	61 (35.6)	55 (29.8)	---	45 (32.2)	68 (36.0)	---
% Broken top	---	28.5	58	59	64	88	---	76	9 (22.4)	---
Sample size[2]	15	14	105	32	86	65	0	29	652	4294

[1] Tree species: PICO = Lodgepole pine, PIPO = ponderosa pine, LAOC = western larch, PSME = Douglas-fir, ABGR= grand fir
[2] Sample size reflects total number of nest trees (live or snag) whereas availability data are only shown for snags

Table 1.3. Mean (standard deviation) and frequency of characteristics in nest plots of four cavity-nesting species and available plots in the Upper Grande Ronde sub-basin, 2003 and 2004. Plot size was converted to match data from 1970s (Bull et al. 1986, Bull 1987) for comparison.

Characteristic	Black-backed Woodpecker		Pileated Woodpecker		Williamson's Sapsucker		Pygmy Nuthatch		Available	
	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004	1970s	2003-2004
%ABGR[1]	27	14	66	62.5	53	55	---	14	50	42
%PIPO	4	21	0	0	5	0	---	48	11	23
%PSME/PIPO	33	57	34	37.5	42	45	---	38	39	36
% Canopy	46	31	70	31.3	60	27.2	---	27.4	64	35.5
	(25.5)	(18.8)	(23.5)	(19.2)	(26.2)	(15.9)		(20.9)	(26.8)	(20)
Total Live/ .1 ha [2]	17	9.7	32	7.67	22	5.7	---	5.9	19	7
	(16.5)	(4.6)	(18.2)	(5.7)	(15.0)	(3.6)		(3.7)	(12.8)	(5.2)
Total Snags/ .1 ha	18	3.4	7.8	7.24	6	7.1	---	1.4	5.0	3.8
	(18.9)	(2.9)	(7.5)	(4.4)	(6.1)	(5.1)		(1.4)	(8.6)	(4.8)
≥ 50 cm dbh	---	0.36	1.9	2.4		2.1	---	0.41	1.0	2.0
		(0.8)	(1.3)	(1.9)		(1.9)		(0.5)	(1.4)	(1.4)
Logs/ .1 ha	---	6.3	---	17	---	15.7	---	4.6	---	12.3
		(4.7)		(8.2)		(8.9)		(4.7)		(9.9)
% Logs	6	---	13	---	10	---	---	---	13	----
	(6.1)		(12)		(9)				(11.3)	
Size logs (LED)	23	32.3	24	36.4	31	35.5	---	37.9	21	35.2
	(7)	(4.9)	(13.6)	(5)	(14.9)	(4.1)		(8.6)	(11.1)	(6.6)
Mean DBH of snags and trees (cm)	---	38	---	43	---	43.8	---	46.7	---	39.4
		(7.2)		(7.1)		(5.6)		(9.1)		(8)
Percent slope	12	10.1	19	13.2	17	10.1	---	6.8	20	15.8
	(10.1)	(3.5)	(11.7)	(10.7)	(14.6)	(11.3)		(6.1)	(15.6)	(12)
Sample size	15	14	105	32	86	65	0	29	367	225

[1] Forest type: ABGR= grand fir, PSME = Douglas-fir, PIPO = ponderosa pine
[2] 1970s live trees, snags, and logs reflect ≥15 cm; current live trees, snags, and logs reflect ≥ 23 cm in diameter

Table 1.4. Best logistic regression models for predicting use of vegetation plots as a nest site for 4 species of cavity nesting birds in the Upper Grande Ronde sub-basin, 2003 and 2004. See Appendix I for all models considered.

Species	Best Model	ΔAICc	K[3]	w_i[4]
Black-backed Woodpecker	Use[1] = -1.993 + 1.149(PSME[2]) - .071(slope) + .0067(small trees/ha) -.0101(logs/ha)	0	6	.64
Pileated Woodpecker[5]	Use= -2.662 + .049 (large snags/ha)	0	3	.51
Pileated Woodpecker	Use = -2.75 + .047 (large snags/ha) + .0008 (logs/ha)	1.93	4	.19
Pileated Woodpecker	Use = -2.83 - .42(ABGR) + .055(large snags/ha) + .011(large trees/ha)	2.18	5	.17
Pygmy Nuthatch	Use= 1.55 + 1.10 (PIPO) - .114(slope) - .0356(small trees/ha) - .028 (large trees/ha) - .014(logs/ha)	0	7	.92
Williamson's Sapsucker	Use= -.818 - .0496(slope) + .042(large snags/ha) – .015(large tree/ha) - .0007(logs/ha)	0	6	.87

[1]Use = Probability a plot was used as nest

[2] Cover type: PSME = Douglas-fir, ABGR = grand fir, PIPO = ponderosa pine

[3]Number of parameters

[4]Akaike weight

[5]The 3 top models are listed for Pileated Woodpeckers due to their high predictive value based on delta AICc. See text for model averaged parameter estimates.

Table 1.5. Best logistic-exposure models for predicting nest success of Pileated Woodpeckers in the Upper Grande Ronde sub-basin, 2003 and 2004. See Appendix II for all models considered

Model	Parameters	ΔAICc	K[2]	w_i[3]	DSR[4]	95 % CI	Nest success[5]
Cavity orientation and aspect [1]	Success= 5.9 - 2.92 (cavity orientation) -1.3 (aspect) + 3.4 (orientation*aspect)	0	5	.42	.9926	.98225, .99697	71%
Number of pileated cavities	Success = 3.87 + .38 (cavities)	0.70	3	.29	.9925	.9841, .99658	70%
Constant survival	Success = 4.76	1.74	2	.17	.9915	.98381, .99559	67%

[1] East or south facing (46-225) vs. north or west (0-45, 226-360) facing
[2] No. of parameters
[3] Akaike weights
[4] Daily survival rate
[5] Nest success = DSR^ # days in nesting cycle (= 47)

Snags $\geq$ 23 cm
20 m

Canopy cover measured in 4
directions, 1-2 m out from nest
tree (or center of plot)

Nest

Live Trees
$\geq$ 23 cm

10 m

50 m
Section

4 m

Down logs ($\geq$ 23 cm LED)
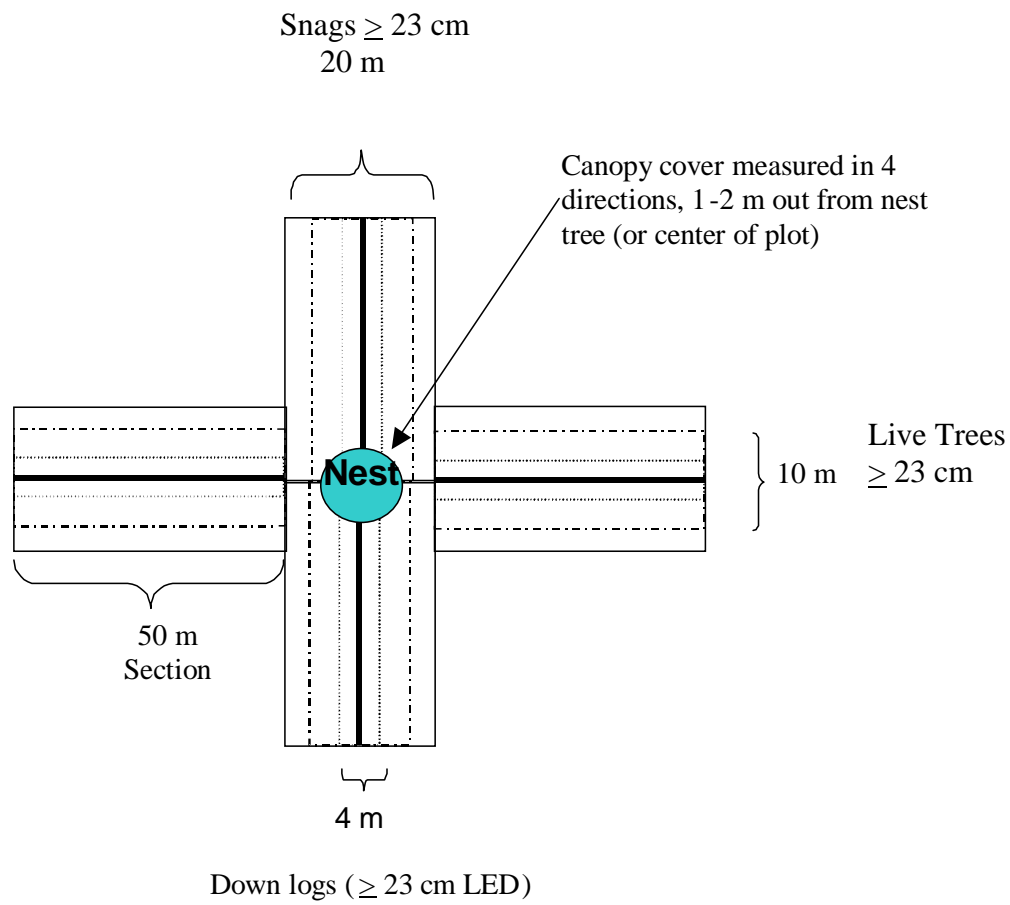
Figure 1.1. Sampling design used for measuring habitat variables in the Upper Grande
Ronde Sub-basin, 2003 and 2004 (adapted from Saab 2003).
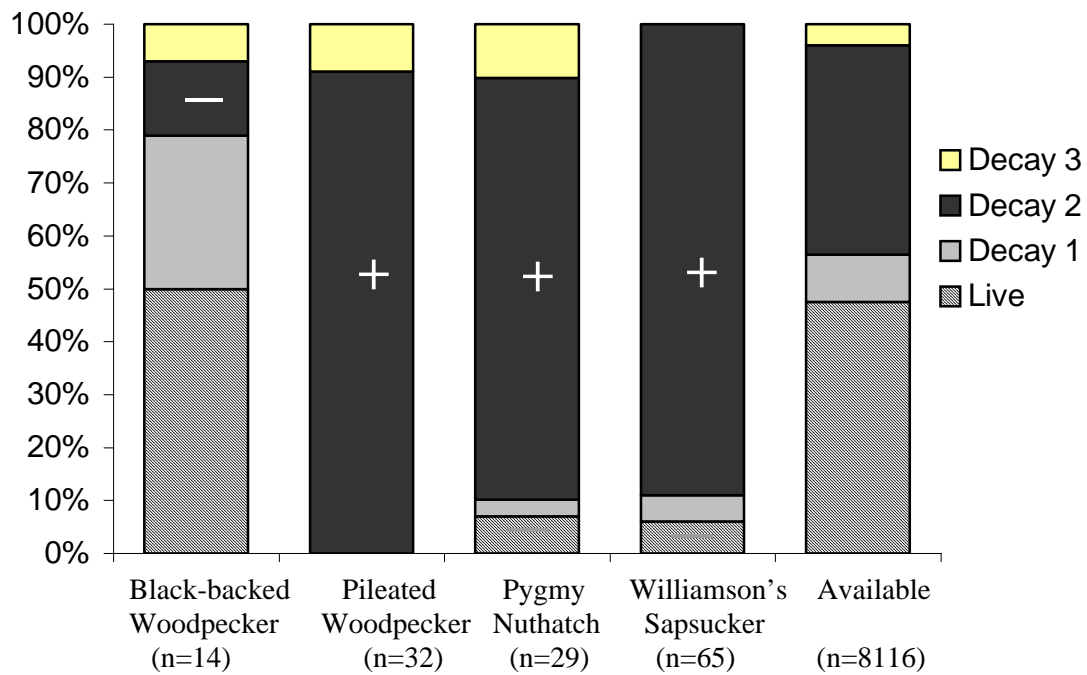
Figure 1.2. Distribution of nest trees and random trees by decay class (Bull et al. 1997) in the Upper Grande Ronde Sub-basin, 2003 and 2004. Not statistically significant for any species. + indicates preference, - indicates avoidance given 95% Bonferroni confidence intervals.
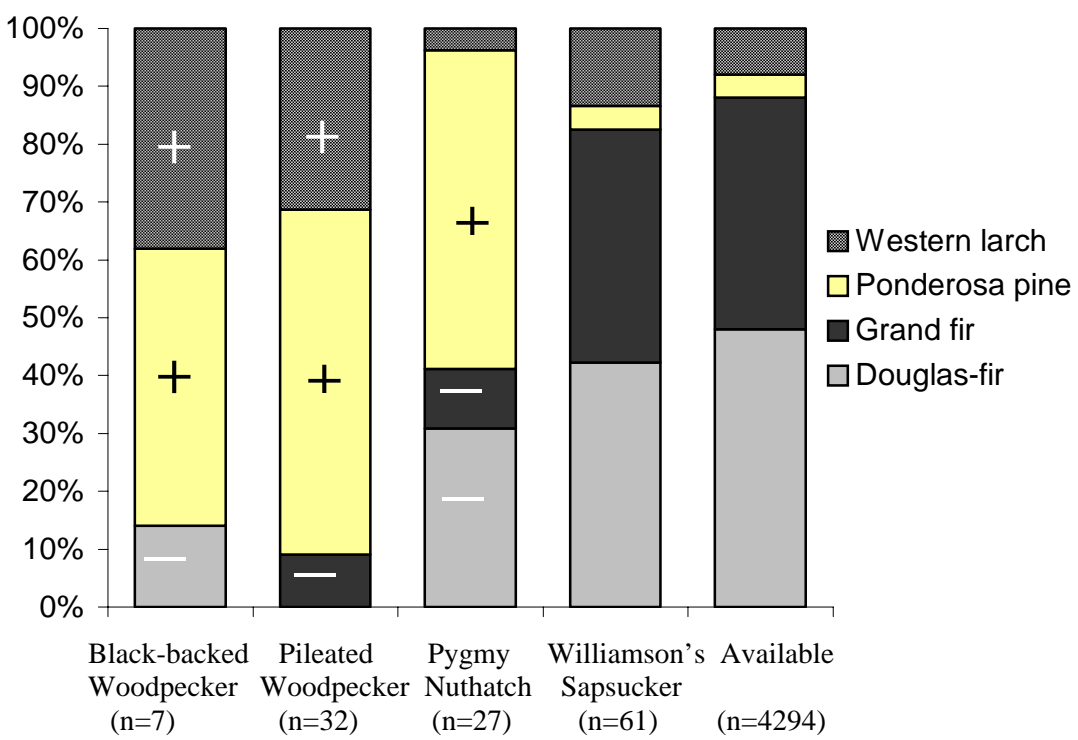
Figure. 1.3. Distribution of nest trees that were snags and available snags species, Upper
Grande Ronde Sub-basin, 2003 and 2004. + indicates preference, - indicates
avoidance given 95% Bonferroni confidence intervals.
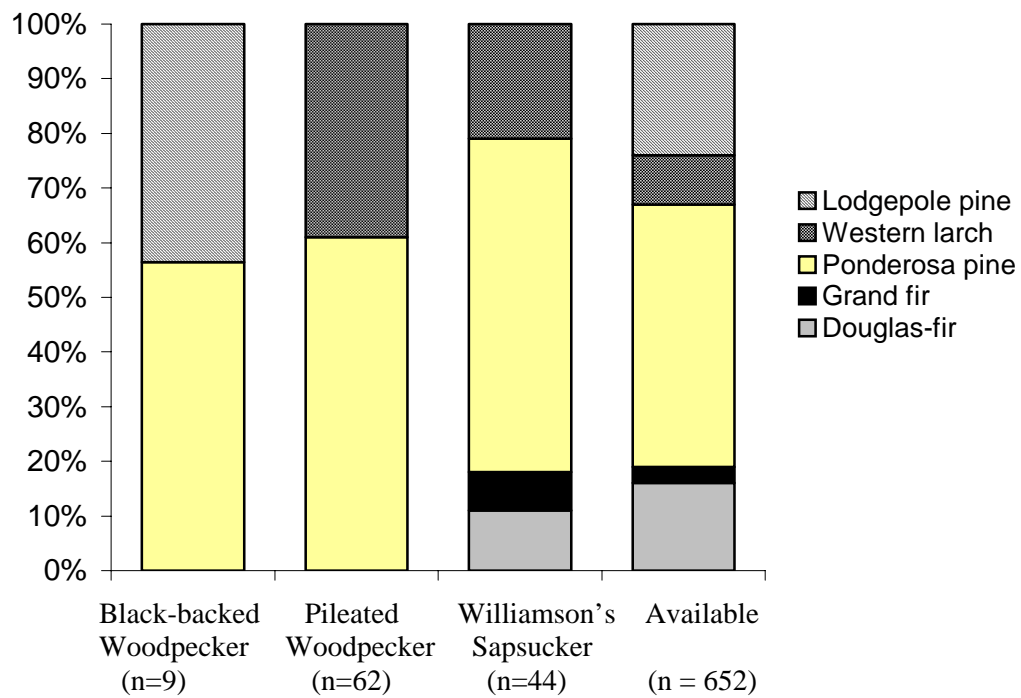
Figure 1.4. Distribution of nest trees that were snags and available snags species in the 1970s, Starkey Experimental Forest (Bull 1980).
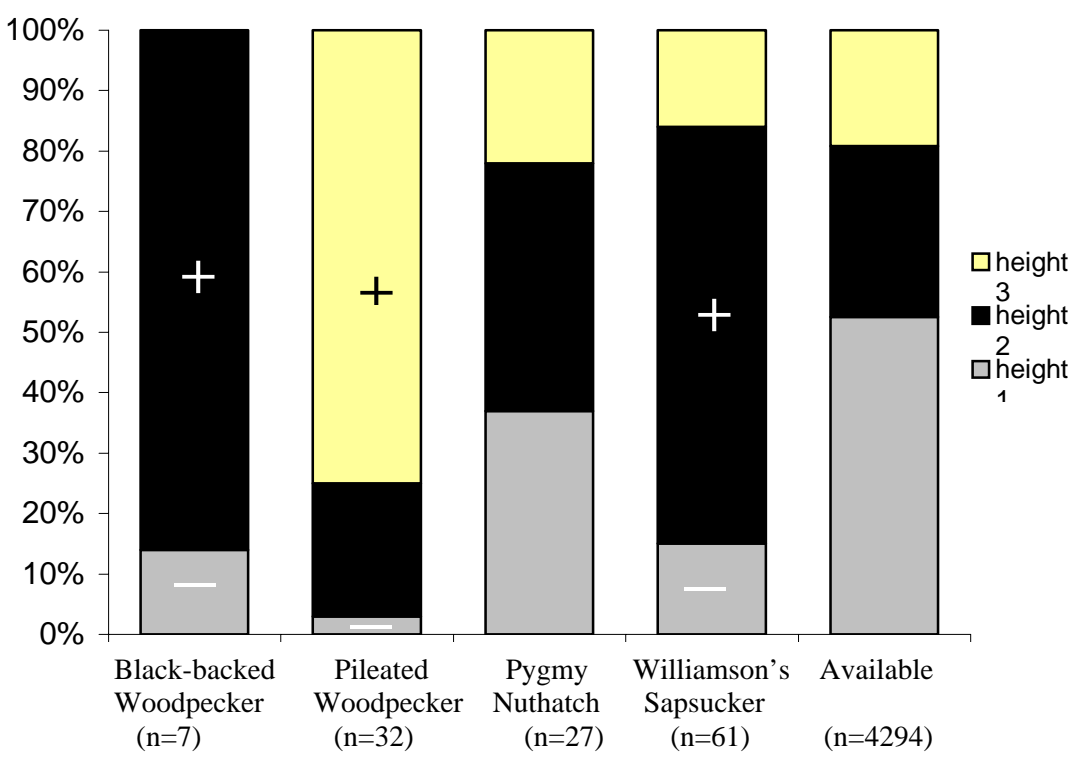
Figure 1.5. Distribution of nest trees that were snags and available snags by height class, Upper Grande Ronde Sub-basin, 2003 and 2004. Height 1= 1.4 –10m; height 2= > 10-20m; height 3 = > 20m. + indicates preference, - indicates avoidance given 95% Bonferroni confidence intervals.
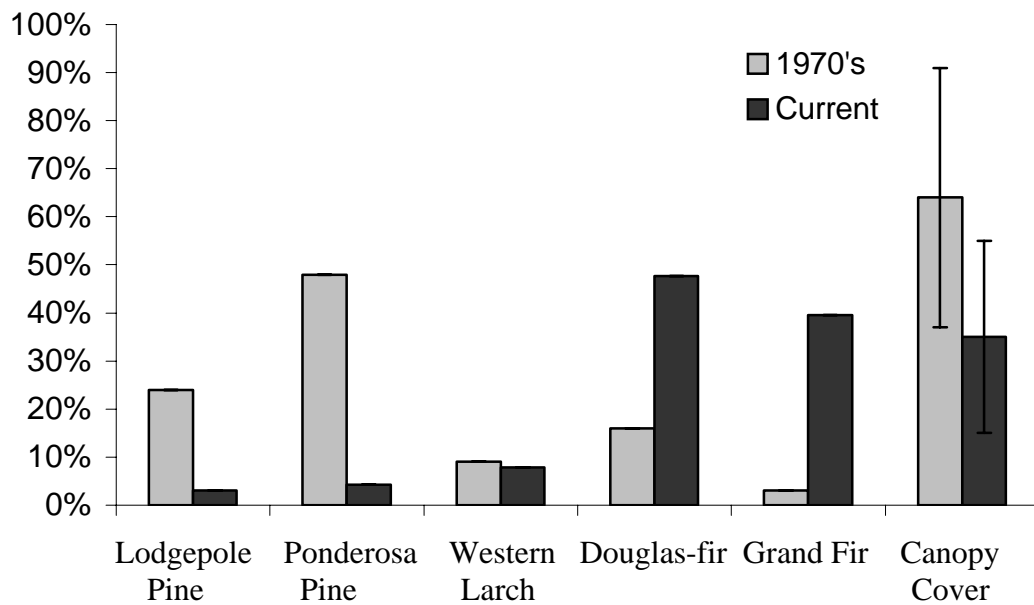
Figure 1.6. Differences in snag species encountered and canopy cover in the Upper Grande Ronde Sub-basin, 2003 and 2004, compared to Bull et al. (1986).

Appendix 1.1. All logistic regression models considered in model selection for predicting use of a plot as a nest location by 4 species of cavity-nesting birds in the Upper Grande Ronde sub-basin, 2003-2004.

Species	Candidate model	ΔAICc	K^4	$w_i{}^5$
Black-backed Woodpecker	Use[1] = PSME[2], slope, small trees/ha, logs/ha	0	6	0.64
	Use = PSME, small snags/ha, small trees/ha, logs/ha	3.39	6	0.12
	Use = canopy layers, slope, small trees/ha, logs/ha	3.82	6	0.09
	Use = PSME, canopy layers, slope, small snags/ha, medium snags/ha, large snags/ha, small trees/ha, medium trees/ha, large trees/ha, logs/ha[3]	4.64	12	0.07
	Use = canopy layers, slope, small snags/ha, small trees/ha, logs/ha	4.70	7	0.06
	Use = slope, small snags/ha, small trees/ha	6.76	5	0.02
Pileated Woodpecker	Use = large snags/ha	0	3	0.51
	Use = large snags/ha, logs/ha	1.95	4	0.19
	Use = ABGR, large snags/ha, logs/ha	2.22	5	0.17
	Use = small snags/ha, med snags/ha, large snags/ha	3.52	4	0.09
	Use = canopy layers, slope, large snag/ha, large tree/ha, logs/ha	5.38	7	0.04
	Use = ABGR, canopy layers, slope, small snags/ha, medium snags/ha, large snags/ha, small trees/ha, medium trees/ha, large trees/ha, logs/ha[3]	12.67	12	0.00
Pygmy Nuthatch	Use = PIPO, slope, small trees/ha, large trees/ha	0	6	0.92
	Use = PIPO, canopy layers, slope, small snag/ha, medium snag/ha, large snag/ha, small trees/ha, medium trees/ha, large trees/ha, logs/ha[3]	4.96	12	0.08
	Use = slope, large snags/ha, logs/ha	12.85	5	0.00
	Use = PIPO, canopy layers, slope, large snags/ha, large trees/ha, logs/ha	15.72	8	0.00
	Use = PIPO, large snags/ha, small trees/ha	24.15	5	0.00
	Use = canopy layers, layers, large snags/ha, small trees/ha	31.9	6	0.00

Williamson's Sapsucker	Use = slope, large snags/ha, large trees/ha, logs/ha	0	6	0.87
	Use = slope, medium snags/ha, medium trees/ha, logs/ha	5.48	6	0.06
	Use = ABGR, canopy layers, slope, small snag/ha, medium snags/ha, large snags/ha, small trees/ha, medium trees/ha, small trees/ha, logs/ha[3]	6.96	12	0.03
	Use = ABGR, large snags/ha	7.13	4	0.02
	Use = small snags/ha, medium snags/ha, logs/ha	7.31	5	0.02
	Use = ABGR, medium snag/ha, large snags/ha, logs/ha	10.78	6	0.00

[1] Use = Probability a plot was used as nest
[2] Cover type: PSME = Douglas-fir, ABGR = grand fir, PIPO = ponderosa pine
[3] Global models
[4] Number of parameters
[5] Akaike weight

Appendix 1.2. All logistic-exposure models considered in model selection for predicting nest success in Pileated Woodpeckers in the Upper Grande Ronde sub-basin, 2003-2004.

Model	ΔAICc	K[2]	w_i[3]
Cavity orientation, aspect, orientation*aspect[1]	0	5	0.42
Number of holes	0.70	3	0.29
Constant survival model	1.74	2	0.17
% bark, % branches, number of holes	4.43	5	0.05
Cavity orientation, ABGR[4], % canopy cover	5.32	5	0.03
Nest height, tree height, nest height*tree height	5.33	5	0.03
Tree height, dbh, ABGR	7.52	5	0.01
Global model	10.61	12	0.00

[1] East or south facing (46-225) vs. north or west (0-45, 226-360) facing
[2] No. of parameters
[3] Akaike weights
[4] grand fir cover type

LITERATURE CITED

Aubry, K.B. and C.M. Raley. 2002. Selection of nest and roost trees by Pileated Woodpeckers in coastal forests of Washington. Journal of Wildlife Management 66(2): 392-406.

Bull, E.L., and E.C Meslow. 1977. Habitat requirements of the Pileated Woodpecker in northeastern Oregon. Journal of Forestry 77: 335-337.

_____. 1980. Resource partitioning among woodpeckers in northeastern Oregon. Masters Thesis. University of Idaho.

_____, S.R. Peterson, and J.W. Thomas. 1986. Resource partitioning among woodpeckers in northeastern Oregon. PNW-444. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____. 1987. Ecology of the Pileated Woodpecker in northeastern Oregon. Journal of Wildlife Management 51: 472-481.

_____, and E.C. Meslow. 1988. Breeding biology of the Pileated Woodpecker-management implications. PNW-RN-474. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____, M.G. Henjum, and R.S. Rohweder. 1988. Nesting and foraging habitat of great gray owls. Journal of Raptor Research 22(4):107-115.

_____, R.S. Holthausen, and M.G. Henjum. 1990. Techniques for monitoring Pileated Woodpeckers. PNW-GTR-269. U.S. Forest Service, Pacific Northwest Research Statioin, Oregon.

_____, R.S. Holthausen, and M.G. Henjum. 1992. Roost trees used by Pileated Woodpeckers in northeastern Oregon. Journal of Wildlife Management 56: 786- 793.

_____, and R.S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in northeastern Oregon. Journal of Wildlife Management 57: 335-345.

_____, C.G. Parks, and T.R. Togersen. 1997. Trees and logs important to wildlife in the interior Columbia River Basin. General Technical Report, PNW-GTR-391. USDA Forest Service, Pacific Northwest Research Station. Portland, Oregon.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: an information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Chapell, C.B., R.C. Crawford, C. Barrett, J. Kagan, D.H. Johnson, M. O'Mealy, G.A. Green, H.L. Ferguson, W.D. Edge, and E.L. Greda, T.A. O'Neal. 2001. Wildlife habitats: descriptions, status, trends, and system dynamics. Pages 22-114 in D.H.

Johnson and T.A. O'Neil, managing directors. Wildlife habitat relationships in Oregon and Washington. Oregon State University, Corvallis.

Conway, C.J. and T.E. Martin. 1993. Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests. Journal of Wildlife Management 57:322-328.

Dudley, J., and V. Saab. 2003. A field protocol to detect habitat change for cavity-nesting birds. RMRS-RP-44 U.S. Forest Service, Rocky Mountain Research Station, Boise, Idaho.

Goggans, R., R.D. Dixon, and L.C. Seminara. 1989. Habitat use by three-toed and Black-backed Woodpeckers Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. Technical Report 87-3-02.

Hosmer, D.W., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. Wiley, New York.

Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A) conifer forests. Conservation Biology 9(5): 1041-1058.

Johnson, D.H.1979. Estimating nest success: the Mayfield method and an alternative. The Auk 96: 651-661.

Johnson, C.G., Jr., and F.Hall. 1990. Plant associations of the Blue Mountains. Region 6- Ecological Area 3. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Kingery, H.E. and C.K. Ghalambor. 2001. Pygmy Nuthatch (Sitta pygmaea). In A. Poole and F. Gill, editors. *In* The birds of North America, No. 567. The Birds of North America, Inc. Philadelphia, Pennsylvania.

Knick, S.T. and J.T. Rotenberry. 2000. Ghosts of habitat past: contribution of landscape change to current habitats used by shrublands birds. Ecology 81(1): 220-227.

Mannan, R.W. and E. C. Meslow. 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeasternern Oregon. Journal of Wildlife Management 48:1219-1238.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. Resource selection by animals: Statistical design and analysis for field studies, Second Edition. Kluwer Academic Publishers.

Martin,T.E., and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73(2): 579-592.

Martin, K., K.E.H.Aitken, and K.L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106: 5-19.

Maurer, B.A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. Journal of Wildlife Management 50(4): 556-566.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.

McClelland, B.R., S.S. Frissell, W.C. Fisher, and C.H. Halvorson. 1979. Habitat management for hole-nesting birds in forest of western larch and Douglas-fir. Journal of Forestry 77: 480-483.

McClelland, B.R. and P.T. McClelland. 1999. Pileated Woodpecker nest and roost trees in Montana: links with old-growth and forest "health". Wildlife Society Bulletin 27(3): 846-857.

McEllin, S.M. 1979. Nest site and population demographies of white-breasted and pigmy nuthatches in Colorado. Condor 81: 348-352.

Morrison, M.L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613-623

Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38(3): 541-545.

O'Neil, T. A., K. A. Bettinger, M. Vander Heyden, B. G. Marcot, C. Barrett, T. K. Mellen, W. M. Vander Haegen, D. H. Johnson, P. J. Doran, L. Wunder, and K. M. Boula. 2001. Structural conditions and habitat elements of Oregon and Washington. Pp. 115-139 in: D. H. Johnson and T. A. O'Neil, eds. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis OR.

Raphael, M.G. and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

Saab, V. A. 2003. Instructions for vegetation measurements at nests and point counts. Forest Service, Rocky Mountain Research Station, Boise, Idaho.

Saab, V.A. and J.G. Dudley. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pin/Douglas-fir forests of southwestern Idaho. RMRS-RP-11 U.S. Forest Service, Rocky Mountain Research Station , Boise, Idaho.

Saab, V.A., J.G. Dudley, and W.L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor 106: 20-36.

SAS. 1999. SAS/STAT software, 8.2. SAS Institute, Cary, North Carolina, USA.

Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson. 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Shaffer, T.L. 2004. A unified approach to analyzing nest success. Auk 121(2): 526-540.

Swetnam, T.W., B.E. Wickman, H.G. Paul, and C.H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. Research paper PNW-RP-484. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Szaro, R.C., and R.P. Balda. 1979. Bird community dynamics in a ponderosa pine forest. Studies in Avian Biology no. 3. Cooper Ornithological Society, Lawrence, Kansas.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4): 893- 901.

Wickman, B.E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. General technical report GTR-295. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wiebe, K.L. 2001. The microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118:412-421.

Wiens, J.A. 2002. Predicting species occurrences: progress, problems, and prospects. *In* Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Wisdom, M.J., R.S. Holthausen, B.C. Wales, C.D. Hargis, V.A. Saab, D.C. Lee, W.J. Hann, T.D. Rich, M.M. Rowland, W.J. Murphy, and M.R. Eames, 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. General technical report PNW-GTR-485. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

CHAPTER 2. Modeling density of cavity-nesting birds from habitat characteristics in forested stands in northeastern Oregon

ABSTRACT

Predictive models are only useful to decision makers when they are based on the appropriate spatial scale.   I created multiple linear regression models describing the relationship between cavity-nesting bird density and habitat to make predictions at the forest stand scale (4 - 65 ha). The 5 species of cavity-nesting birds studied were: the Pileated Woodpecker (*Dryocopus pileatus*), Black-backed Woodpecker (*Picoides arcticus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), White-breasted Nuthatch (*Sitta carolinensis*) and Pygmy Nuthatch (*Sitta pygmaea*). The differences in the best models to predict bird density among the 5 species represented the variation in forest conditions that are needed to sustain communities of cavity-nesting birds. Pileated Woodpecker and Williamson's Sapsucker densities were predicted best by a combination of factors describing grand fir (*Abies grandis*) forest types with high densities of dead trees while White-breasted Nuthatches were most abundant in grand fir stands with lower densities of snags. Density of Pygmy Nuthatches was predicted by a combination of factors that represented ponderosa pine stands with large trees. Black-backed Woodpeckers were rare in all forest types and model predictions were weak. Models created from empirical field data provide a more refined understanding of habitat relationships of cavity-nesting birds than broad-scale approaches such as the Interior Columbia Basin Ecosystem Management Project.

INTRODUCTION

Cavity-nesting birds represent a diverse and specialized community within forests of the Interior Columbia River Basin. Cavity-nesters are often associated with old-growth forests due to the high densities of snags for foraging and nesting (Mannan and Meslow 1984), and are sensitive to management practices that result in snag removal (Zarnowitz and Manuwal 1985). Timber extraction, salvage logging of snags after forest fires, and high road densities, which expose snags to removal for firewood, have greatly decreased snag abundance throughout the Interior Columbia River Basin (Wisdom et al. 2000). The sensitivity to forest management and specialized habitat needs of these birds have likely caused declining trends in populations of cavity-nesting birds (Hejl 1994).

Wildlife-habitat relationship models provide scientists and land managers a basis to predict population dynamics under specific habitat conditions. The predictive ability of these models is highly dependent on temporal and spatial scales (Morrison et al. 1992). Models developed at one scale are not applicable to other scales (see Scott et al. 2002). Researchers associated with the Interior Columbia Basin Ecosystem Management Project (ICBEMP) developed wildlife-habitat relationship models to assess quality, abundance, and distribution of wildlife habitat and to project distributions of terrestrial vertebrates at a coarse scale (1-km^2) and for a broad regional landscape (Wisdom et al. 2000). Land managers, however, make decisions on the scales of a sub-basin, watershed, or forest stand. The goal of this study is to develop models to predict density of cavity-nesting birds under current habitat conditions at the stand scale. This study focuses on 5 species of cavity nesting birds: the Pileated Woodpecker, Black-backed Woodpecker, Williamson's Sapsucker, White-breasted Nuthatch, and Pygmy Nuthatch.

METHODS

Study area

The study area consists of 2 areas located in the Upper Grande Ronde sub-basin (618,000 hectares) and within the Wallowa-Whitman National Forest. In order to apply my results to the variety of forest types and conditions available to cavity-nesting birds in the Blue Mountains of Oregon and Washington, these 2 areas were chosen to capture the ecological variability that results from a gradient of elevation, moisture, and slope aspects typical in this region.

The first area, The Starkey Experimental Forest, is located 35 km south of La Grande, Oregon and comprised 11,400 ha. Starkey ranges between 1070 and 1525 m in elevation and the average precipitation is 50 cm per year (Bull et al. 1986). The area is covered by coniferous forest stands and open grasslands that consist of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis)*, lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) (Bull and Holthausen 1993). Grand fir and Douglas-fir stands were subjected to severe outbreaks of western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir tussock moth (*Orgyia pseudotsuga*) in the 1980's and early 1990's (Swetnam et al. 1992, Wickman 1992). Evidence of outbreaks of budworm is extensive, and intensive timber harvest has created a mosaic of stand types.

The Spring Creek area is 17 km west of La Grande and at 930-1140 m, is lower in elevation than Starkey. Due to past selective forest management, this area is characterized by open stands of live ponderosa pine and grasslands, and contains many large trees (> 50 cm dbh) (Bull et al. 1988). The occurrence of grand fir and Douglas-fir

stands is less common, making this area less subject to outbreaks of western spruce budworm. Consequently, there are fewer dead trees and downed logs.

Field sampling

Bird surveys.

I established line transects in 117 forested stands in 3 cover types: ponderosa pine, Douglas-fir /ponderosa pine, and grand fir. I used a stratified random sampling method with 5 strata based on forest type and size class. Douglas-fir/ponderosa pine and grand fir stands were further stratified based on the dominance of small trees (> 23 cm dbh) or large trees (> 40 cm dbh). Ponderosa pine stands were in one size class (> 40cm diameter at breast height (dbh)). I queried a United States Forest Service vegetation database in a geographic information system (GIS) describing stands in this region and randomly selected 117 stands based on these criteria and reasonable accessibility from roads. The vegetation data were acquired by photo-interpretation from 1996 aerial photographs (1:12,000) that were interpreted in 2001 according to Region 6 (USFS) interpretation protocol. Stands ranged in size from 4.3 to 65.2 hectares. Before surveying, a location on an aerial photograph and a random bearing were established as the beginning of the first transect in the stand. Transects were laid parallel at least 250 m apart in order to sufficiently survey the stand. Transects were identified with flagging that included transect distance (m) and compass bearing written in permanent marker and mapped using a global positioning system in order to be relocated.

Observers surveyed each stand in the Douglas-fir and grand fir forest types (strata 1-4) twice between March 30 to June 1 in 2003 and 2004 (total of 4 surveys) using the variable-width line transect method (Buckland et al. 2001). The 23 stands in the

ponderosa pine forest type (stratum 5) were surveyed in 2004 only. Bird surveys began at a half hour past sunrise and lasted until 1200 hours (Bull et al. 1990) and were not conducted during heavy rain or high winds. While walking marked transects, observers recorded detections of cavity-nesting birds both aurally and visually. Bird species, sex, behavior (i.e. perched, foraging, calling, drumming), type of detection (aural or visual), time, perpendicular distance to transect and location along transect were recorded for each detection. Observers estimated the perpendicular distance of the bird to the transect line using a laser range finder. Before surveying independently, all observers were trained for 2 weeks in distance sampling and bird identification. Observers recorded detections of 8 cavity-nesting bird species, but this study focuses on only 5 of these species. Additionally, many woodpeckers cannot be discerned from one another by drumming patterns alone and therefore a general category (WOOD) was created for these detections.

Immediately after each transect was completed using the distance sampling method, observers walked back in the opposite direction along the transect to conduct playback surveys. Tapes of drumming and calling of 4 species were broadcast at designated locations spaced 250-300 m apart along the transect. The species I targeted by this method were played in order from smallest to largest body size: the White-breasted Nuthatch, Williamson's Sapsucker, Black-backed Woodpecker, and Pileated Woodpecker. Recording times for each species varied slightly ranging from 1 minute (White-breasted Nuthatch) to 2 minutes and 30 seconds (Pileated Woodpecker) of drumming or calling. Observers paused incrementally while broadcasting the calls and drumming and for 1-2 minutes after each species segment to listen for responses.

Broadcasting was discontinued if a response was detected for that species (British

Columbia Ministry of Environment, Land and Parks 1999). Recordings of the three

woodpeckers were obtained locally (White 1992) and a commercial recording was used

for White-breasted Nuthatches (Colver et al. 1999).

 Habitat sampling.

 During the summers of 2003 and 2004, habitat attributes were measured at points

systematically placed throughout the study area. Systematic plots were established in all

117 stands in the 3 forest cover types. Plots were located along bird survey transects and

were spaced at least 250-m apart and at least 50-m from a forest edge as to not sample

non-forest or grassland cover types.

 I measured habitat variables based on information from previous studies that have

identified important attributes for these cavity-nesting birds (Table 2.1). I used variable

width crossed plots with 50-m arms (Figure 2.1) centered on either nest trees or

systematic points (Saab 2003). General measurements such as slope, aspect, percent

canopy cover, number of canopy layers, and cover type were recorded at the plot center.

Aspects were converted to a nominal scale where a value of 1 was given to cooler aspects

(northeasterly: 22°-68°), a value of 2 was given to northwesterly (248°-21°) and

southeasterly (69°-201°), and 3 was given to warmer aspects (southwesterly: 202°-247°).

Only live trees $\geq$ 23 cm dbh and snags at least 1.4 m in height and $\geq$ 23 cm dbh were

measured. For each live tree within 5 meters (.2-ha plot) of the transect line (arm of the

cross), I recorded species and diameter at breast height. For each snag within 10 meters

(.4-ha plot) of the transect line, I recorded species, diameter at breast height, decay class

on a scale of l to 3 (Bull et al. 1997), and height class on a scale of 1 to 3 (1.4 - 10 m, 10

– 19 m, or > 20 m). Downed logs $\geq$ 23 cm dbh were measured if their large end was within 2 meters (.08-ha plot) on either side of the transect line. For each log I recorded species, decay class (1-3: Bull et al. 1997), and least end diameter (led). In addition to taking exact measurements, I later categorized live trees, snags, and logs as small (23 – 37 cm in diameter), medium (38-49 cm), or large ($\geq$ 50 cm) based on O'Neil et al. (2001). All plot measurements are described further in Table 2.1.

Data analysis

Bird Abundance.

Observations from the line transects (without the playback data) were analyzed in the software program, DISTANCE version 4.0 (Thomas et al. 2003). Data were prepared for analysis by truncating observations where the detection probability fell below 10 percent. This software package allowed me to obtain a modeled probability density function {$f(y)$} that differed among bird species and observers and that was not biased by the playback method. This probability density function measures the effective area surveyed based on perpendicular distances of the birds detected to a line transect.

I used the playback method to improve density estimates of the 4 species targeted by correcting for the number of birds missed within the effective area surveyed. I assumed a true number of birds along each transect by taking the number of birds from the line transect method and adding any more birds detected using the playback method. The true number of birds was therefore the largest number detected by either method, not a summation of the 2 methods. This method depends on the assumption that the use of the playback did not change the effective area surveyed, but allowed observers to detect individuals that were not calling or drumming, but present during the line transect survey.

Density estimates were calculated for each bird species at each visit using this combined method and a probability density function adjusted for the observer that was obtained from the line transect data. These estimates were averaged over all visits to obtain density estimates for each species in each stand.

Hypotheses Testing.

I used multivariate analysis of variance (MANOVA) to test the null hypothesis that bird density does not differ among species and among strata (Zar 1999). All of the 8 species of cavity-nesting birds recorded during field sampling were considered for this analysis. Given a significant ($P \leq .10$) MANOVA, I continued to test for differences in density among strata for each species by analysis of variance (ANOVA) using the Tukey-Kramer test to detect differences among means. All of these analyses were performed in the SAS statistical program (SAS Institute 1999).

Models.

From the habitat variables measured in field sampling, I created a set of uncorrelated variables in a factor analysis. This analysis was performed in order to reduce the number of variables to consider in the models (Johnson 1998). I determined the number of factors that existed in the data by the principal components method. Factors were considered further if their eigen value was > 1. These factors were then rotated with the Varimax procedure in order to be more interpretable (Johnson 1998).

I used multiple linear regression models to predict bird density in a stand from the factors that described the habitat. Models were created for 5 species: Black-backed Woodpeckers, Pileated Woodpeckers, Pygmy Nuthatches, White-breasted Nuthatches and Williamson's Sapsuckers. For each of the 5 bird species, a global model that

included all of the factors that were retained from the factor analysis was created. The fit

of these models was assessed by R^2 and the residuals were examined for normality.

Given a proper fit of the global models, a small set of *a priori* candidate models were

evaluated. Candidate models were chosen based on ecological plausibility for each of

the bird species. Models were assessed using Akaike's Information Criterion (AIC) by

comparing ΔAICc and choosing the model with the lowest AICc value (Burnham and

Anderson 2002). Factor analysis and regression modeling were performed using the SAS

statistical program (SAS Institute 1999).

RESULTS

Bird surveys in 2003 and 2004 resulted in a total of 2861 unclustered detections

of 8 cavity-nesting species. Considering all 8 species, densities differed among the 5

strata ($F = 29.88$, df = 44, $P < .0001$). Red-breasted nuthatches occurred in the highest

densities and Pileated Woodpeckers in the lowest densities. When considered alone,

Williamson's sapsuckers ($F = 31.62$, df = 4, $P < .0001$) and Pileated Woodpeckers ($F = 8.35$, df = 4, $P < .0001$) differed significantly among strata. The Tukey-Kramer test

revealed that these species both occurred in significantly (*alpha* = 0.10) lower densities in

stratum 5 (ponderosa pine) than in the other 4 strata and in higher densities in the grand

fir stands (Table 2.2).

A total of 225 habitat plots in 117 forest stands were sampled in 2003 and 2004

(Table 2.3). The 28 variables measured in these plots were reduced to 8 uncorrelated

factors that explained 74% of the variation in an initial principal components analysis. I

applied a factor analysis using the Varimax rotation method to develop an ecological

interpretation of the 8 factors (Table 2.4). Factor 1 represents a gradient of "snag

importance" due to the inclusion of the variables that described snags and logs. Factor 2

is defined by "live tree importance" due to the inclusion of variables describing higher

densities of live trees and greater percentages of canopy cover. Factor 1 is more

representative of grand fir and Douglas-fir stands, while factor 2 represents ponderosa

pine stands. Factor 3 is defined by "size importance" characterized by positive factor

loadings for the sizes of trees, snags, and logs and a negative loading for small trees. I

defined factor 4 as the "larch importance" factor because it describes a stand with Height

3 (> 20m) and Decay 1 (least decayed) snags and the presence of western larch and live

grand fir. The combination of these variables is characteristic of a stand where western

larch snags dominate since most of the shorter and more decayed snags are grand fir or

Douglas-fir. Factor 5 characterizes stands that have a cold (northeasterly) aspect and not

a northwesterly or southeasterly aspect. Factor 6 simply characterizes the density of live

Douglas-fir. Factor 7 characterizes stands that have a warm (southwesterly) aspect and

not a northwesterly or southeasterly aspect. Factor 8 is characterized by a positive

loading for percent slope and a negative loading for the density of live grand fir.

Multiple linear regression models including all 8 factors to predict bird density

(global models) were created for each of the 5 species. The global model for Black-

backed Woodpecker density resulted in a poor fit ($R^2 = 0.04$) and therefore model

selection was not pursued. The best model for predicting Pileated Woodpecker density

($R^2 = 0.19$) included a positive relationship with snags (factor 1), size (factor 3) and larch

(factor 4) and a negative relationship with live trees (factor 2). This was the best model

by a ΔAICc of 3.06 (Appendix 2.1) and had an Akaike weight of 0.79 (Table 2.5). The

global model ($R^2 = 0.28$) was the best model for predicting Pygmy Nuthatch density with

a ΔAICc of 6.74 (Appendix 2.1). This model had an Akaike weight of 0.95. The ΔAICc

between the 2 top models for predicting White-breasted Nuthatch and Williamson's

Sapsucker densities was not large enough to select one of these models over another

(Table 2.5, Appendix 2.1). The global model for Williamson's Sapsucker density had an

R^2 of 0.44. I considered the fit of the global model for White-breasted Nuthatches to be

enough to warrant model selection, but the amount of variation explained was low ($R^2 =$

0.17).

DISCUSSION

The dramatic habitat changes that have occurred in the Upper Grande Ronde sub-

basin of northeastern Oregon over the past several decades have created a unique

opportunity to understand the response of the cavity-nesting bird community. After

decades of fire suppression, logging and outbreaks of forest insects such as the western

spruce budworm, forests in this region have changed in both structure and composition.

Typically, grand fir and Douglas-fir stands are dense with live trees and closed canopies.

Trees in these stands in my study area were mostly dead and had little overhead canopy

cover.

Cavity- nesting birds rely on dead trees and logs for nesting, roosting and

foraging. The 2 grand fir strata (strata 3 and 4) had noticeably more snags per hectare

than the Douglas-fir and ponderosa pine strata (strata 1, 2, and 5) (Table 2.3). The higher

densities of Pileated Woodpeckers and Williamson's Sapsuckers in the grand fir stands

were related to the higher densities of snags and logs in this forest type. This is reflected

by the importance of factor 1 (snag importance) in the best models for predicting density

of both of these species. Other authors have noted snag density as a predictor of density

in these 2 species. In Arizona, Conway and Martin (1993) found that snag density was the largest contributor to a Habitat Suitability Index for Williamson's Sapsucker nesting habitat. Bull and Holthausen (1993) found that the density of snags $\geq$ 51 cm was the best predictor of Pileated Woodpecker density. The best model for predicting Pileated Woodpecker density given my data did not indicate a positive relationship with the importance of size. Although large trees are needed for nesting (see Chapter 1), foraging habitat of Pileated Woodpeckers may be less restrictive based on dbh and more dependent on high densities of snags and logs.

Even before severe outbreaks of western spruce budworm in grand fir forests in northeastern Oregon, these stands contained important habitat components for Pileated Woodpeckers and Williamson's sapsuckers in this region. Bull et al. (1986) found that the majority of Williamson's Sapsucker nests were in grand fir forest types. Additionally, previous studies established that Pileated Woodpeckers relied on old-growth grand fir stands for nesting, roosting, and foraging and occurred in higher densities in grand fir than in ponderosa pine forest (Bull 1987, Bull and Holthausen 1993). This was attributed to the greater availability of large snags and logs and to the importance of dense canopy cover in this forest type. Although earlier research conclusions imply that dense canopy cover is an important habitat attribute for Pileated Woodpeckers, my results indicate that the percentage of canopy cover is correlated with the density of live trees (factor 2) and that live tree density is not positively related to predicting density. The grand fir forest types that these birds prefer were likely the locations of the densest forest canopy before the severe outbreaks of western spruce budworm, whereas currently these same stands have a very open canopy. Therefore, I

believe that the importance of canopy cover in previous research was likely a surrogate

for correlated attributes of habitat in forest types that contained the best nesting and

foraging opportunities for these birds. The changes in forests in this region over the last

30 years have resulted in an abundance of dead trees and logs. Regardless of the

decrease in canopy cover, the availability of these resources potentially has improved the

habitat conditions for many cavity-nesting species in the short-term (1 to 3 decades).

Pygmy Nuthatches and White-breasted Nuthatches occurred in moderate densities

throughout all forest types that I studied. Pygmy Nuthatches are usually associated with

old-growth ponderosa pine forest (Wisdom et al. 2000, Szaro and Balda 1979, Kingery

and Ghalambor 2001). The best model for predicting density described a typical

ponderosa pine stand with a warm aspect and shallow slope and bird densities were

highest in the ponderosa pine stratum, although not significantly ($P = .85$). The negative

relationship with factor 3 (size importance) was unexpected due to their usual preference

for large trees, but there was little difference in mean dbh among strata (Table 2.3). The

density of large live trees (> 50 cm) was included in factor 2 (live tree importance).

Since most large live trees were found in ponderosa pine forests (Table 2.3), the positive

correlation with this factor also reflects the Pygmy Nuthatch's preference for ponderosa

pine stands with large trees.

Contrary to Pygmy Nuthatches, White-breasted Nuthatches are less specialized to

ponderosa pine forests. White-breasted Nuthatches occur in both deciduous and

coniferous forest types throughout their range (Pravosudov and Grubb 2001) and have

been classified as a habitat generalist in comparison to other cavity-nesting birds

(Rapheal and White 1984). In a ponderosa pine forest, Szaro and Balda (1979) described

their adaptation to habitat modification as "behaviorally plastic". The White-breasted

Nuthatch rarely excavates its own nest cavities and breeding densities have been

associated with the availability of nest sites (McEllin 1979). The abundance of primary

cavity-nesting birds and decayed trees with natural cavities allows the White-breasted

Nuthatch to populate a variety of forest types in the Upper Grande Ronde sub-basin. The

generalist characteristics of this bird may explain the lack of clarity in interpreting the

best models for predicting density and an overall low amount of variation explained by

the model. Both of the best models included positive correlation with stands with a

northeasterly aspect (factor 5) and larch (factor 4), but a slight negative correlation with

snags and logs (factor 1). Grand fir stands are more likely to occur on this aspect and

contain western larch. The combination of these parameters therefore describes a grand

fir stand without a high proportion of dead trees. Additionally, the global model reflected

a negative relationship with both snags and live trees and implies that White-breasted

nuthatches occur in higher densities in areas with fewer stems/ha.

Black-backed Woodpeckers occurred in low densities in all forest types that I

studied and densities were not explained by habitat models. This elusive species is

considered to be a "burn specialist" and occurs in irruptive populations in areas with

outbreaks of wood-boring insects (Dixon and Saab 2000, Hutto 1995, Murphy and

Lenhausen 1998). In Oregon, Black-backed Woodpeckers have been found in highest

densities in lodgepole pine forests, especially those affected by mountain pine beetle

(Dixon and Saab 2000, Bull et al. 1986, Goggans et al. 1989). The habitat data collected

in the Upper Grande Ronde sub-basin does not represent lodgepole pine forests, areas

with recent beetle outbreaks, or forest fires. It is likely that the information directly

depicting the availability of forage and not habitat characteristics that describe the deadness, tree size or forest type of a stand would provide for a better model to predict Black-backed Woodpecker density. Portions of this study area were recently treated for fuels reduction through forest thinning and prescribed burning. Black-backed Woodpeckers did occur in these areas, but I was not able to quantify their use of these areas in terms of burned or not burned, nor could I determine if these prescribed burns mimic ecological patterns favorable to Black-backed Woodpeckers in naturally occurring burns. Although no habitat model could adequately explain Black-backed Woodpecker density, the abundance of dead trees likely provided an opportunity for this bird to exist in low population numbers throughout the study area. Regardless of the inability to predict density for this species, my observations add to the knowledge of the abundance of Black-backed Woodpeckers in a post-disturbance (western spruce budworm) ecosystem where stand-replacing fire has been absent.

Over the past several decades, the scientific community has identified the need for looking beyond population density to understand habitat quality (Van Horne 1983, Maurer 1986). Regardless of this recognition, rarely do studies incorporate survival and reproduction parameters due to the additional effort needed to collect these data (Bock and Jones 2004). Nest success of Pileated Woodpeckers in this study area (70%; see Chapter 1) was not well predicted by habitat conditions surrounding nests. The top 2 models included variables describing the nest tree, but given values in ΔAICc, a constant survival model (intercept only) was also considered competitive (see Chapter 1). Although density does provide useful information about populations and has been found to be correlated with breeding success in birds, Bock and Jones (2004) found that the

disconnect between abundance and reproductive success is most probable in habitat that has undergone anthropogenic disturbance. Estimates of nest success of other cavity-nesting birds in the study area would provide a more in depth understanding of habitat quality.

MANAGEMENT IMPLICATIONS

Cavity-nesting birds and mammals comprise a diverse and interdependent ecological community. Primary cavity-nesting birds play an essential role in providing nests for both birds and mammals that do not excavate their own nests (Martin et al. 2004). The diversity in results of this study represents the differences in habitat requirements amongst the 5 cavity-nesting birds I studied. Clearly, a variety of forest conditions and habitat attributes at multiple scales are needed to sustain a range of cavity-nesters. Therefore, land managers should maintain a mixture of forest conditions.

Although densities of attributes such as snags and logs vary between forest types, the availability of these resources are important to every cavity-nesting bird. Forest management practices such as logging and prescribed burning should be sensitive to retention of various sizes, heights, and decay classes of snags. Additionally, allowing forests to burn naturally provides critical habitat for several species of cavity-nesting birds (Saab et al. 2004, Hutto 1995). In order to provide a mosaic of forest conditions for cavity-nesters, a variety of management approaches are needed.

The conditions in grand fir and Douglas-fir forests where western spruce budworm outbreaks were severe provide an abundance of snags and logs for cavity-nesters, but the benefits may be short-term. Additionally, the effects of these disturbances on other forest vertebrates are unknown. Current snag densities in mixed

conifer stands in the Upper Grande Ronde Sub-basin exceed target densities used by managers in Oregon and Washington to sustain populations of cavity-nesting birds (Mellen et al. 2003). However, the rarity of large live trees in many of these stands leaves little potential for snag recruitment as these existing snags continue to decay and fall. Therefore, retaining large live trees in these stands and across the landscape is critically important.

Although many parallels can be drawn between this stand-scale approach to habitat relationships of cavity-nesting birds and the broad-scale assessment from the Interior Columbia Basin Ecosystem Management Project (Wisdom et al. 2000, Raphael et al. 2001), the collection of empirical data allowed for more refined models. Source habitat for Williamson's Sapsuckers and Pileated Woodpeckers was generally described by ICBEMP as late-seral stages in a variety of elevations and forest types (Wisdom et al. 2000). Ponderosa pine forests were included as a source habitat for Williamson's sapsuckers, where as my study indicates that they were relatively absent from this forest type (Table 2.2). Although Raphael et al. (2001) acknowledged Pygmy Nuthatches to be more restrictive in their habitat requirements than White-breasted Nuthatches, source habitat for both species was generally restricted to low-elevation ponderosa pine forests (Wisdom et al. 2000). While my results confirm this relationship for Pygmy Nuthatches, White-breasted Nuthatches occurred in significantly lower densities in ponderosa pine forests than in Douglas-fir and grand fir forest types. Wisdom et al. (2000) described a variety of forest conditions as source habitat for Black-backed woodpeckers. The inclusion of data describing recently burned forest was unavailable at a broad-scale. Although this type of data was also absent in my analysis, it could be accounted for at the

stand-scale in future studies. Although the importance of snag density was

acknowledged for all cavity-nesting bird species, broad-scale habitat relationships

generally described forest types considered to contain snags (Wisdom et al. 2000). By

allowing for measurement of snags, fine-scale habitat relationships based on field data

provided a better understanding of this and other specific habitat requirements of cavity-

nesting birds. Broad-scale approaches could therefore be improved by methods to

measure and map key resources, such as snags, at a larger spatial scale.

Table 2.1. Habitat characteristics measured in each plot in the Upper Grande Ronde sub-basin, 2003 and 2004.

Variables	Method
Dominant forest cover type	Johnson and Hall 1990
Number of canopy layers	visual count
Live trees/ha and snags/ha in 3 size classes:	O'Neil et al. 2001
DBH (23-37 cm, 38-49 cm, 50 cm and >)	
Percent Canopy Cover (%)	Densiometer
Percent slope	Clinometer
Aspect (°)	Compass
Trees, snags, and log $\geq$ 23 cm:	
Species	
Decay class	Bull et al. 1997
Tree height (snags only) in 3 classes	visual assessment
($\leq$ 10 m, > 10-20m, > 20m)	
Diameter at breast height (DBH)	DBH tape
or large end diameter (LED)	

Table 2.2. Mean densities (birds/100 ha) and standard errors of 8 species of cavity-nesting birds in 5 strata sampled in the Upper Grande Ronde sub-basin, 2003 and 2004.

Species	Douglas-fir/ ponderosa pine (>40 cm)	Douglas-fir/ ponderosa pine (>23 cm)	Grand fir (> 40 cm)	Grand fir (> 23 cm)	Ponderosa pine (> 40 cm)
Black-backed Woodpecker	3.47 A[1] ± 1.04	2.23 A ± 0.76	4.01 A ± 1.53	1.07 A ± 0.70	2.48 A ± 1.11
Hairy Woodpecker	3.72 A ± 0.73	2.13 A ± 0.42	4.38 A ± 1.00	4.67 A ± 1.10	1.72 A ± 0.80
Northern Flicker	7.39 A ± 1.09	4.30 A ± 1.08	5.43 A ± 0.70	7.12 A ± 1.00	4.24 A ± 0.92
Pileated Woodpecker	2.49 AB ± 0.37	2.11 B ± 0.50	4.94 AC ± 0.87	5.26 C ± 0.94	0.34 B ± 0.16
Pygmy Nuthatch	7.17 A ± 5.61	8.32 A ± 4.84	5.92 A ± 2.55	5.23 A ± 1.90	10.19 A ± 2.66
Red-breasted Nuthatch	37.49 A ± 4.36	31.40 A ± 3.71	31.17 A ± 4.10	34.76 A ± 3.52	30.46 A ± 5.38
White-breasted Nuthatch	14.13 A ± 2.37	10.67 A ± 2.30	13.33 A ± 2.55	13.51 A ± 2.16	5.78 B ± 1.94
Williamson's Sapsucker	19.90 AB ± 2.28	18.47 A ± 2.39	27.55 B ± 1.28	26.96 B ± 2.4	3.19 C ± 1.13
WOOD	0.55 A ± 0.18	1.06 A ± 0.33	0.83 A ± 0.25	1.75 A ± 0.62	0.62 A ± 0.48

[1] Means sharing the same letter are not statistically different from each other; Tukey-Kramer test for differences (*alpha* = .10)

Table 2.3 Mean and standard deviation of habitat variables measured in 325 plots in 5 strata in the Upper Grande Ronde sub-basin, 2003 and 2004.

Habitat variable	Douglas-fir/ ponderosa pine (>40 cm)		Douglas-fir/ ponderosa pine (>23 cm)		Grand fir (> 40 cm)		Grand fir (> 23 cm)		Ponderosa pine (> 40 cm)	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
% Canopy	35.8	17.2	31.9	14.7	25.8	17	23.5	11.9	55.1	15.1
Canopy layers	1.8	0.4	1.90	0.3	1.70	.47	1.85	.41	1.93	0.2
% Slope	18.3	11.1	14.4	11	13.6	10.8	17.6	16	15.5	7.1
Aspect [1]	1.9	0.8	2.0	0.8	1.6	0.7	1.7	0.8	2.1	0.8
DBH snags (cm)	39.8	6.6	37.7	6.5	40.8	8.7	37.8	5.7	37.1	10.2
Snags/ ha	48.9	26.5	33.9	22.9	68.7	45.6	81.4	46.9	4.24	4.6
PSME snags/ha [2]	34.7	25.0	24.8	21.0	22.6	16.8	32.5	19.0	0.7	1.9
ABGR snags /ha	6.7	9.6	3.3	4.1	40.2	29.5	44.8	35.4	0.0	--
PIPO snags /ha	3.4	3.4	2.1	2.4	0.4	0.8	0.6	1.1	3.4	4.6
LAOC snags/ha	3.6	4.0	3.5	6.3	5.3	6.3	4.5	5.0	0.1	0.4
Snag/ha (23-37 cm)	27.8	19.6	27.2	28.1	36.7	26.2	48.7	25.8	2.8	3.3
Snag/ha (38-49 cm)	9.2	6.8	7.9	10.1	16.5	15.7	15.5	12.1	1.1	1.5
Snag/ha ($\geq$ 50 cm)	11.8	10.4	5.4	4.5	14.9	15.1	13.3	14.9	0.5	0.6
Decay1 snags/ha	11.1	9.4	5.7	2.0	9.1	7.2	11.2	8.0	1.4	1.8
Decay2 snags/ha	32.9	20.3	25.6	19.5	55.9	40.1	64.1	44.7	2.3	3.8
Decay3 snags/ha	7.1	4.0	5.1	3.8	7.0	6.1	6.9	5.3	5.7	6.3
Height1snags/ha	23.4	14.9	17.5	11.4	39.0	30.4	44.6	31.1	2.1	2.6
Height2 snags/ha	15.0	10.4	10.2	7.9	16.7	12.7	22.3	13.8	1.5	1.9
Height3 snags/ha	10.9	7.4	6.3	6.2	13.0	11.1	16.2	11.5	0.6	1.1
DBH live tree (cm)	44.2	6.7	40.0	6.5	42.3	7.8	42.6	7.1	41.0	5.2
Live trees/ha	74.4	34.1	83.4	35.6	59.3	30.6	53.9	25.9	136.2	50.7
PSME live/ha	17.5	20.4	24.4	21.4	2.0	1.8	11.3	12.0	5.2	14.8
ABGR live/ha	3.6	6.6	3.1	5.0	1.6	1.7	7.9	9.3	0.0	0.0
PIPO live/ha	33.7	22.3	40.1	28.6	2.8	2.8	15.7	19.2	124.7	56.8

LAOC live/ha	18.3	18.1	14.1	19.5	4.3	3.2	16.6	18.3	6.1	12.9
Live/ha (23-37 cm)	39.8	34.1	45.9	24.9	30.8	22.4	25.8	17.0	69.7	39.8
Live/ha (38-49 cm)	15.0	30.2	19.6	9.7	13.7	8.6	13.3	10.7	39.3	17.6
Live/ha ($\geq$ 50 cm)	22.2	8.8	16.6	10.7	14.7	9.8	15.0	10.1	31.1	20.4
LED log (cm)	36.7	4.3	36.6	5.3	35.3	4.7	33.9	3.4	32.7	6.3
Logs/ha	147.2	73.9	88.8	42.5	179.8	103.2	190.0	105.7	40.9	7.8

[1] Aspects closer to 1 represent cooler aspects (Northeastern) and those closer to 3 represent warmer aspects (Southwest)

[2] PSME= Douglas-fir, ABGR= grand fir, PIPO= ponderosa pine, LAOC= western larch

Table 2.4 Factor loadings from the Varimax rotation for the variables describing habitat for cavity-nesting birds in the Upper Grande Ronde sub-basin, 2003 and 2004.

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
Decay2snag	0.94							
Height1snag	0.93							
Height2snag	0.84							
ABGRsnag	0.81							
MEDsnag	0.80							
SMsnag	0.80							
LRGsnag	0.73		0.45					
PSMEsnag	0.71							
Logs/ha	0.66							
Height3snag	0.64			0.49				
Decay1snag	0.51			0.51				
LRGlive		0.77						
MEDlive		0.73						
PIPOlive		0.71		-0.41				
% Canopy		0.69						
PIPOsnag		0.66						
DBHsnag			0.79					
DBHlive			0.78					
LEDlog			0.66					
Canopy layers			-0.44					
SMlive		0.41	-0.60					
LAOClive				0.73				
LAOCsnag	0.41			0.57				
ABGRlive				0.46				-0.43
NE aspect					0.89			
NW/SE aspect					-0.85		-0.49	
PSMElive						0.78		
SW aspect							0.98	
Slope								0.78
Variation explained	7.30	3.05	2.90	2.09	1.69	1.64	1.49	1.42
Percent of total	31.5	10.8	7.7	6.0	5.4	4.5	4.4	4.2
Cumulative	31.5	42.3	50.0	56.0	61.4	65.9	70.3	74.4

Table 2.5. Best models for predicting bird density for 4 species of cavity-nesting birds based on factors describing habitat characteristics at the stand level in the Upper Grande Ronde sub-basin, 2003 and 2004.

Species	Best Model	ΔAICc	K[1]	w_i[2]	R^2
Pileated Woodpecker	Birds/ha = 3.04 + 0.99(factor 1) – 1.01(factor 2) -0.16(factor 3) + 0.87 (factor 4)	0	6	.79	.19
Pygmy Nuthatch	Birds/ha = 2.54 – 1.66(factor 1) + 1.92 (factor 2) – 1.03(factor 3) – 1.51(factor 4) + 0.06(factor 5) – 1.64(factor 6) + 0.89(factor 7) – .30(factor 8)[3]	0	10	.95	.28
White-breasted Nuthatch	Birds/ha = 11.72 – 0.12(factor1) – 1.66(factor2) + 0.85(factor3) + 2.75(factor4) + 2.17(factor5)	0	7	.53	.16
White-breasted Nuthatch[4]	Birds/ha = 11.72 – 0.12(factor1) + 2.75(factor4) + 2.17(factor5)	.40	5	.45	.12
Williamson's Sapsucker	Birds/ha = 19.38 + 4.37(factor1) – 6.29(factor2) + 2.42(factor3) + 2.98(factor4) + 1.33(factor5) – 0.65(factor6) – 2.60(factor7) – 1.30(factor8)[3]	0	10	.71	.44
Williamson's Sapsucker	Birds/ha = 19.38+ 4.37(factor1) – 6.29(factor2) + 2.42(factor3) + 2.98(factor4)	1.93	6	.29	.38

[1] No. of parameters

[2] Akaike weight

[3] Global model

[4] 2 models are given when the delta ΔAICc between models was < 4
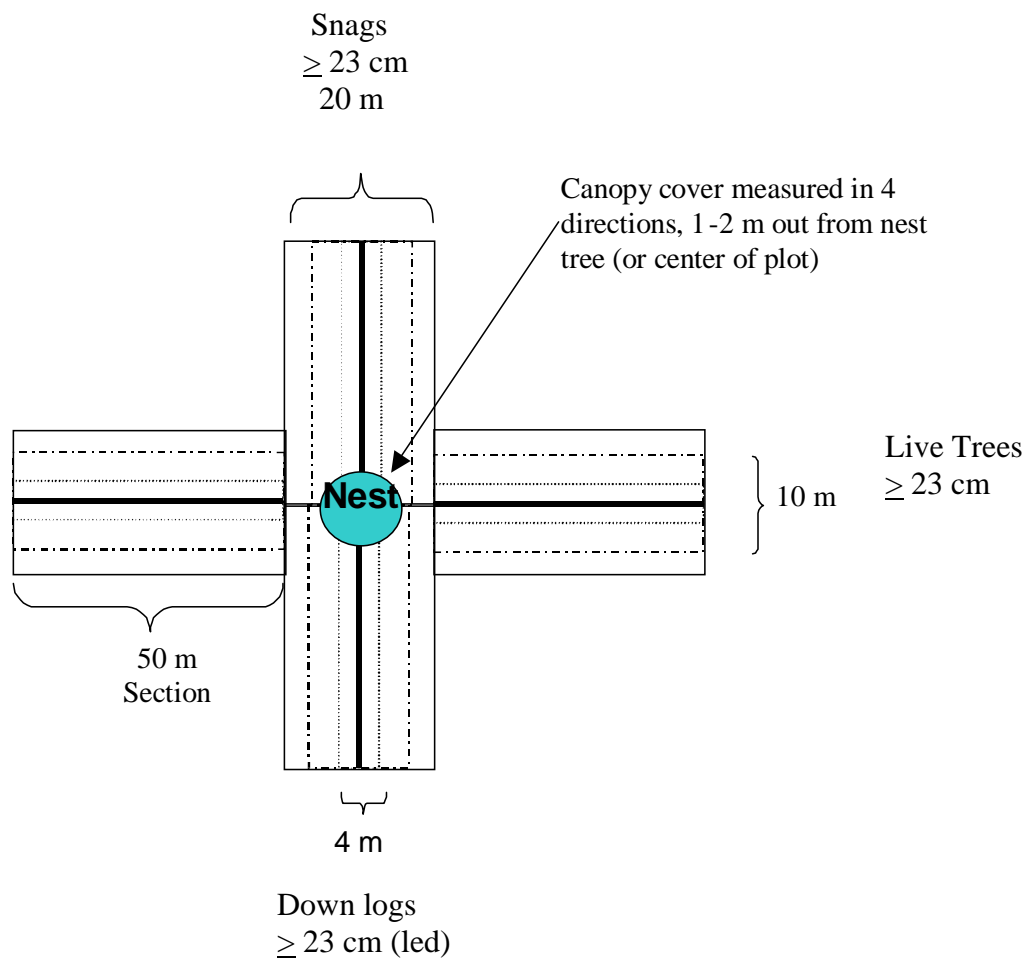
Figure 2.1. Sampling design used for measuring habitat variables in the Upper Grande Ronde Sub-basin, 2003 and 2004. (Saab 2003)

Appendix 2.1. All multiple regression models considered in model selection for predicting density at the stand-scale by 4 species of cavity-nesting birds in the Upper Grande Ronde sub-basin, 2003-2004.

Species	Candidate model	ΔAICc	K[3]	w_i[4]
Black-backed Woodpecker	Density[1] = snag importance, live PSME/ha	0	4	0.51
	Density = size importance, live PSME/ha	0.68	4	0.36
	Density = live tree importance, live PSME/ha, SW slope, slope	3.44	6	0.09
	Density = snag importance, size importance, live PSME/ha, SW slope, slope	5.48	7	0.03
	Density = snag importance, live tree importance, size importance, larch importance, NE slope, live PSME/ha, SW slope, slope[2]	11.13	10	0.00
Pileated Woodpecker	Density = snag importance, live tree importance, size importance, larch importance	0	6	0.81
	Density = snag importance, live tree importance	3.06	4	0.17
	Density = snag importance, live tree importance, size importance, larch importance, NE slope, live PSME/ha, SW slope, slope	6.36	10	0.03
	Density = size importance, larch importance	13.88	4	0.00
	Density = size importance, larch importance, NE slope	14.84	5	0.00
Pygmy Nuthatch	Density = snag importance, live tree importance, size importance, larch importance, NE slope, live PSME/ha, SW slope, slope	0	10	0.95
	Density = snag importance, live tree importance, size importance	6.74	5	0.03
	Density = live tree importance, size importance, live PSME/ha, SW slope, slope	8.67	7	0.01
	Density = live tree importance, size importance, SW slope	12.00	5	0.00
	Density = live tree importance, size importance, SW slope, slope	13.98	6	0.00
White-breasted Nuthatch	Density = snag importance, live tree importance, size importance, larch importance, NE slope	0	7	0.52
	Density = snag importance, larch importance, NE slope	0.32	5	0.45
	Density = snag importance, live tree importance, size importance, larch importance, NE slope, live PSME/ha, SW slope, slope	6.16	10	0.02
	Density = live tree importance, size importance	12.78	4	0.00
	Density = live tree importance, size importance, SW slope, slope	13.14	6	0.00

Williamson's Sapsucker	Density = snag importance, live tree importance, size importance, larch importance, NE slope, live PSME/ha, SW slope, slope	0	10	0.71
	Density = snag importance, live tree importance, size importance, larch importance	1.77	6	0.29
	Density = live tree importance, larch importance, live PSME/ha	21.61	5	0.00
	Density = snag importance, size importance	37.55	4	0.00
	Density = snag importance, size importance, NE slope	38.50	5	0.00

[1] Density = birds/ 100 ha
[2] Global model
[3] Number of parameters
[4] Akaike weight

LITERATURE CITED

Bock, C.E. and Z.F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2 (8): 403-410.

British Columbia Ministry of Environment, Land and Parks. 1999. Inventory methods for woodpeckers. Standards for Components of British Columbia's Biodiversity No. 19. The Province of British Columbia, Published by the Resource Inventory Committee, Victoria, BC, Canada. http:// srmwww.gov.bc.ca/risc/pubs/tebiodiv /woodpeckers/index.htm

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L.Thomas. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford, UK.

Bull, E.L., S.R. Peterson, and J.W. Thomas. 1986. Resource partitioning among woodpeckers in Northeast Oregon. PNW-444. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____. 1987. Ecology of the Pileated Woodpecker in Northeast Oregon. Journal of Wildlife Management 51: 472-481.

_____, M.G. Henjum, and R.S. Rohweder. 1988. Nesting and foraging habitat of great gray owls. Journal of Raptor Research 22(4):107-115.

_____, R.S. Holthausen, and M.G. Henjum. 1990. Techniques for monitoring Pileated Woodpeckers. PNW-GTR-269. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____, and R.S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in Northeast Oregon. Journal of Wildlife Management 57: 335-345.

_____, C.G. Parks, and T.R. Togersen. 1997. Trees and logs important to wildlife in the interior Columbia River Basin. General Technical Report, PNW-GTR-391. USDA Forest Service, Pacific Northwest Research Station. Portland, Oregon.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: an information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Colver, K.J., D. Stokes, and L. Stokes. 1999. Stokes field guide to bird songs: western region. Time Warner AudioBooks, New York.

Conway, C.J. and T.E. Martin. 1993. Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests. Journal of Wildlife Management 57:322-328.

Dixon, R.D. and V.A. Saab. 2000. Black-backed Woodpecker (*Picoides arcticus*). *In* A. Poole and F. Gill, editors, The birds of North America, No. 509. The Birds of North America, Inc. Philadelphia, Pennsylvania.

Goggans, R., R.D. Dixon, and L.C. Seminara. 1989. Habitat use by three-toed and Black-backed Woodpeckers Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. Technical Report 87-3-02.

Hejl, S.J. 1994. Human-induced changes in bird populations in coniferous forests in western North America during the past 100 years. Studies in Avian Biology 15:232-246.

Hutto, R.L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A) conifer forests. Conservation Biology 9(5): 1041-1058.

Johnson, D.E. 1998. Applied Multivariate Methods for Data Analysis. Brooks/Cole Publishing Company, Pacific Grove, California.

Johnson, C.G., Jr., and F.Hall. 1990. Plant associations of the Blue Mountains. Region 6-Ecological Area 3. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Kingery, H.E. and C.K. Ghalambor. 2001. Pygmy Nuthatch (Sitta pygmaea). In A. Poole and F. Gill, editors. *In* The birds of North America, No. 567. The Birds of North America, Inc. Philadelphia, Pennsylvania.

Mannan, R.W. and E. C. Meslow. 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. Journal of Wildlife Management 48:1219-1238.

Martin, K., K.E.H.Aitken, and K.L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. Condor 106: 5-19.

Maurer, B.A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. Journal of Wildlife Management 50(4): 556-566.

McEllin, S.M. 1979. Nest site and population demographies of white-breasted and pigmy nuthatches in Colorado. Condor 81: 348-352.

Mellen, K., B.G. Marcot, J.L. Ohmann, K. Waddell, S.A. Livingston, E.A. Willhite, B.B. Hostetler, C.Ogden, and T.Dreisbach. 2003. DecAID, the decayed wood advisor for managing snags, partially dead trees, and down wood for biodiversity in forests of Washington and Oregon. Version 1.10. USDA Forest Service, Pacific Northwest Region and Pacific Northwest Research Station; USDI Fish and Wildlife Service,

Oregon State Office; Portland, Oregon.
http://wwwnotes.fs.fed.us:81/pnw/DecAID/DecAID.nsf

Morrison, M.L., B.G. Marcot, R.W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications, second edition. The University of Wisconsin Press. Madison, Wisconsin.

Murphy, E.C., and W.A. Lenhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management 62(4): 1359-1372.

O'Neil, T. A., K. A. Bettinger, M. Vander Heyden, B. G. Marcot, C. Barrett, T. K. Mellen, W. M. Vander Haegen, D. H. Johnson, P. J. Doran, L. Wunder, and K. M. Boula. 2001. Structural conditions and habitat elements of Oregon and Washington. Pp. 115-139 in: D. H. Johnson and T. A. O'Neil, eds. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis OR.

Pravosudov, V.V. and T.C. Grubb. 1993. White-breasted Nuthatch (Sitta carolinensis). *In* The birds of North America, No. 54 (A. Poole and F.Gill, editors). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Raphael, M.G. and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 86.

_____, M.J. Wisdom, M.M. Rowland, R.S. Holthausen, B.C. Wales, B.G. Marcot, and T.D. Rich. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia river basin. Forest Ecology and Management 153: 63-88.

Saab, V. A. 2003. Instructions for vegetation measurements at nests and point counts. Forest Service, Rocky Mountain Research Station, Boise, Idaho.

Saab, V.A., J.G. Dudley, and W.L. Thompson. 2004. Factors influencing occupancy of nest cavities in recently burned forests. The Condor 106: 20-36.

SAS. 1999. SAS/STAT software, 8.2. SAS Institute, Cary, North Carolina, USA.

Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson. 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Swetnam, T.W., B.E. Wickman, H.G. Paul, and C.H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. Research paper PNW-RP-484. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Szaro, R.C., and R.P. Balda. 1979. Bird community dynamics in a ponderosa pine forest. Studies in Avian Biology no. 3. Cooper Ornithological Society, Lawrence, Kansas.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2003. Distance 4.0. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4): 893- 901.

White, D. 1992. A guide to the vocalizations of woodpeckers of Northeastern Oregon. USDS Forest Service. Pacific Northwest Research Station, La Grande, OR.

Wickman, B.E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. General technical report GTR-295. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wisdom, M.J., R.S. Holthausen, B.C. Wales, C.D. Hargis, V.A. Saab, D.C. Lee, W.J. Hann, T.D. Rich, M.M. Rowland, W.J. Murphy, and M.R. Eames. 2000. Source habitats for terrestrial vertebrates of focus in the Interior Columbia Basin: Broad-scale trends and management implications. General technical report PNW-GTR-485. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Zarnowitz, J.E. and D.A. Manuwal. 1985. The effects of forest management on cavity-nesting birds in the northwestern Washington. Journal of Wildlife Management 49 (1): 255-263.

CHAPTER 3. Estimating density by combining distance sampling and playback methods

ABSTRACT

Variable-width line transects and point counts dramatically improve density estimates of bird populations compared to fixed plot methods. Distance sampling allows the observer to estimate the detection probability of bird species and to account for the variability of this function between species. An assumption of distance sampling is that birds do not move from the initial observation location during the survey. Therefore, eliciting a response by mimicking songs or calls violates this assumption as this often results in drawing a bird in to the observer. However, passive sampling may not adequately detect many cavity-nesting species, such as woodpeckers, rare species or species that occur in small populations sizes or vocalize infrequently. I estimated densities of several species of cavity-nesting birds using variable-width line transects in forested stands in northeastern Oregon. I used playback tapes of calls and drumming immediately after concluding line transects for 4 of the species encountered: Black-backed Woodpeckers (*Picoides arcticus*), Pileated Woodpeckers (*Dryocopus pileatus*), White-breasted Nuthatches (*Sitta carolinensis*), and Williamson's Sapsuckers (*Sphyrapicus thyroideus*). Counts of birds that responded to the tapes were tallied and compared to those counted using the line transect method. 61% of the total detections of Black-backed Woodpeckers and 48% of the Pileated Woodpecker detections were only acquired using the playback method. Rare species such as these are therefore not accurately surveyed using traditional methods alone. I combined these 2 survey methods by assuming the total number of birds detected (number from the transect and any additional birds from the playbacks) to be the true number of birds within an effective

survey area (as calculated using only the distance data). I then estimated density based on the true number of birds within that effective survey area. I modeled the relationship between these 2 estimates by regressing the true density on the density of birds as estimated by the line transect method alone. The resulting model could be used to predict true density given estimates resulting from distance sampling and provides a less biased estimate.

INTRODUCTION

The abundance of individuals is an important parameter for monitoring, managing and studying wildlife populations. Over the past several decades, methods for estimating abundance in bird populations have advanced (Ralph and Scott 1981, Reynolds et al. 1980). Current counting techniques based on fixed-radius plots produce indices that are assumed to represent relative abundance in bird populations (Hutto et al. 1986). However, researchers have noted the need for the application of empirical methods to obtain reliable measures of bird abundance (Burnham 1981, Rosenstock et al. 2002, Thompson 2002). Variable-width line transects and point counts dramatically improve density estimates compared to fixed plot methods by estimating the effective area surveyed for each species. Distance sampling allows observers to estimate the detection probability of each bird species and to account for the variability of this function (Buckland et al. 2001).

Population trends of species that are rare or that occur in low densities are difficult to monitor. Species such as woodpeckers and nuthatches are often undetected in population surveys (Hejl 1994). The playback method aids in detecting birds by broadcasting songs or calls in order to elicit a response. This method is used commonly

for index counts in birds that are rare, elusive, or vocalize infrequently. This technique has been applied to raptors, nocturnal species, and waterbirds (Johnson et al. 1981, Gibbs and Melvin 1993). An assumption of distance sampling is that birds do not move from the initial location during the survey (Buckland et al. 2001). Therefore, the playback method violates this assumption as it may result in drawing a bird in to the observer and is not suitable for estimating density by itself. However, it has been suggested that playback responses could be used to adjust other census techniques (Falls 1981).

The premise of distance sampling is that the detection function ($g(y)$ in line transects) will account for the decrease in the probability of detecting an individual as its distance (y) from the transect line is increased. This function varies by factors such as, an individual observer's ability to identify and detect species, habitat attributes, and properties of a bird's vocalization (high pitched for example) (Franzreb 1981, Buckland et al. 2001). In some cases a bird that has a high probability of being detected may not vocalize. The probability of detecting a species, as calculated by distance sampling, in this case is negatively biased. Although distance sampling accounts for individuals that are not detected, an important assumption is that those on or near the transect line are not missed ($g(0) = 1.0$, Burnham et al. 1981, Buckland et al. 2001).

Due to their relatively large body size, loud calls and drumming behavior, and often striking plumage, most woodpeckers are easily detectable at great distances by trained observers. However, in contrast to many songbirds, woodpeckers vocalize infrequently, and often occur in low population densities. Other less conspicuous cavity-nesting species, such as the White-breasted Nuthatch, vocalize quietly and are more easily missed by observers (Pravosudov and Grubb 1993). The goal of this research was

to develop a method for sampling cavity-nesting birds that produced a more accurate density estimate by combining distance sampling and playback methods. I apply this method to 4 species that vary in prevalence and detectability. The specific objectives were to: 1) compare the percentage of detections of cavity-nesting birds by the line transect and playback methods and 2) model the relationship between density estimates obtained from the line transect method and from combining the line transect and playback methods.

METHODS

Study area

The study area consists of 2 areas located in the Upper Grande Ronde sub-basin (618,000 hectares) and within the Wallowa-Whitman National Forest. In order to apply my results to the variety of forest types and conditions available to cavity-nesting birds in the Blue Mountains of Oregon and Washington, these two areas were chosen to capture the ecological variability that results from a gradient of elevation, moisture, and slope aspects typical in this region.

The first area, The Starkey Experimental Forest, is located 35 km south of La Grande, Oregon and comprised 11,400 ha. Starkey ranges between 1070 and 1525 m in elevation and the average precipitation is 50 cm per year (Bull et al. 1986). The area is covered by coniferous forest stands and open grasslands that consist of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis)*, lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) (Bull and Holthausen 1993). Grand fir and Douglas-fir stands were subjected to severe outbreaks of western spruce budworm (*Choristoneura occidentalis*)

and Douglas-fir tussock moth (*Orgyia pseudotsuga*) in the 1980's and early 1990's
(Swetnam et al. 1992, Wickman 1992). Evidence of outbreaks of budworm is extensive,
and intensive timber harvest has created a mosaic of stand types.

The Spring Creek area is 17 km west of La Grande and at 930-1140 m, is lower
in elevation than Starkey. Due to past selective forest management, this area is
characterized by open stands of live ponderosa pine and grasslands, and contains many
large trees (> 50 cm dbh) (Bull et al. 1988). The occurrence of grand fir and Douglas-fir
stands is less common, making this area less subject to outbreaks of western spruce
budworm. Consequently, there are fewer dead trees and downed logs.

Field sampling

I established line transects in 117 forested stands in 3 cover types: ponderosa pine,
Douglas-fir /ponderosa pine, and grand fir. I used a stratified random sampling method
with 5 strata based on forest type and size class. Douglas-fir/ponderosa pine and grand
fir stands were further stratified based on the dominance of small trees (> 23 cm dbh) or
large trees (> 40 cm dbh). Ponderosa pine stands were in one size class (> 40cm
diameter at breast height (dbh)). I queried a United States Forest Service vegetation
database in a geographic information system (GIS) describing stands in this region and
randomly selected 117 stands based on these criteria and reasonable accessibility from
roads. The vegetation data were acquired by photo-interpretation from 1996 aerial
photographs (1:12,000) that were interpreted in 2001 according to Region 6 (USFS)
interpretation protocol. Stands ranged in size from 4.3 to 65.2 hectares. Before
surveying, a location on an aerial photograph and a random bearing were established as
the beginning of the first transect in the stand. Transects were laid parallel at least 250 m

apart in order to sufficiently survey the stand. Transects were identified with flagging

that included transect distance (m) and compass bearing written in permanent marker and

mapped using a global positioning system in order to be relocated.

Observers surveyed each stand in the Douglas-fir and grand fir forest types (strata

1-4) twice between March 30 to June 1 in 2003 and 2004 (total of 4 surveys) using the

variable-width line transect method (Buckland et al. 2001). The 23 stands in the

ponderosa pine forest type (stratum 5) were surveyed in 2004 only. Bird surveys began

at a half hour past sunrise and lasted until 1200 hours (Bull et al. 1990) and were not

conducted during heavy rain or high winds. While walking marked transects, observers

recorded detections of cavity-nesting birds both aurally and visually. Bird species, sex,

behavior (i.e. perched, foraging, calling, drumming), type of detection (aural or visual),

time, perpendicular distance to transect and location along transect were recorded for

each detection. Observers estimated the perpendicular distance of the bird to the transect

line using a laser range finder. Before surveying independently, all observers were

trained for 2 weeks in distance sampling and bird identification. Observers recorded

detections of 8 cavity-nesting bird species, but this study focuses on only 4 of these

species. Additionally, many woodpeckers cannot be discerned from one another by

drumming patterns alone and therefore a general category (WOOD) was created for these

detections.

Immediately after each transect was completed using the distance sampling

method, observers walked back in the opposite direction along the transect to conduct the

playback surveys. Tapes of drumming and calling of 4 species were broadcast at

designated locations spaced 250-300 m apart along the transect. The species I targeted

by this method were played in order from smallest to largest body size: the White-breasted Nuthatch, Williamson's Sapsucker, Black-backed Woodpecker, and Pileated Woodpecker. Recording times for each species varied slightly ranging from 1 minute (White-breasted Nuthatch) to 2 minutes and 30 seconds (Pileated Woodpecker) of drumming or calling. Observers paused incrementally and for 1-2 minutes after each species segment to listen for responses. Broadcasting was discontinued if a response was detected for that species (British Columbia Ministry of Environment, Land and Parks 1999). Recordings of the 3 woodpeckers were obtained locally (White 1992) and a commercial recording was used for White-breasted Nuthatches (Colver et al. 1999).

Data analysis

Observations from the line transects (without the playback data) were analyzed in the software package program, DISTANCE version 4.0 (Thomas et al. 2003). Data were prepared for analysis by truncating observations where the detection probability fell below 10 percent. This software package allowed me to obtain a modeled probability density function {*f(y)*} that differed among bird species and observers and that was not biased by the playback method. This probability density function is a measure of the effective area surveyed and is evaluated at 0 meters {*f(0)*}. The sample used to obtain *f(0)* was the recorded distances of individual birds that were detected while vocalizing or observed during the survey.

In order to calculate density, I corrected the number of birds along the transect within the effective survey area using the additional information obtained from the playback method. I assumed the true number of birds along each transect was described by taking the number of birds from the line transect method and adding any more birds

detected using the playback method. The true number of birds was therefore the largest

number detected by either method, not a summation of the 2 methods. I calculated

density using the formula for distance sampling:

$$\hat{D} = \frac{n * \hat{f}(0)}{2L}$$ (Buckland et al. 2001)

Where:

D = density

n = number of individuals as obtained from combining line transect and
playback counts

$f(0)$ = probability density function, or 1/effective survey width as obtained
from the line transect data

L = total line length

I modeled the relationship between the 2 survey methods by regressing the

density estimates calculated from combining the line transect and playback methods (true

density) on the estimates calculated from the line transect method alone. The original

regression models for each bird species were created only using the data collected in

2003. This allowed me to use the data collected in 2004 to validate and update the

models (Harell 2001).

I validated the regression models by applying them to the density estimates

obtained from the line transects alone in 2004 to yield an adjusted, or predicted, density.

This predicted density was regressed on the true density as estimated from data collected

in 2004 and evaluated using R^2 and the root mean squared error. After model validation,

the 2003 and 2004 data were combined to form the final models. These final models

could then be used to predict true density estimates given data collected from a variable-

width line transect. All linear regressions were performed using the SAS statistical package (SAS Institute 1999).

RESULTS

Observers surveyed 46,935 m of transect and 184 playback stations in 2003 and 60,006 m of transect and 309 playback stations in 2004. The playback method was most effective in detecting Black-backed and Pileated Woodpeckers over the line transect alone (Figure 3.1). The playback method also increased the number of detections of Williamson's Sapsuckers and White-breasted Nuthatches (Figure 3.1). The playback method resulted in an equal or greater number of individuals detected over the transect 97% of the time in the case of Black-backed Woodpeckers, 93% of the time for Pileated Woodpeckers, 80% of the time for White-breasted Nuthatches, and 81% of the time for Williamson's Sapsuckers.

The initial models constructed on the 2003 data fit the 2004 data reasonably well (Table 3.1). Although models fit at varying levels in the validation process, models for all 4 species had low mean squared errors and coefficients remained similar between 2003 and 2004. The final models of the relationship between the number of detections from the transect and the actual number of birds present of each species yielded squared correlation coefficients that explained 39 % to 69 % of the variation (Figure 3.2).

DISCUSSION

The predictive power of wildlife-habitat relationship models relies on accurate estimates of population parameters. When developing predictive models with data collected through field observations, it is important to recognize prediction error. Several studies have shown that sample size, detectability of a species, and commonness of a

species primarily determine errors of commission (Karl et al. 2002, Marcot et al. 1983).

The use of the playback proved to be an important tool in detecting cavity-nesting species

in this study and was most helpful in detecting 2 rare species that occurred in the lowest

population densities, the Black-backed and Pileated Woodpecker. Other count methods

may be sufficient when management or research goals do not require accurate census

data (Verner 1985). However, reducing sampling bias and improving census methods

reduces the chance of prediction error.

The models developed for the 4 species that I focused on varied in their predictive

abilities. Overall, model predicted mean density estimates had improved precision over

both the line transect and combined method density estimates (Table 3.1). The 2003

model predicted mean density estimates were exactly equal to the true density estimates

in the 2004 data for Black-backed Woodpeckers and Williamson's Sapsuckers (Table

3.1). Additionally, the models over predicted White-breasted Nuthatch density by only

11%. The 2003 model did not predict true density of Pileated Woodpeckers in 2004 very

well likely due to the variation in the number of detections of this species between years

(more in 2003 than 2004). The final models (Figure 3.2) were improved by including

data from both years.

In addition to the assumptions required for distance sampling (see Buckland et al.

2001), this combined method also has some assumptions. The probability density

function evaluated at $y = 0$ is the inverse of the effective survey area. In order to apply

this combined method, the playback method must not attract birds into the effective

survey area that were not already present during the line transect survey period. In other

words, the shape of the probability density function must remain the same. Field tests

could be performed to assess this assumption. It is important that there is standardization of playback equipment and recordings to avoid violating this assumption (Turcotte and Desrochers 2002). Similar to distance sampling, field procedures during the playback method must minimize double counting.

Although distance sampling provides a more accurate density estimate over fixed-plot methods, traditional distance sampling alone may not adequately detect many cavity-nesting species. These birds may go undetected due to infrequent calling or drumming even when they are on or near the line transect. The use of this combined method allowed me to model the number of non-calling and non-drumming birds and account for these birds in the density estimates. In comparing 50-m fixed-radius point count data with a period of playback of black-capped chickadee (*Poecile atricapilla*) mobbing calls, Gunn et al. (2000) found that a combined count of both pre-playback and post-playback data gave a more accurate census 75% of the time.   Turcotte and Desrochers (2002) demonstrated the usefulness of playbacks during the nonbreeding season and suggested its use for rare and secretive birds during the breeding season as well. Other recent advances in population surveys include double observer surveys (Bart and Earnst 2002) and double observer with distance sampling (Kissling 2004). By reducing detection bias, these methodological improvements provide more reliable population estimates and facilitate meeting conservation, management, and monitoring goals.

Table 3.1. Validation results for predicting true density (birds/ha) of 4 cavity-nesting bird species. Density and standard error were estimated from the line transect data alone, from combining line transect and playback data, and from a predictive regression model.

	Black-backed Woodpecker	Pileated Woodpecker	White-breasted Nuthatch	Williamson's Sapsucker
Mean transect density 2003[1]	0.024 ± 0.059	0.021 ± 0.025	0.085 ± 0.041	0.142 ± 0.037
Mean true density 2003[2]	0.044 ± 0.038	0.046 ± 0.030	0.141 ± 0.046	0.240 ± 0.043
Mean transect density 2004[1]	0.010 ± 0.035	0.013 ± 0.022	0.111 ± 0.096	0.127 ± 0.033
Mean true density 2004[2]	0.031 ± 0.036	0.023 ± 0.024	0.144 ± 0.035	0.227 ± 0.033
Mean predicted true density 2004[3]	0.031 ± 0.004	0.039 ± 0.003	0.162 ± 0.012	0.227 ± 0.008
Difference between predicted and true density	0 %	+ 41%	+ 11%	0 %
R^2	0.32	0.53	0.84	0.40
Root Mean Squared Error	0.06	0.03	0.11	0.20

[1] Density estimated from line transect data alone

[2] Density estimated from combining line transect and playback data

[3] Model was created from 2003 combined transect and playback data and applied to 2004 transect data
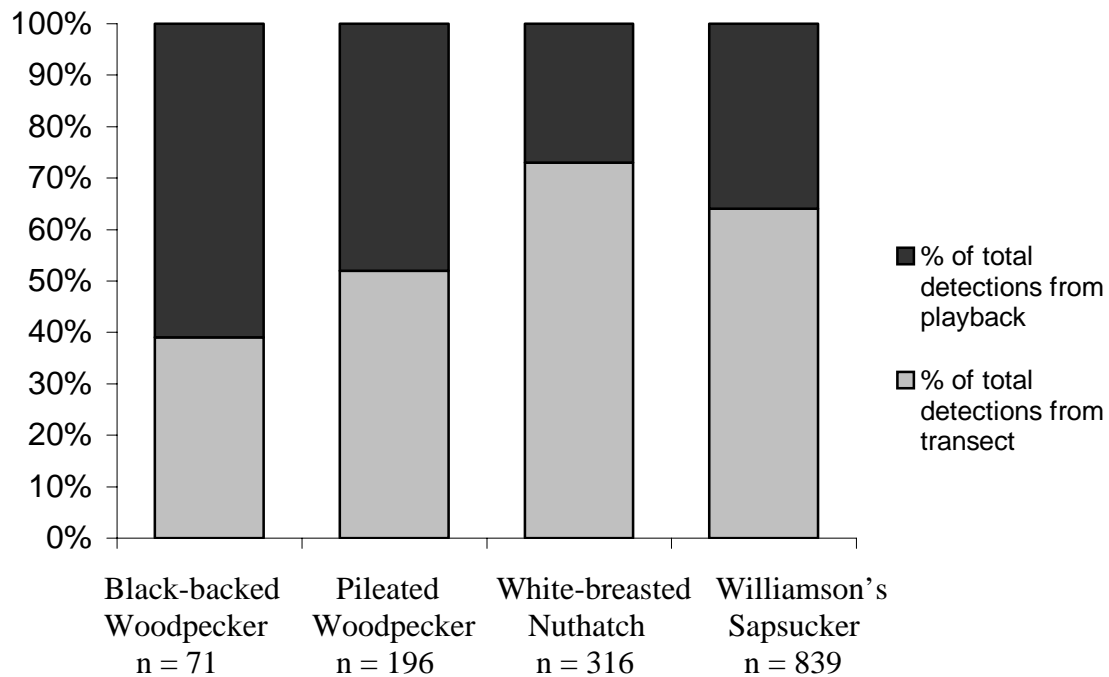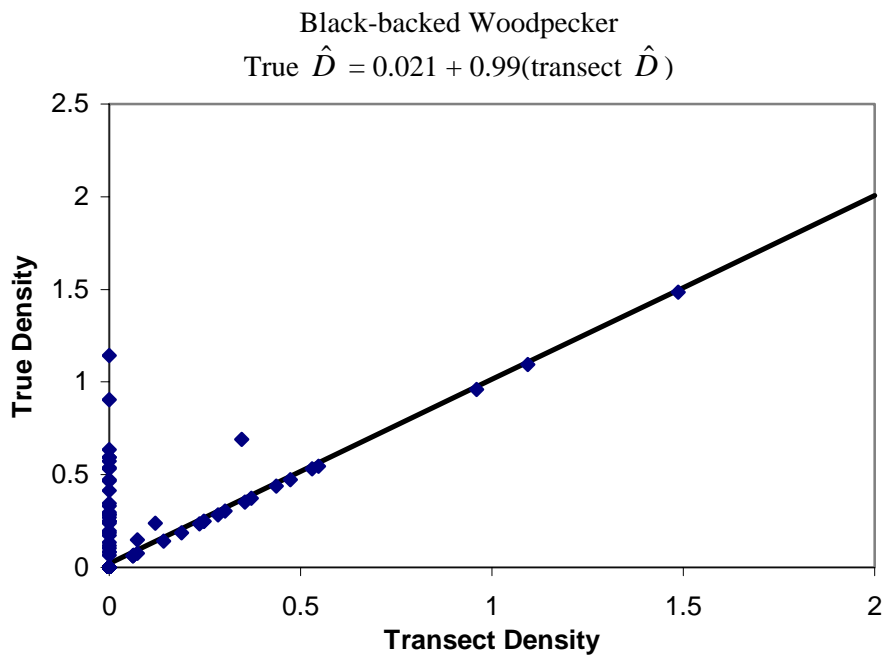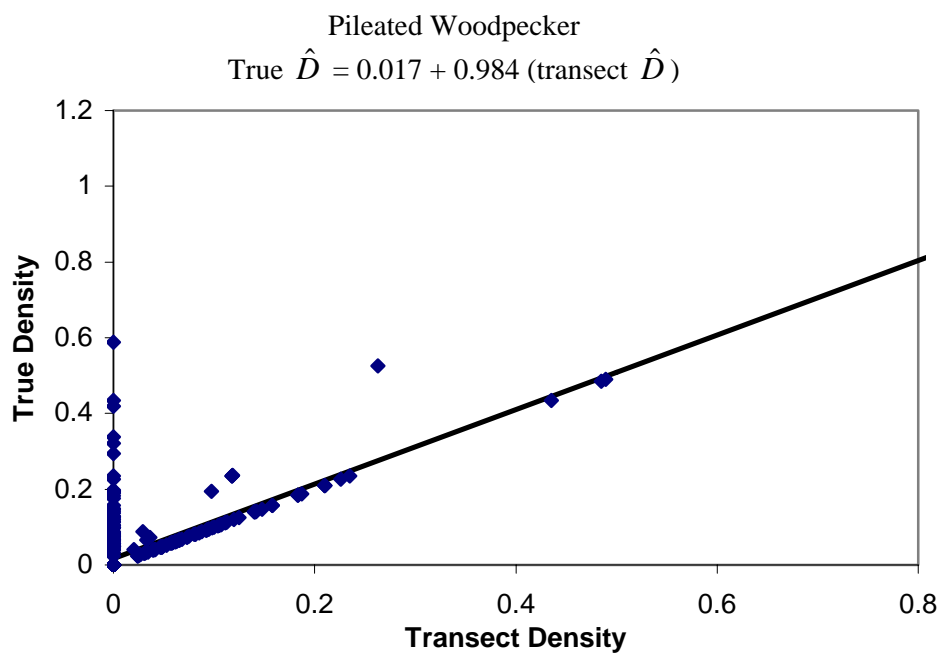
Figure 3.1. Percentage of total detections (2003 and 2004) from the line transect method and the playback method. See text for species codes.
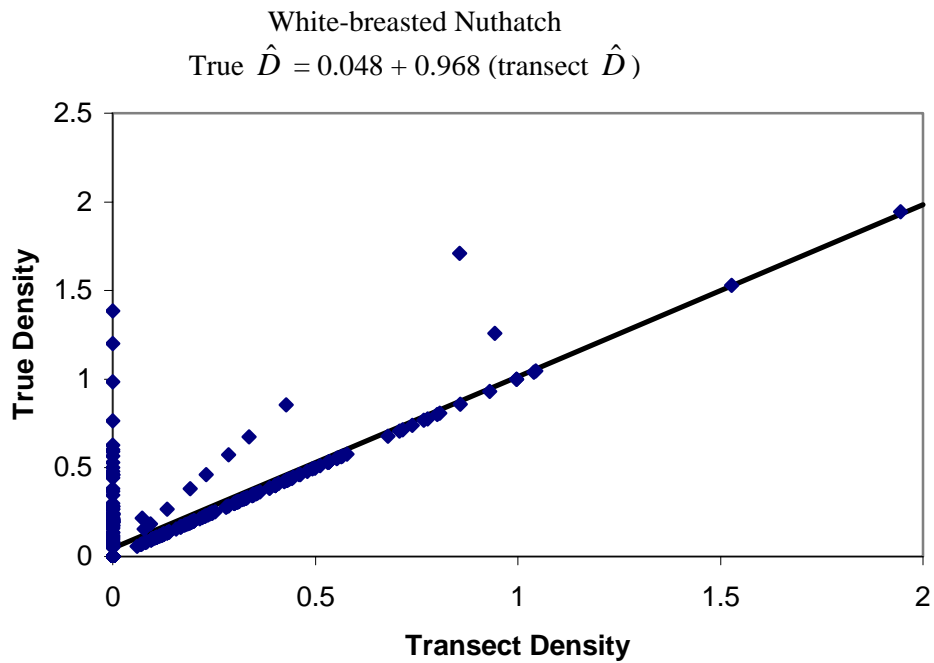
A

Black-backed Woodpecker
True $\hat{D} = 0.021 + 0.99$(transect $\hat{D}$)

B

Pileated Woodpecker
True $\hat{D} = 0.017 + 0.984$ (transect $\hat{D}$)

C

White-breasted Nuthatch

True $\hat{D} = 0.048 + 0.968$ (transect $\hat{D}$)

D

Williamson's Sapsucker

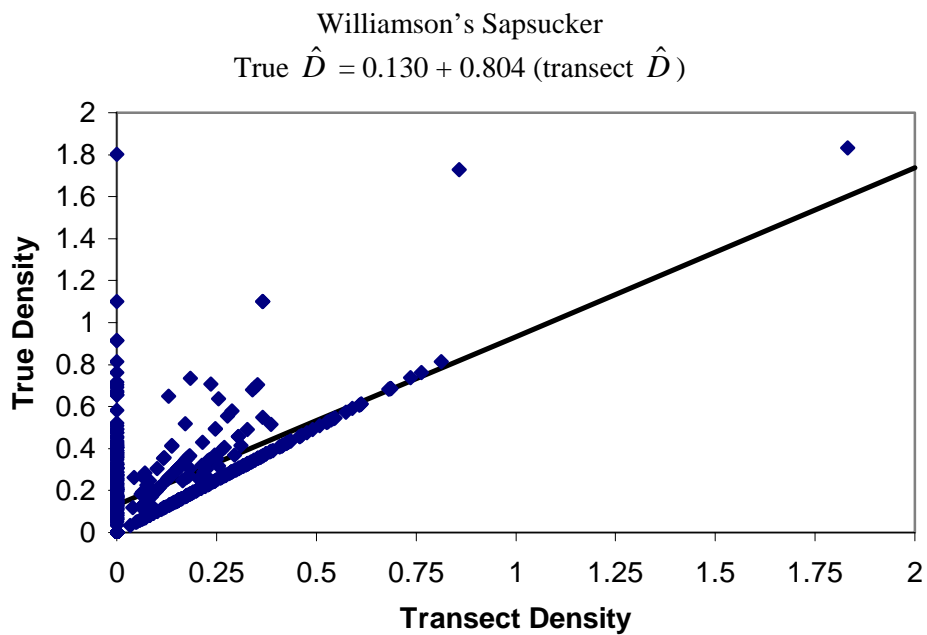True $\hat{D} = 0.130 + 0.804$ (transect $\hat{D}$)

Figure 3.2. Final regression models based on data collected in 2003 and 2004 for 4 cavity-nesting bird species.

A.) $R^2 = .0.51$ RMSE = 0.1016 B.) $R^2 = 0.45$ RMSE = 0.0567 C.) $R^2 = 0.69$ RMSE = 0.1409 D.) $R^2 = 0.39$ RMSE = 0.1833

LITERATURE CITED

Bart, J. and S. Earnst. 2002. Double sampling to estimate density and population trends in birds. Auk 119 (1): 36-45.

British Columbia Ministry of Environment, Land and Parks. 1999. Inventory methods for woodpeckers. Standards for Components of British Columbia's Biodiversity No. 19. The Province of British Columbia, Published by the Resource Inventory Committee, Victoria, BC, Canada. http:// srmwww.gov.bc.ca/risc/pubs/tebiodiv /woodpeckers/index.htm

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L.Thomas. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford, UK.

Bull, E.L., S.R. Peterson, and J.W. Thomas. 1986. Resource partitioning among woodpeckers in northeasternern Oregon. PNW-444. U.S. Forest Service, Pacific Northwest Research Station, Oregon.

_____, M.G. Henjum, and R.S. Rohweder. 1988. Nesting and foraging habitat of great gray owls. Journal of Raptor Research 22(4):107-115

_____, R.S. Holthausen, and M.G. Henjum. 1990. Techniques for monitoring Pileated Woodpeckers. PNW-GTR-269. U.S. Forest Service, Pacific Northwest Research Statioin, Oregon.

_____, and R.S. Holthausen. 1993. Habitat use and management of Pileated Woodpeckers in northeasternern Oregon. Journal of Wildlife Management 57: 335-345.

Burnham, K.P. 1981. Summarizing remarks: environmental influences. Studies in Avian Biology 6: 324-325.

Burnham, K.P., D.R. Anderson, and J.L. Laake. 1981. Line transect estimation of bird population density using a Fourier series. Studies in Avian Biology 6: 466-482.

Colver, K.J., D. Stokes, and L. Stokes. 1999. Stokes field guide to bird songs: western region. Time Warner AudioBooks, New York.

Falls, B.J. 1981. Mapping territories with playback: an accurate census method for songbirds. Studies in Avian Biology 6: 86-91.

Franzerb, K.E. 1981. The determination of avian densities using the variable-strip and fixed-width transect surveying methods. Studies in Avian Biology 6:138-145.

Gibbs, J.P. and S.M. Melvin. 1993. Call-response surveys for monitoring breeding waterbirds. Journal of Wildlife Management 57(1): 27-34.

Gunn, J.S., A. Desrochers, M. Villard, J. Bourque, and J. Ibarzal. 2000. Playbacks of mobbing calls of Black-capped Chickadees as a method to estimate reproductive activity of forest birds. Journal of Field Ornithology 71(3): 472-483.

Harrell, F.E. Jr. 2001. Regression Modeling Strategies: with applications to linear models, logistic regression, and survival analysis. Springer-Verlag, New York.

Hejl, S.J. 1994. Human-induced changes in bird populations in coniferous forests in western North America during the past 100 years. Studies in Avian Biology 15:232-246.

Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breedding season use. Auk 103: 593-602.

Johnson, R.R., B.T. Brown, L.T. Haight, and J.M. Simpson. 1981. Playback recordings as a special avian censusing technique. Studies in Avian Biology 6: 68-75.

Karl, J.A., L.K. Svancara, P.J. Heglund, N.M. Wright, and J.M. Scott. 2002. Species commonness and the accuracy of habitat-relationship models. Pages 573-580 in J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, F.B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C.

Kissling, M. 2004. Effects of forested buffer width on breeding bird communities in coastal forest of Southeast Alaska with a comparison of avian sampling techniques. University of Idaho, Masters Thesis.

Marcot, B.G., M.G. Raphael, and K.H. Berry. 1983. Monitoring wildlife habitat and validation of wildlife-habitat relationships models. Transactions of the North American Wildlife and Natural Resources Conference 48:315-329.

Pravosudov, V.V. and T.C. Grubb. 1993. White-breasted Nuthatch (Sitta carolinensis). *In* The birds of North America, No. 54 (A. Poole and F.Gill, editors). Philadelphia: The Academy of Natural Sciences; Washingtion, D.C.: The American Ornithologists' Union.

Ralph, C.J. and J.M. Scott (editors). 1981. Estimating Numbers of Terrestrial Birds. Studies in Avian Biology No.6. The Cooper Ornithological Society.

Reynolds, R.T., J.M. Scott, and R.A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82: 309-313.

Rosenstock, S.S., D.R. Anderson, K.M. Giesen, T. Leukering, and M.F. Carter. 2002. Landbird counting techniques: current practices and an alternative. Auk 119(1): 46-53.

SAS. 1999. SAS/STAT software, 8.2. SAS Institute, Cary, North Carolina, USA.

Swetnam, T.W., B.E. Wickman, H.G. Paul, and C.H. Baisan. 1995. Historical patterns of western spruce budworm and Douglas-fir tussock moth outbreaks in the northern Blue Mountains, Oregon, since A.D. 1700. Research paper PNW-RP-484. U.S.Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H. and Bishop, J.R.B. 2003. Distance 4.0. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Thompson, W.L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. Auk 119(1): 18-25.

Turcotte, Y. and A. Desrochers. 2002. Playbacks of mobbing calls of Black-capped Chickadees help estimate the abundance of forest birds in winter. Journal of Field Ornithology 73(3): 303-307.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247-302.

White, D. 1992. A guide to the vocalizations of woodpeckers of Northeastern Oregon. USDS Forest Service. Pacific Northwest Research Station, La Grande, OR.

Wickman, B.E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. General technical report GTR-295. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.