AN ABSTRACT OF THE THESIS OF

Daniel L. Gumtow-Farrior for the degree of Master of Science in Forest Science presented on 24 April, 1991.

Title: Cavity Resources in Oregon White Oak and Douglas-Fir Stands in the Mid-Willamette Valley, Oregon

Abstract approved: William McComb
William C. McComb

Previous studies of bird communities in the mid-Willamette Valley, Oregon, indicated that Oregon white oak (Quercus garryana) stands supported more cavity-using bird species than sympatric stands of Douglas-fir (Pseudotsuga menziesii). Mature Oregon oak stands are being harvested and few are regenerating.

I compared cavity availability for hole-using fauna among 10 types of stands in the mid-Willamette Valley and adjacent Coast Range foothills (6 Oregon white oak, 3 Douglas-fir and 1 mixed Oregon oak/Douglas-fir). Thirty stands (3/type of stand) were classified by their predominant tree species, average diameter class (20.0-to-

34.9 cm, 35.0-to-49.9 cm, and 50.0+ cm at breast height) and area (groves <4 ha, stands >4 ha). Origin, location and estimated size were recorded for 735 cavities found in 3300 trees. Sixty-three percent of the trees examined were Oregon oak, but 93.7% of the cavities were in Oregon oak.

Most cavities (70%) were products of decay following infection. Two-thirds of the cavities had entrance hole diameters between 2.5-to-5.0 cm. Groves of medium- and large- diameter oaks and stands of large-diameter oaks had the most cavities. Cavity availability was higher in the oak stands than in the Douglas-fir and mixed stands.

Declines in densities of cavities through a progressive replacement of larger Oregon white oak by smaller, managed Douglas-fir will unquestionably reduce the abundance of cavities in the mid-Willamette Valley. Maintenance of existing oak stands and regeneration of Oregon oak in the mid-Willamette Valley may be desirable to maintain habitat for indigenous cavity-using fauna.

Cavity Resources in Oregon White Oak and Douglas-Fir Stands in the Mid-Willamette Valley, Oregon

by

Daniel L. Gumtow-Farrior

A THESIS

Submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed 24 April, 1991

Commencement June 1991

ACKNOWLEDGEMENTS

Several people have helped to make this study possible. I thank Dr. W. C. McComb, my major advisor, for his guidance, support and scientific example. I also thank Dr. E. C. Meslow, Dr. D. S. deCalesta, and Dr. D. E. Hibbs, members of my committee, for their insights and contributions to this study. I also thank Dr. D. R. Buhler for serving as my graduate council representative.

Stan Dill kindly loaned me his tree-climbing equipment and taught me how to use it. Tom Sabin graciously addressed my frequent questions regarding computers and statistics. Bill Ripple and Dennis Isaacson provided me access to and instruction in the interpretation of aerial photography. Jeff Garver and the staff of the OSU Research Forests provided mensurational data for stands in McDonald and Dunn Forests. W. I. Stein, D. Minore and D. Dollarhide freely shared with me their knowledge and ideas regarding tree regeneration and diseases. Many landowners gave me consent to work on their property.

Funding for this study was provided by Oregon State University's Forest Research Laboratory, the North American Bluebird Society, the Oregon Department of Fish & Wildlife and the U. S. Fish and Wildlife Service. I would especially like to thank Charlie Bruce of ODF&W and

Palmer Sekora of the USF&WS.

I thank my friends for their stimulation and support, and my family members (with special regards to Mr. and Mrs. Gumtow) for kindnesses too numerous to list. I dedicate this thesis to Cathy, my wife and fellow biologist, without whose loving constancy this work would not have been possible.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
OBJECTIVES	12
STUDY AREA	13
METHODS	16
Definition of a cavity	16
Stand selection	16
Sampling protocol	19
Cavity correction factor	23
Data analysis	25
RESULTS AND DISCUSSION	27
Stand selection	27
Cavity correction factor	32
Tree-level results	36
Cavities per tree	36
Cavities per snag	36
Excavated cavities	42
Non-excavated cavities	44
Properties of trees influencing susceptibility to cavity formation	45
Stand-level results	50
Cavity abundance among stand types	50
Predicting availability of cavities among stands for cavity-nesters	55
Cavity abundance and stand dynamics	66
CONCLUSIONS	69
MANAGEMENT RECOMMENDATIONS	70
LITERATURE CITED	71
APPENDICES	82

LIST OF FIGURES

Figure		Page
1.	Stylized representation of open-form Oregon white oak (*Quercus garryana*)	3
2.	Stylized representation of closed-form Oregon white oak (*Quercus garryana*)	5
3.	Distribution of Oregon white oak in North America. Crosshatching designates study area in mid-Willamette Valley, Oregon (map from Thilenius 1968)	14
4.	Diameter distributions (cm dbh) for 10 types of stands in the mid-Willamette Valley, Oregon	29
5.	Cavities/tree by dbh class for Oregon white oak and Douglas-fir in the mid-Willamette Valley, Oregon, based on *n* = 15 Douglas-fir and 689 Oregon white oak cavities and *n* = 1108 Douglas-fir and 2072 Oregon white oak trees	37
6.	Cavities by origin in Oregon white oak, Douglas-fir and mixed Oregon white oak/ Douglas-fir stands in the mid-Willamette Valley, Oregon	40
7.	Densities of cavities (cavities/ha, $P < 0.01$) for Oregon white oak, Douglas-fir and mixed Douglas-fir/Oregon white stands in the mid-Willamette Valley, Oregon	53

LIST OF TABLES

Table		Page
1.	Selected comparisons of characteristics of cavity- and non-cavity trees in North America	8
2.	Cavities/tree (SE) among 3 diameter classes of Oregon white oak and Douglas-fir in the mid-Willamette Valley, Oregon, based on classifications of holes into 5 categories used to construct a cavity correction factor	33
3.	Cavities/tree (range) by dbh class and species in the mid-Willamette Valley, Oregon	39
4.	Densities of cavities (>2.5 cm entrance diameter) in 10 types of stands in the mid-Willamette Valley, Oregon (n = 30)	52
5.	Maximum percentages of roosting pairs of woodpeckers potentially supported among 10 types of stands (n=30) in the mid-Willamette Valley, Oregon, as determined by densities of excavated cavities with appropriate entry diameters	58
6.	Maximum percentages of pairs of facultative and secondary-nesting species potentially supported by the cavity resources among 10 types of stands (n=30) in the mid-Willamette Valley, Oregon	61

LIST OF APPENDICES

APPENDIX Page

1. Cavity features used by cavity-using species in upland Oregon white oak and Douglas-fir woodlands in the mid-Willamette Valley, Oregon 82

2. Features of 10 types of stands (n=30) in the mid-Willamette Valley, Oregon 86

CAVITY RESOURCES IN OREGON WHITE OAK AND DOUGLAS-FIR STANDS IN THE MID-WILLAMETTE VALLEY, OREGON

INTRODUCTION

Oregon white oak (*Quercus garryana*) has the longest north-south distribution among native oaks in western North America (Stein, *in press*). Oregon oak occurs from southern British Columbia to the valleys of central California, and attains its best development as a dominant vegetation form on the valley floor and foothills of Oregon's Willamette Valley (Thilenius 1968). However, some oak stands are suppressed by faster-growing Douglas-fir (*Pseudotsuga menziesii*) that have extended into low elevation oak sites that are no longer burned (Franklin and Dyrness 1973).

About 98% of Oregon oak in western Oregon is privately owned (Popino and Gedney 1984). Douglas-fir is a conspicuous landscape feature on the periphery of the Willamette Valley, and it is managed for timber. Oregon oak comprises 2.2% and Douglas-fir 61.4% of the total volume of growing stock on private timberlands in west-central Oregon from the crest of the Cascade Range west to the coast (Gedney et al. 1987).

There have been several significant floral shifts since the 1840's when Europeans settled the Willamette Valley. Before settlers cut the once-extensive Willamette River floodplain forest (gallery forest), the forest contained tree species (e.g., bigleaf maple (Acer macrophyllum), Oregon ash (Fraxinus latifolia), and black cottonwood (Populus trichocarpa) (Johannessen et al. 1971)) that could have been important cavity resources, (Gumtow-Farrior, this study and unpub. data). Annual prairie fires set by the Kalapuyah Indians to enhance their food-gathering efforts prior to 1850 are believed to have played a major role in promoting and maintaining solitary, thick-barked Oregon white oak ("open-form oak," Figure 1) and Douglas-fir by preventing establishment of competing vegetation.

Ring-growth studies indicate that Indians set fires in the Willamette Valley since at least 1647 (Sprague and Hansen 1946). Wilkes (1844) recorded eyewitness accounts of several early pioneers who observed Indians setting prairie fires every summer. Fire control following pioneer settlement of the Willamette Valley from the 1850's onward is thought to have fostered development of oak forests (i.e., "closed-form oak" Figure 2) (Sprague and Hansen

Figure 1. Stylized representation of open-form Oregon white oak (Quercus garryana).

Figure 1.

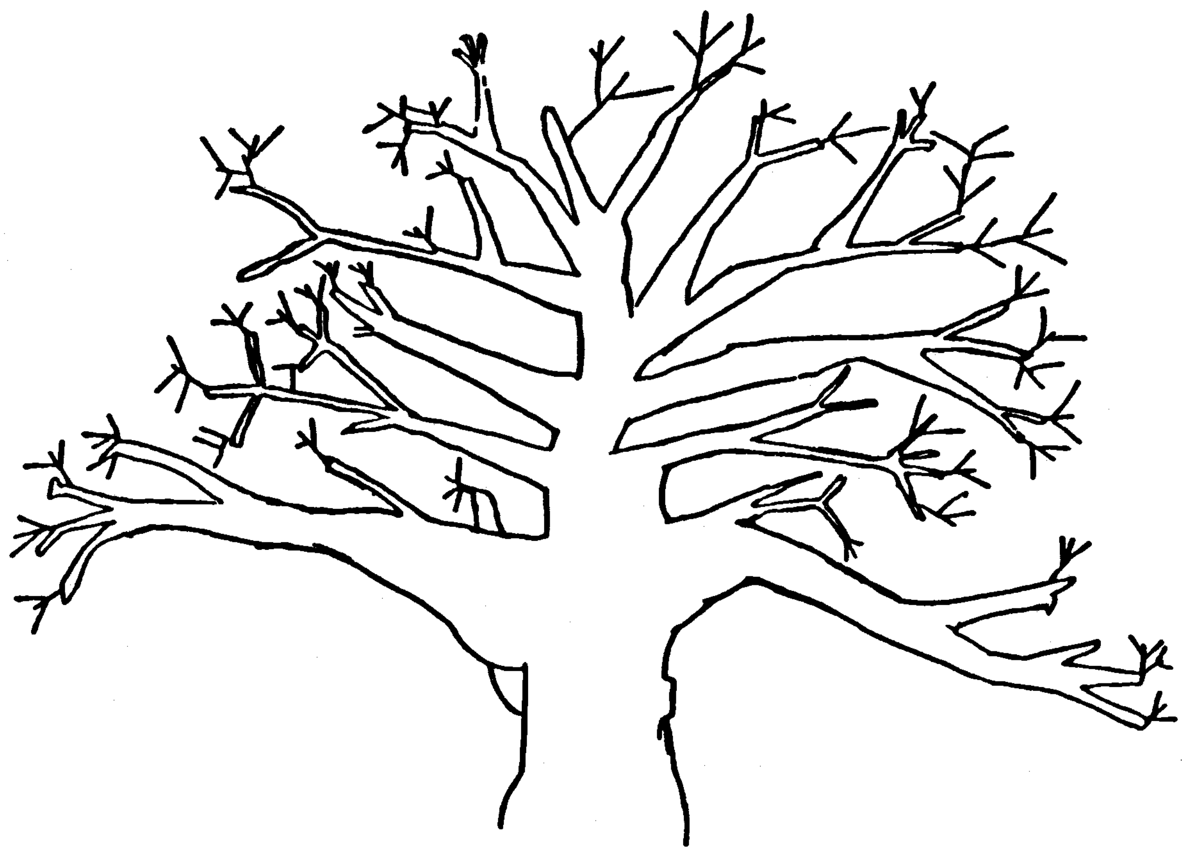
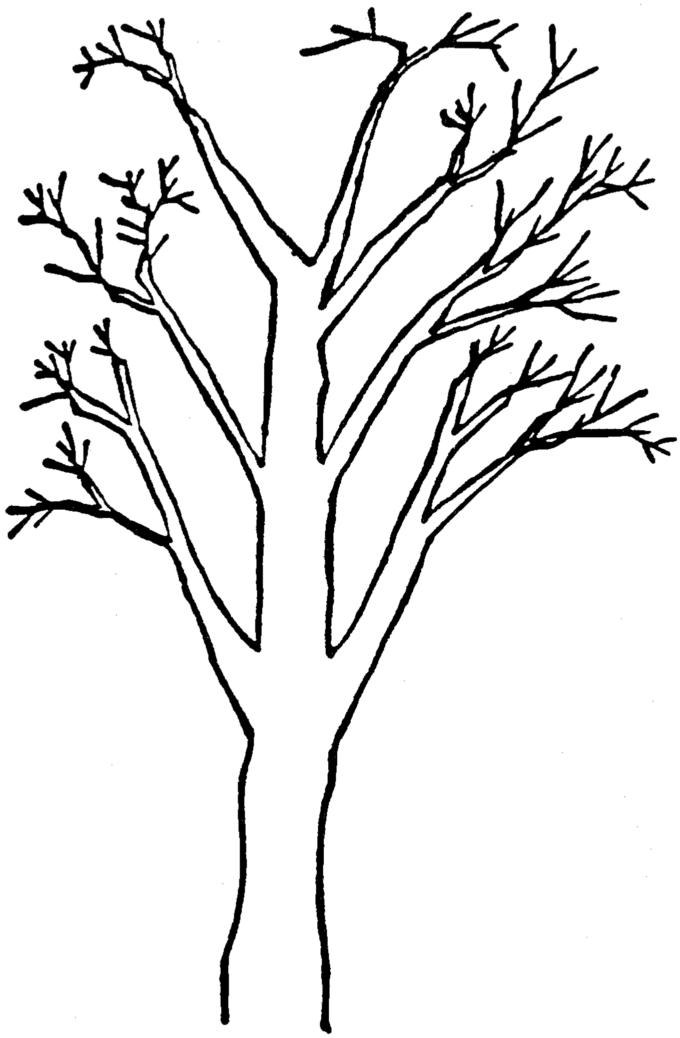


Figure 2. Stylized representation of closed-form Oregon white oak (_Quercus garryana_).

Figure 2.



1946, Habeck 1961, Thilenius 1968, Anderson 1970, Johannessen et al. 1971, Franklin and Dyrness 1973, Cole 1977). The net effect of the concurrent dimunition of the riparian gallery forest and expansion of upland closed-form oak forests on the volume of hardwood in the mid-Willamette Valley has not been documented. Precise estimates of the current total area of Oregon white oak habitat in the mid-Willamette Valley were not found (Stein, in press), but I surmised from regional reports provided by Gedney et al. (1986, 1987) that the figure is < 8900 ha. Although written records were not kept by 2 private landowners whom I interviewed, these landowners cut at least 500 ha of Oregon oak in the mid-valley (> 5% of the total) between 1980 and 1989, and replanted these stands with Douglas-fir. I have seen other privately-owned oak stands that have been converted to Douglas-fir.

Tree-cavity abundance and characteristics important to cavity-using vertebrates have been documented for many North American habitats (Table 1), but not for Oregon white oak and Douglas-fir stands in the Willamette Valley and adjacent foothills. In Oregon's mid-Willamette Valley, approximately 28 cavity-using bird species use Oregon white oak woodlands during some portion of the

Table 1. Selected comparisons of characteristics of cavity and non-cavity trees in North America.

Variable	Conclusion	Location	Author (s)
dbh	spreading Oregon oak (Quercus garryana) > 50 cm dbh had more cavities than Douglas-fir. (Pseudotsuga menziesii) or smaller-diameter oak.	Oregon	This study
	40- to 90-cm dbh plains cottonwood trees (Populus sargentii) had 83% of the cavities.	Colorado	Sedgwick and Knopf (1986)
	cavity trees were 7.5- to 12.5-cm dbh larger than sound trees.	Missouri	Dalke (1948)
	dbh of woodpecker nest trees > than adjacent non-nest trees.	Vermont	Runde and Capen (1987)
	woodpeckers nested in large trees in a trembling aspen (Populus tremuloides)/Douglas-fir forest.	Br. Col.	Harestad and Keisker (1989)
	cavities generally occurred in 30- to 60-cm-dbh trees.	Missouri	Gysel (1961)
	diameters of cavity trees were 75% larger than noncavity trees.	W. Virg.	Carey (1983)
	dbh of nest trees > that of randomly-selected non-nest trees.	Flor., S. Car.	McComb et al. (1986)
	mean dbh of cavity trees was 22.6% greater than mean noncavity-tree dbh.	Conn.	McComb and Noble (1980)
Cavity densities (cav/ha)	25.1-117.4 in Oregon white oak stands, 2.4-24.0 for Douglas-fir stand for cavity entrance diameters > 2.5 cm.	Oregon	This study
	25.9-80.8 in hardwood stands for cavity entrance diameters > 2.5 cm.	S. Car.	McComb et al. (1986)
	14.5 in pine-hardwood stands for cavity diameters > 2.5 cm dbh.	S.Car.	McComb et al. (1986)
	12.4-13.1 for hemlock (Tsuga canadensis) and pine (Pinus strobus) community; entrance diameters not given.	Conn.	McComb and Noble (1980)

Table 1. Continued.

Variable	Conclusion	Location	Author (s)
Cavity densities (cav/ha)	4.4 in a hardwood community for cavity entrance diameters > 3.0 cm.	Colorado	Winternitz and Cahn (1983)
	4.2 in a plains cottonwood community for cavity entrance diameters > 3.0 cm.	Colorado	Sedgwick and Knopf (1986)
	3.7-24.2 in hardwood stands for cavity entrance diameters > 1.3 cm.	Michigan	Gysel (1961)
	3.4-4.8 in hardwood stands for cavity entrance diameters > 2.5 cm.	Calif.	Waters et al. (1990)
	2.1-5.8 in pine plantations and natural stands for cavity entrance diameters > 2.5 cm.	S. Car.	McComb et al. (1986
	<1-3 in a conifer-dominated community for cavity entrance diameters > 3.0 cm.	Calif.	Raphael and White (1984)
	0.2 in a hardwood community for cavity entrance diameters > 3.7 cm.	Arizona	Brush (1983)
Vigor	presence of disease predicted presence of excavated and nonexcavated cavities.	Oregon	This study
	woodpeckers required decayed heartwood in deciduous trees for excavating nest cavities.	W. Virg.	Conner et al. (1976)
	woodpeckers selected decayed nest trees.	Brit C.	Harestad and Keisker (1989)
	trees with excavated cavities had the most rot or the poorest vigor.	W. Virg.	Carey (1983)
	75% of nonexcavated cavities were in trees of poor vigor.	Michigan	Gysel (1961)
	woodpeckers disproportionately nested in trees with heartwood decay.	Vermont	Runde and Capen (1987)
	length of dead limbs was correlated (r=0.89) with the frequency of cavities by tree dbh class.	Colorado	Sedgwick and Knopf (1986)
	nest trees of primary cavity-using birds had more wounds and broken limbs than non-nest trees.	Calif.	Waters et al. (1990)

Table 1. Continued.

Variable	Conclusion	Location	Author (s)
Cavity Diameter	83% of 735 cavity entrances were 2.5-7.5 cm in diameter.	Oregon	This study
	> 90% of cavity entrances were 3.0-7.0 cm in diameter.	Colorado	Sedgwick and Knopf (1986)
	83% of 989 hardwood cavity entrances were 1.25-9.75 cm in diameter.	Colorado	Gysel (1961)
	55-70% of dens in 4 forest types had entrances <12.5 cm in diameter.	Florida, S. Car.	McComb et al. (1986)
Species Contrasts	Oregon white oak produced more cavities/tree than Douglas-fir.	Oregon	This study
	blue oak (Quercus douglasii) and interior live oak (Quercus wislizenii) had more cavities/tree than digger pine (Pinus sabiniana).	Calif.	Waters et al. (1990)
	trembling aspen had more cavities/tree than Douglas-fir.	Brit. C.	Harestad and Keisker (1989)

year, 22 cavity-using bird species use Douglas-fir stands of the adjacent Coast Range foothills, and 19 cavity-using bird species use both types of habitat (Appendix 1). Approximately 11 species of cavity-using mammals inhabit Oregon oak stands, 12 occupy Douglas-fir habitats, and 11 are found in both habitats (Brown 1985). Acorn woodpeckers (Melanerpes formicivorus) appear to occur only in oak habitats in the mid-Willamette Valley. Douglas-squirrels (Tamiasciurus douglasii) occupy Douglas-fir and mixed oak/Douglas-fir types of stands (Brown 1985).

Given the potential importance to cavity-using wildlife of cavity production by Oregon oak and Douglas-fir, it is important to be able to predict how these contributions might change under management activities that decrease Oregon white oak and favor Douglas-fir.

OBJECTIVES

The objectives of this study were to examine upland Oregon white oak, Douglas-fir, and mixed Oregon oak/Douglas-fir stands in the mid-Willamette Valley that differed in area and tree diameter class in order to determine abundances of: a) excavated and nonexcavated cavities, b) cavities per tree by size class and species, and c) cavity densities in the different types of stands.

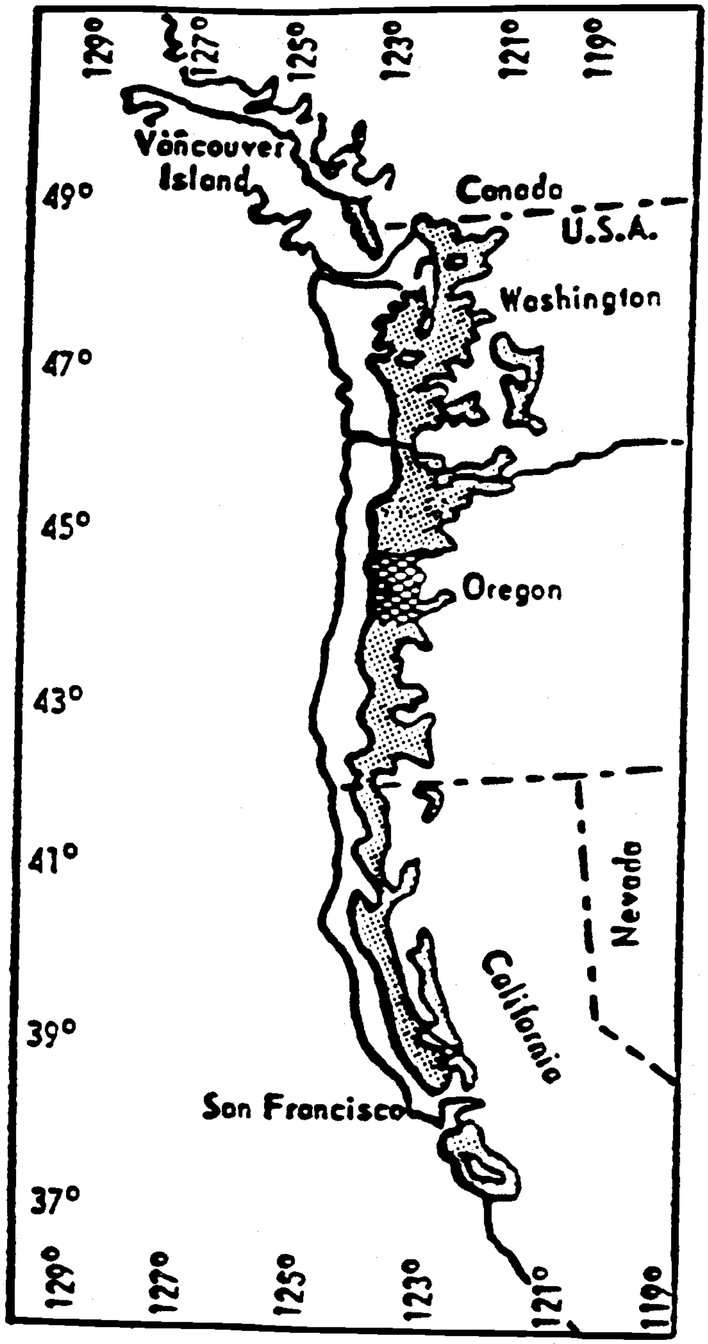
STUDY AREA

The mid-Willamette Valley is located in western Oregon and is bounded on the west by the Oregon Coast Range and on the east by the Cascade Range. The geography, physiography, geology and climate of the Willamette Valley have been described by Thilenius (1968) and Towle (1982). Average elevation of the valley bottom is 90 m, and the upper elevations of the adjacent Coast Range foothills usually do not exceed 400 m. Oregon white oak extends to approximately 200 m in elevation and Douglas-fir are found along this entire elevational gradient.

The Willamette Valley is approximately 50 km wide and 200 km long; the mid-Willamette Valley is approximately 60 km long, extends between roughly Rickreall on the north and Monroe on the south, and is centered around Corvallis (Figure 3). The climate of the Willamette Valley is characterized by moist, cool winters and warm, dry summers.

Figure 3. Distribution of Oregon white oak in North America. Crosshatching designates study area in mid-Willamette Valley, Oregon (map from Thilenius 1968).

Figure 3.


129°
127°
125°
123°
121°
119°
Vancouver
Island
Canada
U.S.A.
49°
Washington
47°
45°
Oregon
43°
41°
Nevada
California
39°
San Francisco
37°
129°
127°
125°
123°
121°
119°

METHODS

Definition of a Cavity

Because I had insufficient time to measure them, hole dimensions were estimated. Cavities were tree holes that seemed to have horizontal depths $\geq$ 7.5 cm with entrances $\geq$ 2.5 cm wide. Cavities of this size accomodate the smallest secondary cavity-using bird and mammal species in the mid-Willamette Valley (Appendix 1). Other workers have delineated minimum cavity entrance diameters as 2.5-3.0 cm (McComb et al. 1986, Sedgwick and Knopf 1986).

Stand Selection

Classifications of stands as Oregon white oak, Douglas-fir or mixed Oregon oak/Douglas-fir were based on color aerial photographs and site visits. Stands were classified as Oregon white oak when Oregon white oak crown cover was $\geq$ 70%, as Douglas-fir when Douglas-fir crown cover was $\geq$ 70%, and as mixed Oregon oak/Douglas-fir when Oregon oak crown cover was from 30-70% inclusive (Brown 1985). Types of stands were either groves (oaks $\leq$ 4 ha bordered by fields, roads, or both) or stands (oak, Douglas-fir, or mixed Oregon oak/Douglas-fir > 4 ha). The area of each grove and stand was estimated using a dot grid on an aerial photograph. The mid-Willamette Valley was stratified into northern, central and southern blocks. Three upland groves or stands (1 from each block) that were similar in area, average tree diameter, and species composition were replicates for each of the 10 types of stands (treatments). I chose 20.0 cm dbh as a minimum tree size for sampling purposes because preliminary examinations indicated that only rarely did Willamette Valley oaks < 20 cm dbh have cavities. Aerial photographs from 1980 and extensive reconnaissance driving in 1990 indicated that the mixed type of stand was not well distributed in the mid-valley except in the northern block, thus the 3 replicates of this type of stand were all in the northern block.

Unable to locate prior mensurational data for oak groves and stands, and lacking the time for a thorough quantitative pre-survey, I measured the dbh of 12-15 oaks in each grove and stand that appeared to be closest to the stand mean, then used these values as the basis for assigning each stand to 1 of 3 diameter classes: small (20.0- to 34.9-cm dbh), mid (35.0- to 49.9-cm dbh), and large (50.0+ cm dbh). The same method was used with Douglas-fir, except when quadratic mean diameters were known. Quadratic mean diameters for the hardwood and

Douglas-fir components of the mixed stands were known. Mixed stands were classified on the basis of Oregon oak diameters in order to review how cavity resources of Oregon oak changed as Oregon oak stands succumbed to Douglas-fir dominance.

Oregon white oak stands (or portions of stands) that had been systematically thinned were avoided since only the healthiest trees (those least likely to have cavities) were usually retained and cavity surveys in these stands would probably underestimate cavity densities compared to pre-thinning conditions. Conversely, if cavity surveys occurred in stands in which only the "poorest quality" specimens remained following a "high-grading" of merchantable timber, then cavity densities would be overestimated.

With 2 exceptions, I avoided portions of stands that were cut or cleared. Some mature oaks were harvested from a portion of the central stand of large-diameter oak (See Appendix 2). A scattering of various diameter trees had been removed from a large portion of the northern stand of large-diameter oak; it was sampled nonetheless because this was the only stand of large-diameter oak found in the northern block that had not been heavily thinned and the structure of this stand was similar to that of the other large-diameter oak stands (i.e., dead, obviously diseased, and apparently healthy trees were distributed throughout it).

I endeavored to sample 9 unthinned Douglas-fir stands, but found only 6 unthinned, upland Douglas-fir stands (2 per diameter class in the central and southern block); thus each of the 3 types of Douglas-fir stands contained 1 thinned stand from the northern block. Only vigorous Douglas-fir were retained during thinning, consequently I may have underestimated Douglas-fir cavity densities compared to pre-thinning conditions.

I preferentially selected federal and state-owned stands. When these did not meet the criteria of my sampling design, appropriate privately-owned groves or stands were used. No attempt was made to differentiate between grazed and ungrazed stands because it was not possible to verify the grazing history of all stands.

Sampling Protocol

From a randomly-chosen starting position, 25 equidistant sampling points were located on a field grid established along the 4 cardinal directions. The point-quarter sampling technique (Cottam and Curtis 1956) was used to identify the tree (regardless of species except in the mixed stands) nearest point-center in each quadrant irrespective of whether the tree was alive or dead (a snag). The point-quarter technique is valid only in habitats where stems are randomly distributed. I was unable to determine whether distributions of stems in the 30 stands were random, uniform, or aggregated because I recorded only point-to-plant distances, not plant-to-plant distances. In each stand, 100 trees $\geq$ 20 cm dbh (regardless of species) were examined for cavities. However, 200 trees (100 oak and 100 Douglas-fir) were sampled in each of the 3 mixed stands.

The following data were recorded for each tree:

1) Diameter-at-breast-height (dbh);

2) Total number of cavities seen;

3) Edge or interior tree; any tree that was within 10 m of an edge was classified as an edge tree, otherwise it was an interior tree;

4) Disease. A tree was categorized as diseased if any of several obvious signs of disease were present. Examples of such signs were rotting branch stubs (Nietro et al. 1985) which I defined as broken branches $\leq$ 45.0 cm long, poorly healed wounds, presence of fungal conks, a broken top, evidence of heartrot or rootrot, (Runde and Capen 1987), or existing cavities that did not appear to

be compartmentalized (walled off from the rest of the tree) (Shigo 1976);

5) Percentage of mortality by volume. All trees with any natural pruning were assigned 1% mortality. In all other cases, the proportion of dead tree volume to whole tree volume was visually estimated to the nearest 5 percent. Snags were recorded as having 100% mortality by volume;

6) Number of dead branches thought to be $\geq$ 8 cm in diameter. Counting dead branches requires comparatively more time than visually scanning a tree and estimating percentage of mortality by volume (see above), so dead branches were counted only for a subsample of trees (n = 305 oak, 17 Douglas-fir); and

7) Tree growth form. I assigned each oak tree to either open-form or closed-form as described by Thilenius (1968) and Stein (in press) (Figures 1 and 2).

The following information was recorded for each cavity:

1) Estimated diameter of the entry hole (cm). Calibrations of my estimates were based on my prior experience with estimating and then measuring cavity entrance diameters in the Willamette Valley (unpub. data)

and elsewhere. The lesser of the 2 diameters was used for cavities with oblong or otherwise irregular entrances;

2) Origin of cavity (excavated or nonexcavated). Excavated cavities were created by woodpeckers and nonexcavated cavities were not created by woodpeckers (Waters et al. 1990).

Trees were scanned for cavities from the ground with and without binoculars. Searches were suspended when heavy rain or highly reflective cloud cover reduced visibility to unsatisfactory levels.

Cavity searches in deciduous stands are preferably conducted in the winter because deciduous trees drop their leaves in winter thereby enhancing visibility (Carey 1983). My stands were sampled during the leafless period (winter) and full-leaf period (summer), but not during periods of partial leafout because visibility under these conditions can change dramatically on a daily basis (e.g., visibility can improve with decreasing foliage cover in the autumn or deteriorate with increasing foliage cover in the spring). Entry restrictions at 2 U.S. Fish and Wildlife Service National Wildlife Refuges resulted in 5 oak stands that were accessible only during the summer. The remaining 25 stands were sampled in winter. The bias inherent in sampling during both summer and winter was minimized by developing an oak cavity correction factor based on trees sampled during both summer and winter.

Cavity Correction Factor

Some cavities cannot be seen from the ground and some tree holes can be misconstrued as cavities, so a correction factor (Gysel 1961) for ground counts of cavities was developed. Ground surveys were defined as surveys where an observer on the ground examined upright trees for cavities. Sixteen Oregon white oaks ($\bar{x}$ = 33.1 cm dbh, SE = 6.4 cm) from the northern block (not one of the replicate stands) were included in the cavity correction factor, as were 12 oaks in the central block ($\bar{x}$ = 66.4 cm dbh, SE = 11.7 cm), and 12 in the southern block ($\bar{x}$ = 58.2 cm dbh, SE = 11.5 cm).

Data for the oak cavity correction factor were obtained by recording entrance diameters, locations and origins of cavities for oaks in each block. Cavity information for the northern block was recorded in winter before and after oaks were felled. Oaks in the central and southern blocks were randomly selected from among the largest living trees in these blocks. Trees were climbed to 50-60% of their height using ropes and spurs during the same season that the ground counts were conducted in the stand (southern block in summer, central block in winter). All cavities observed by the climber were described to a helper on the ground who recorded the information. Cavity data from earlier ground surveys were not reviewed prior to climbing, but were compared after the climbing was completed.

The cavity correction factor for Douglas-fir was based on a winter ground survey of a 22-ha, 120-year-old, unmanaged Douglas-fir stand in the northern block (not one of the replicate stands). In this foothill stand, 55 Douglas-fir (x = 82.9 cm dbh, SE = 21.1) were surveyed for cavities before and after felling. A cavity correction factor for bigleaf maple was not developed.

Oregon white oak and Douglas-fir were sampled equally in the mixed stands, and the cavity correction factor for mixed stands was the average of the correction factors for oak and Douglas-fir. In each case, the factor was multiplied by original ground estimates of cavity densities to provide corrected estimates of cavity densities for comparisons among the types of stands. Due to time limitations, diameter-specific correction factors were not developed for either Oregon oak or Douglas-fir. Corrections were based more on the largest-diameter oak and Douglas-fir, thus the correction factor probably overestimated cavity abundances in the smaller-diameter trees.

Data Analysis

Plots of predicted versus residual values (SAS Institute Inc., 1987) of cavity abundance among stands were strongly nonnormal. Nonparametric procedures were used because data transformations ($\log_{10}$, inverse, and square root) failed to correct the nonnormality (Sabin and Stafford 1990).

Cavity abundances were compared among 10 types of stands using the Wilcoxon rank sums procedure (SAS Institute, Inc. 1987) based on tree species, diameter classes, and oak growth forms using the q-statistic to assess significant ($P < 0.05$) differences among treatments (Hollander and Wolfe 1973).

I used Spearman's rank correlation coefficient (r_s) to identify both linear and nonlinear relationships (Devore and Peck 1986) between: a) dbh and number of cavities, b) dbh and cavity entrance diameter, c) percentage of tree estimated to be dead and number of cavities, d) dead branch count and number of cavities, and e) percentage of tree estimated to be dead and number of dead branches.

Variables useful for predicting the probability of the occurrence of excavated and nonexcavated cavities in trees were identified using logistic regression. Dead branch counts and estimated percentage mortality by volume were each used in a regression equation to determine which factor might be a better predictor of cavity occurrence.

RESULTS AND DISCUSSION

Stand Selection

Franklin and Dyrness (1973) observed that "even where natural vegetation remains [in the Willamette Valley] it has been largely molded by human activities." All oak groves and stands I surveyed were modified to varying degrees by fire-control programs initiated after pioneer settlement, and some were also influenced by grazing, clearing, logging or some combination of these factors (Appendix 2). Four oak groves (2 small-, 1 mid-, and 1 large-diameter) had been grazed. One small- and 1 large-diameter oak grove and 2 oak stands, (1 small-diameter and 1 large-diameter) were partially grazed. Livestock browsing on oak branches could potentially wound trees and increase their susceptibility to disease, but I could not document or determine the extent or effects of this practice on cavity formation. Four oak stands (2 mid-diameter and 2 large-diameter) had a few trees removed for firewood or were partially cleared.

I did not age trees, but some oak stands I sampled clearly had mixtures of small-and large-diameter trees that indicated that the stands were probably 2-aged. According to Stein (<u>in press</u>) and Thilenius (1968), many

Oregon oak stands actually are 2-aged stands consisting of a majority of small-diameter, closed-form trees 60-150 years of age and scattered large-diameter, open-form trees 270-330 years of age. Large-diameter, open-form oak were in all oak stands, but their proportions varied (Figure 4).

With one exception (mid-diameter oak stands), at least 50% of the stems within each type of oak stand were within the desired dbh class (Figure 4). In one respect this type of oak stand was more like the small-diameter type of oak stand because the mid-diameter stands actually had nearly half of their stems in the small-diameter class. In another respect, the mid-diameter type of oak stand was quite different from the small-diameter oak type of oak stand in that the former had 267% more of its stems in the 35.0- to 49.9-cm dbh class than did the latter type of stand (40.3% versus 15.3%). Since most Oregon oak stands in the Willamette Valley originated after 1850 (Thilenius 1968), it is possible that insufficient time has elapsed from then to now for some trees to have grown large enough to be included in my mid-diameter category.

Figure 4. Diameter distributions (cm dbh) for 10 types of stands in the mid-Willamette Valley, Oregon.

Figure 4.

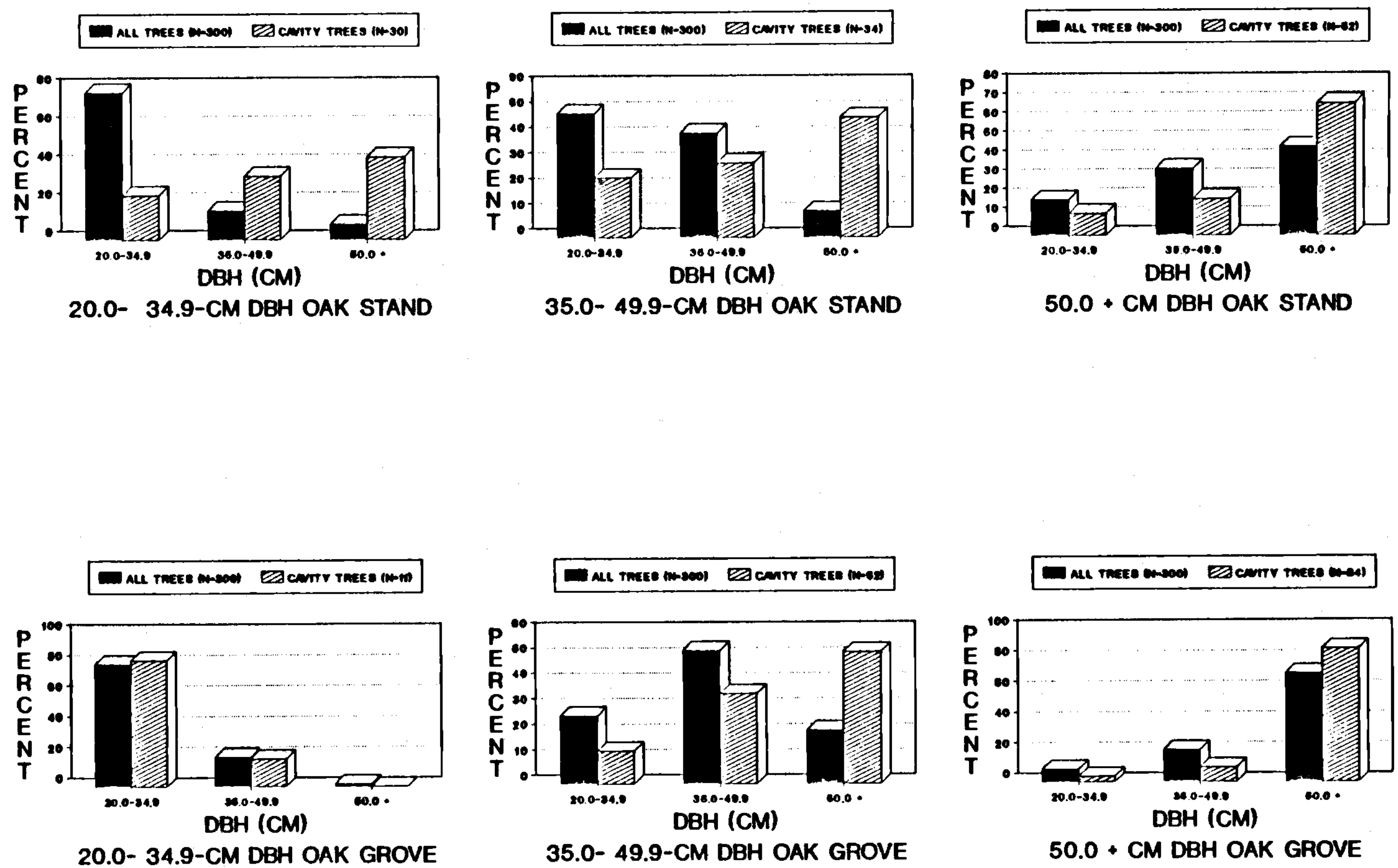
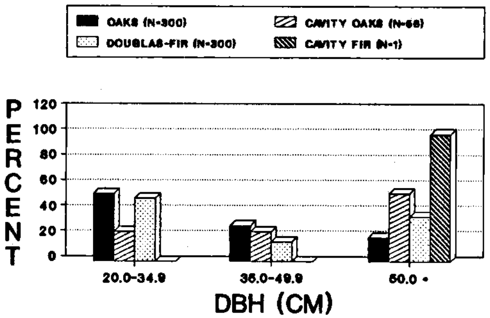
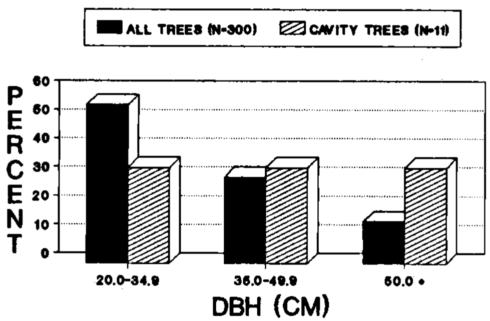

ALL TREES (N=300)
CAVITY TREES (N=30)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
20.0- 34.9-CM DBH OAK STAND
ALL TREES (N=300)
CAVITY TREES (N=34)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
35.0- 49.9-CM DBH OAK STAND
ALL TREES (N=300)
CAVITY TREES (N=62)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
50.0 + CM DBH OAK STAND
ALL TREES (N=300)
CAVITY TREES (N=11)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
20.0- 34.9-CM DBH OAK GROVE
ALL TREES (N=300)
CAVITY TREES (N=62)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
35.0- 49.9-CM DBH OAK GROVE
ALL TREES (N=300)
CAVITY TREES (N=84)
PERCENT
20.0-34.9
35.0-49.9
50.0 +
DBH (CM)
50.0 + CM DBH OAK GROVE

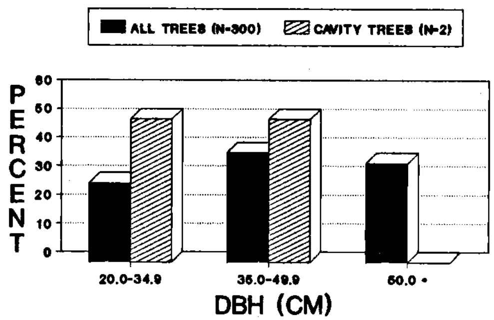
Figure 4. Continued.



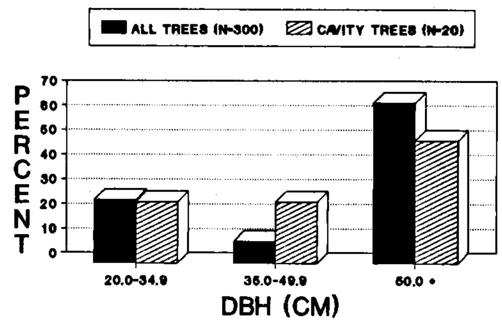
35.0- 49.9-CM DBH MIXED STAND



20.0- 34.9-CM DBH D-FIR STAND



35.0- 49.9-CM DBH D-FIR STAND



50.0 + CM DBH D-FIR STAND

Cavity Correction Factor

Three comparisons were used to develop a cavity correction factor (see Table 2):

1) Holes incorrectly classified from the ground as cavities. All of the hole openings were ≥ 2.5 cm in diameter, but 19.5% of them were < 7.5 cm deep and thus did not satisfy the definition of cavities. Oak of all diameter classes had holes that when viewed from the ground were misclassified as cavities;

2) Cavities that could be seen only by climbing trees (18.2%); this result is consistent with Gysel's (1961) finding that 20% of the cavities in Michigan oak-hickory (Quercus spp, Carya glabra) and maple-beech (Acer saccharinum, Fagus grandifolia) stands could be found only through climbing trees.

Climbing trees can enhance some views that from the ground are obstructed by complex branching, dense vegetation or unfavorable terrain. On the other hand, some cavities that are plainly visible from the ground (e.g., those on distal ends of long, horizontally-inclined branches) are not evident when climbing a bole.

3) Cavities that were plainly visible but were overlooked during the ground search (1.3%). While 1 cavity was plainly visible but was overlooked, other

Table 2. Cavities/tree (SE) among 3 diameter classes of Oregon white oak and Douglas-fir in the mid-Willamette Valley, Oregon, based on classifications of holes into 5 categories used to construct a cavity correction factor.

Diameter Class (cm dbh)	Species	Holes Classified correctly	Holes Classified incorrectly	Cavities Seen only from tree	Cavities Seen only from ground	Cavities Overlooked from ground	Correction Factor
20.0-34.9							
(11)[1]	Oregon white oak (<u>Quercus</u> <u>garryana</u>)	0.91 (0.19)	0.36 (0.43)	----------	----------	----------	0.91
(0)	Douglas-fir (<u>Pseudotsuga</u> <u>menziesii</u>)	----------	----------	----------	----------	----------	
35.0-49.9							
(8)	Oregon white oak	0.25 (0.16)	0.75 (0.53)	0.50 (0.19)	----------	----------	0.38
(0)	Douglas-fir	----------	----------	----------	----------	----------	
50.0 +							
(21)	Oregon white oak	0.48 (0.16)	0.23 (0.11)	0.47 (0.16)	1.19 (0.47)	0.05 (0.05)	0.98
(55)	Douglas-fir	1.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	1.00
Totals	Oregon white oak						0.96
	Douglas-fir						1.00

[1]Sample sizes of trees within each diameter class are shown in parentheses beneath the diameter class description.

cavities may not have been visible due to poison oak (<u>Rhus diversiloba</u>) liana. Poison oak liana obscured > 33% of the boles of 14 Oregon white oak (2.8% of the 500 trees) surveyed in the summer. Seven of these oaks were 35.0- to 50-cm dbh. One large oak with liana coverage was included in the cavity correction factor but this single tree was probably insufficient to account for the decreased visibility from liana coverage.

The correction factor consisted of 2 parts: a) corrected classifications of holes originally observed during ground surveys, and b) classifications of holes corrected after climbing trees. The correction factor (f) and revised estimates of cavity abundance (E_r) were computed using the following formulae:

$f = a + b$, and $E_r = (f) \times (Di)$, where:

$a = (x + xy)$, and $b = (a)(z)$, and

$x = 0.805$ (the proportion of holes correctly classified as cavities; $1.0 - 0.195 = 0.805$);

$y = 0.013$ (the proportion of cavities originally overlooked from the ground);

$z = 0.182$ (the proportion of cavities that could be seen only by climbing a tree or inspecting a felled tree), and

D_i = initial cavity density estimate from ground survey.

The correction factor (f) for Oregon white oak was determined to be 0.963 (96.3%). Multiplying ground counts of oak cavities by 0.963 provided estimates that were corrected for holes that were not truly cavities, cavities that were overlooked during ground observations, and cavities that could be seen only by climbing trees.

No cavities were found in 55 Douglas-fir (x = 82.4 cm dbh, SE = 21.3) either before or after felling, thus original cavity counts in Douglas-fir stands were retained. I later discovered that more than half (56%, 19/34) of the cavities in the Douglas-fir stands were in bigleaf maple. The substantial contribution from bigleaf maple to the cavity resource in some Douglas-fir stands was not anticipated so a correction factor for bigleaf maple was not developed.

As mixed stands provided indication of how cavity resources changed as Oregon white oak succumbed to Douglas-fir dominance, Oregon oak and Douglas-fir were sampled equally (n = 300 Oregon oak and n = 300 Douglas-fir) in mixed-species stands and were the only species sampled in the mixed stands. The cavity correction factor for mixed stands (0.982) was based on the averages of the oak and Douglas-fir correction factors (0.963 + 1.00/2) = 0.982.

Tree-level results

Cavities per tree.-- Oregon white oak had more cavities/tree (0.33, SE=0.02, $P < 0.001$, Figure 5) than bigleaf maple (0.22, SE=0.07) and Douglas-fir (0.01, SE=0.01); these 3 species accounted for 98.4% of the cavities. Cavities/tree increased with increasing dbh ($r=0.53$ and $r=0.49$, respectively, $P < 0.0001$) of Oregon oaks and bigleaf maples (Table 3). Douglas-fir between 35.0 and 49.9 cm dbh had no cavities, but ≥ 50.0-cm dbh Douglas-fir had significantly more cavities/tree than did 20.0- to 34.9-cm dbh Douglas-fir ($P < 0.015$).

Open-form oak had more cavities/tree ($\bar{x}=0.71$, SE=0.07) than closed-form oak ($\bar{x}=0.16$, SE=0.02) ($P < 0.0001$). Large-diameter open-form oak only comprised 24% of the oak-cavity trees, but produced 61% of the oak cavities (Figure 6).

Cavities per snag.-- Oak snags averaged 0.46 cavities/snag (SE = 0.2). The mean diameter of oak snags ($n=97$) was 34.9 cm dbh (SE = 3.0). Douglas-fir snags averaged 0.53 cavities/snag (SE = 0.6), which was more

Figure 5. Cavities/tree by dbh class for Oregon white oak and Douglas-fir in the mid-Willamette Valley, Oregon, based on $\underline{n}$ = 15 Douglas-fir and 689 Oregon white oak cavities and $\underline{n}$ = 1108 Douglas-fir and 2072 Oregon white oak trees.

Figure 5.

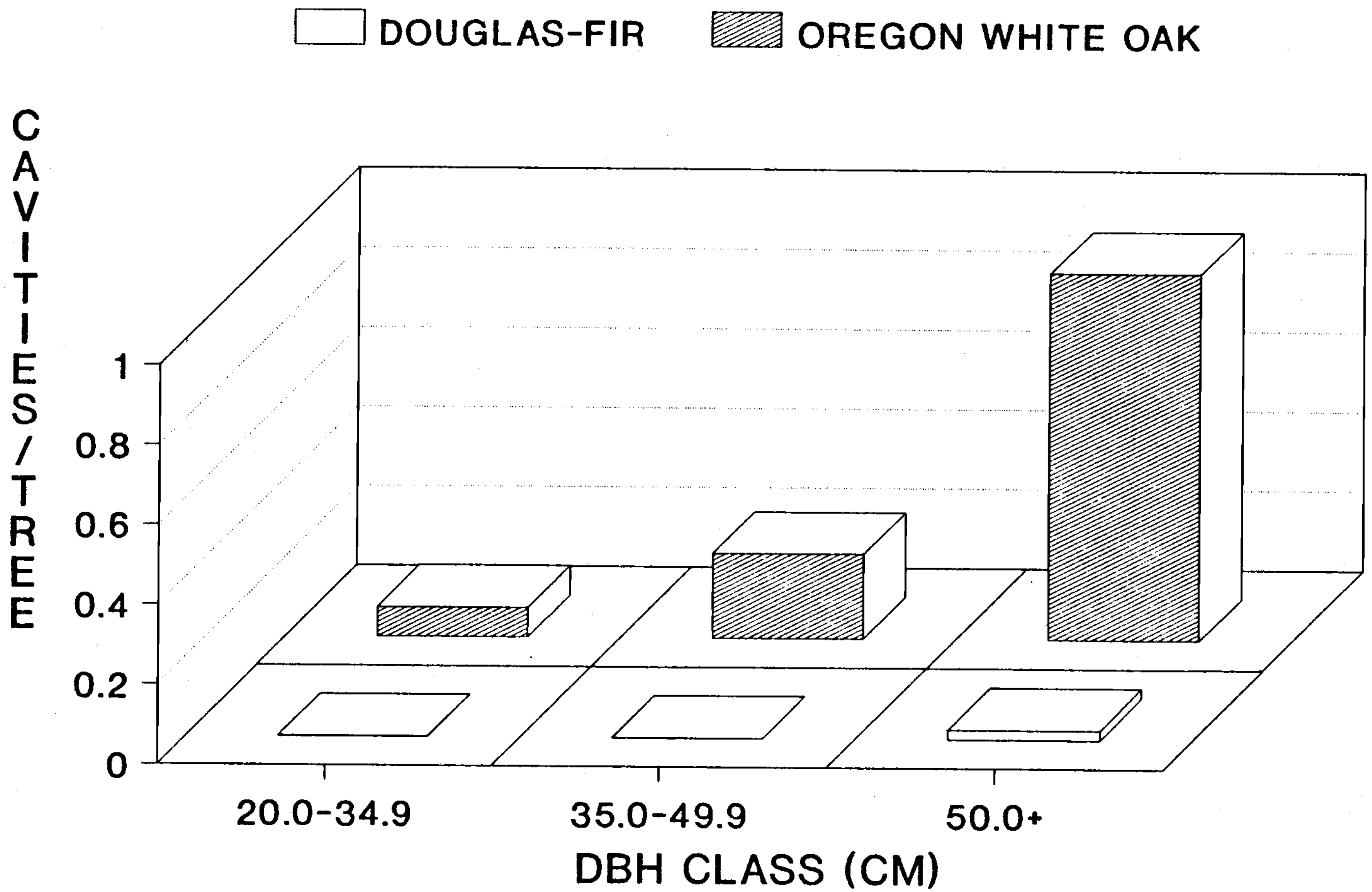

DOUGLAS-FIR
OREGON WHITE OAK
CAVITIES/TREE
1
0.8
0.6
0.4
0.2
0
20.0-34.9
35.0-49.9
50.0+
DBH CLASS (CM)

Table 3. Cavities/tree (range) by dbh class and species in the mid-Willamette Valley, Oregon.

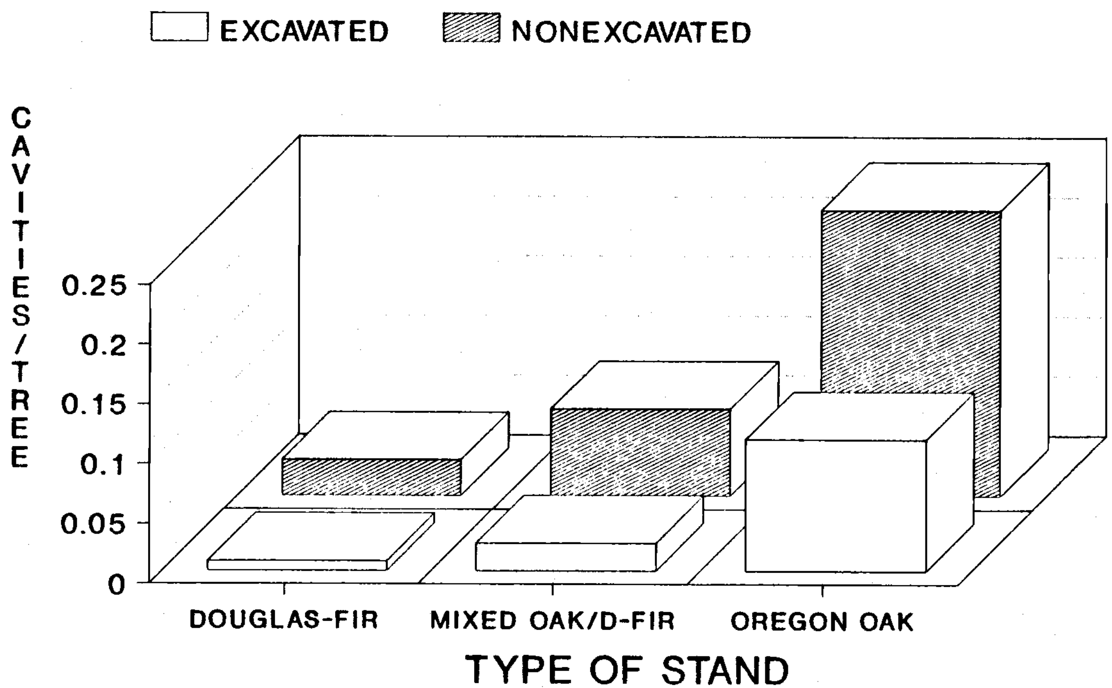
	dbh class (cm)											
	20.0-34.9				35.0-49.9				50.0 +			
Tree Species	x[*]	n	E	N	x	n	E	N	x	n	E	N
Oregon white oak	0.07 A	964	20	51	0.22 B	569	44	77	0.92 C	510	147	350
(Quercus garryana)	(0-5)				(0-5)				(0-15)			
Douglas-fir	0.01 A	432	3	2	0.00 B	265	0	0	0.02 C	411	3	7
(Pseudotsuga menziesii)	(0-3)				(0)				(0-2)			
bigleaf maple	0.08 A	53	2	2	0.31 B	26	2	6	1.00 C	7	3	7
(Acer macrophyllum)	(0-1)				(0-2)				(0-4)			
Other[+]	0.50	12	0	6	0.00	0	0	0	1.50	4	0	6
	(0-5)				(0)				(0-6)			
Totals	0.06 A	1472	25	61	0.15 B	865	83	46	0.54 C	963	150	370
	(0-5)				(0-5)				(0-15)			

[*]x=mean cavities/tree, n=sample size, E=excavated cavities, N=nonexcavated cavities; means among dbh classes of a species and totals denoted by different letters differ (Kruskal-Wallis test, $P < 0.001$ for Oregon white oak, $P < 0.0152$ for Douglas-fir, $P < 0.0165$ for bigleaf maple, $P < 0.001$ for totals).

[+]other species were Oregon ash (Fraxinus latifolia) and mazzard cherry (Prunus avium).

Figure 6. Cavities by origin in Oregon white oak, Douglas-fir and mixed Oregon white oak/Douglas-fir stands in the mid-Willamette Valley, Oregon.

Figure 6.



EXCAVATED
NONEXCAVATED
CAVITIES/TREE
0.25
0.2
0.15
0.1
0.05
0
DOUGLAS-FIR
MIXED OAK/D-FIR
OREGON OAK
TYPE OF STAND

than 6 times the highest value of cavities/live Douglas-fir tree. The mean diameter of Douglas-fir snags (n=13) was 42.6 cm dbh (SE=10.2).

Excavated cavities.-- Excavated cavities comprised 30% of the cavities among the 10 types of stands; 95% of the excavated cavities had 2.5- to 7.4-cm entrances (83.6% from 2.5-4.9 cm, 11.4% from 5.0-7.4 cm). Dead limbs and dead percentage were both significant ($P < 0.0001$) predictors of excavated cavities in Douglas-fir trees ($R^2 = 0.80$, 0.91, respectively) and dead percentage was also a useful predictor of Douglas-fir cavity diameters ($R^2 = 0.91$). Most of the aboveground volume of managed Douglas-fir is in the bole, and the branches are generally too small for excavation. High estimates of dead percentages for Douglas-fir reflect highly diseased boles with could favor cavity-excavtors. All excavated coniferous cavities (5/5, 36% of all coniferous cavities) occurred in only 2 snags (31.1 and 53.5 cm dbh).

Disease and dbh were the most important predictors of the presence of excavated cavities in Oregon white oak ($P < 0.0001$ for disease and dbh); other workers (e.g., Carey 1983, Conner et al. 1976, Harestad and Keisker 1989, Waters et al. 1990) have documented similar patterns (Table 1). Carey (1983) reported that the number of dead branches was not a good indicator of cavities in an Eastern mixed-species deciduous forest. I found a similar pattern (P = 0.47, n = 282) in Oregon white oak stands. Sedgwick and Knopf (1986), however, found that dead limbs (or sections of limbs that were dead) > 10 cm in diameter in apparently healthy plains cottonwoods (Populus sargentii) provided nesting substrate for primary cavity nesters. Trees > 55 cm dbh were more important as cavity substrate than smaller trees because dead limb length gradually increased from 0.04 m for the smallest trees to 8 m for the largest cottonwoods (Sedgwick and Knopf 1986). In my study, estimates of dead percentage were strongly associated with the number of dead limbs (P < 0.002), but not with excavated cavities (P > 0.6): it is likely that more dead limbs were available to woodpeckers than could possibly be used.

The percentage of excavated cavities in oak snags (29.5%) was similar to the percentage in living oak trees (30.0%). Sedgwick and Knopf (1986) and Carey (1983) suggested that in some unmanaged hardwood stands the dead and dying portions of live trees are probably more important to cavity-nesting birds than are snags. Nine of 14 excavator species in the mid-Willamette Valley that use Oregon white oak, Douglas-fir or mixed oak/Douglas-fir stands are classified as weak excavators (Appendix 1) and thus rely on highly decayed wood as excavation substrate. Eleven woodpecker species typically excavate 2.5- to 5.0-cm diameter cavities (7 of the 9 weak excavators and 4 of 5 strong excavators (Appendix 1). Based on entrance diameters of excavated cavities, these 11 species (78.6% of the excavators) probably created > 80% of the excavated cavities (Appendix 1).

Northern flickers (Colaptes auratus) were probably responsible for most of the 5.0- to 7.4-cm excavated cavities (11.8% of the total excavated cavities) (Brown 1985). Lewis' woodpeckers (Melanerpes lewis) commonly use existing cavities (Bull 1986, Galen 1989), excavate only in extremely decayed wood, and probably produced a small proportion of 5.0- to 7.4-cm cavities. Pileated woodpeckers (Dryocopus pileatus), the largest woodpecker in this region, undoubtedly produced all excavated cavities $\geq$ 7.5 cm (5.4% of the total) (Brown 1985).

Nonexcavated Cavities.-- Presence of disease, dbh, and and an open-form predicted occurrence of nonexcavated oak cavities ($P < 0.0001$ for disease and dbh, $P < 0.0388$ for tree form, maximum likelihood ratio = 1). The predilection for open-form oak to have more nonexcavated cavities than closed-form oak has also been observed by Waters (1988) in California savannas. In the savannas, nonexcavated cavities occurred mostly in the heavily bifurcated interior live oak (Quercus wislizenii) (which were open-grown and architecturally similar to open-form Oregon white oak), while excavated cavities were generally in blue oak (Quercus lobata) (which were closed-form and structurally resembled closed-form Oregon white oak).

Disease and dbh predicted presence of nonexcavated cavities in Douglas-fir and bigleaf maple ($P < 0.0001$). While nonexcavated cavities are uncommon in coniferous forests (Bull 1986), 60% of the Douglas-fir cavities were nonexcavated. Nonexcavated cavities comprised 70% of all cavities and were more abundant than excavated cavities among all types of stands ($P < 0.0001$, Wilcoxon Rank Sums); 81% of the nonexcavated cavities had 2.5- to 7.4-cm diameter entrances (61.6% from 2.5-4.9 cm, 19.6% from 5.0-7.4 cm). This pattern is similar to that observed in a plains cottonwood ecosystem where > 90% of all cavity entrances were 3.0-7.0 cm in diameter (Sedgwick and Knopf 1986).

Properties of trees influencing susceptibility to cavity formation.-- Baumgartner (1939) described the process of the formation of nonexcavated cavities as beginning with damage to the tree (e.g., trunk wounding or limb loss) that facilitates subsequent stub and heartwood decay. When decay is extensive, some birds and mammals (including squirrels) may remove rotted wood from decay pockets, and squirrels may maintain the original wound through gnawing. Woodpeckers, on the other hand, may excavate holes in decay pockets that are yet too sound to allow other kinds of animals to simply remove decomposed wood fibers in order to enlarge openings.

While events that favor cavity development are apparently stochastic (Carey 1983), factors such as branching architecture, patterns of decay, and growth habits can influence susceptibilities of trees to cavity-forming processes. For example, large-diameter, deliquescent oaks have deep crowns (Thilenius 1968) and long, massive branches that may parallel the ground. Gravity, wind, snow, or declining vigor can cause large branches to break (Smith 1986), and under such circumstances the architecture of these oaks increases their likelihood of broken limbs and boles. Heartrot fungi (e.g., Basidiomycetes), required by woodpeckers for excavating cavities (Conner 1978, Harestad and Keisker 1989), typically invade trees through dead branch stubs, and their windborn spores may more readily colonize large, exposed wounds (Boyce 1961). Thus, large-diameter open-form oaks that become damaged can present increased surface areas favorable to fungal infections that produce cavities.

Conversely, closed-form oak have 1 main bole and smaller, more vertical branchings than their open-form counterparts. The closed-form structure may reduce limb loss and the chance of infection and development of cavities. Similarly, managed Doulgas-fir probably have few cavities in part because they typically have relatively small, pliable branches that probably heal quickly when broken (Boyce 1961).

Other differences in decay processes between deciduous and coniferous species following successful infection (Peace 1962, Harestad and Keisker 1989) may contribute to the disparities in cavity characteristics between Oregon white oak and Douglas-fir. For example, decay in decidouous species begins in the heartwood (inner wood), and the heartwood of Oregon white oak is classified as highly resistant to decay (USDA 1988). But if heartrot infection does degrade the heartwood of deciduous species, the sapwood continues to provide structural support for the heartwood cavity. Thus, hardwoods produce cavities that tend to be more durable than softwood cavities (Waters et al. 1990).

Decay in conifers, on the other hand, is initiated in the sapwood (outer wood) and proceeds to the heartwood which in Douglas-fir is extremely resistant to wood-rotting fungi (Clark 1957). Consequently, when the heartwood is sufficiently decayed for cavities to develop, the remaining sapwood is usually so highly degraded that it provides only minimal structural reinforcement for a heartwood cavity.

Alternately, cavities are sometimes excavated in coniferous sapwood. Bull (1986) noted that some ponderosa pine (*Pinus ponderosa*) have sapwood thick enough that woodpeckers excavate their entire cavity in the sapwood and avoid heartwood. Nelson (1989) stated that decay in Douglas-firs > 94 cm dbh may produce durable sapwood cavities because of the greater thickness of the sapwood relative to the heartwood.

Differences in site quality throughout the study area could affect growth habits and thus influence the propensities of Oregon white oak and Douglas-fir to form cavities, but I did not address considerations of site quality. Nonetheless, some generalizations from the literature regarding growth habits of these 2 species may be useful in understanding their cavity dynamics. For example, mature Oregon white oak are not especially tall (they rarely exceed 30 m in height) or large (they typically grow to a maximum of 60.0- to 90.0-cm dbh) (Silen 1958, Fowells 1965, Miller and Lamb 1985), but the complex branching architecture of open-form individuals fosters dense concentrations of cavities: 7 open-form oaks in this study each had > 10 cavities/tree.

Once cavities have formed in oak, and barring cutting, windthrow or loss of the tree due to excessive rot, the tree, and hence the cavity, may persist for extended periods. Oregon oak are generally expected to live 300-500 years (Silen 1958, Fowells 1965, Minore 1979, Miller and Lamb 1985). Open-form trees > 90 cm dbh were probably > 300 years old (Stein, in press, Thilenius 1968). These large oaks were at or had surpassed their upper limit of average diameter growth; old oaks that were declining in vigor could be stressed and thus more susceptible to cavity-forming decay processes than old, healthy oaks.

Unmanaged Douglas-fir can grow higher (60 m high), larger (> 4 m dbh) and live longer (750-1200 years) (Fowells 1965, Franklin 1979) than Oregon white oak. A remnant old-growth stand of Douglas-fir in my study area produced > 50% of the cavities found among the 9 Douglas-fir stands inspected in this study, but most of the Douglas-fir stands in the study area are managed stands. The 3 thinned stands of Douglas-fir were characterized by erect, sparsely-branched trees that had no cavities. Neither were any cavities seen in a stand of 120-year-old, unthinned and apparently healthy Douglas-fir in the study area with average dbh = 85.8 cm (SE=24.1, n=104).

In addition to the role of obvious morphological influences on development of cavities, Highley and Kirk (1979) suggested that genetic differences in susceptibiilty to heartrot exist within species, so both genetic features and environmental variables may predispose some individuals to heartrot.

Stand-level results

Cavity abundance among stand types.-- The Oregon white oak, Douglas-fir and mixed oak/Douglas-fir types of stands apparently provide cavities for small-bodied animals, such as chickadees (*Parus* spp.), nuthatches (*Sitta* spp.), house finches (*Carpodacus mexicanus*), northern flying squirrels (*Glaucomys sabrinus*), and deer mice (*Peromyscus maniculatus*) (Appendix 1). Only 1 excavated cavity larger than 10 cm was found, while 60 nonexcavated cavities (11.6% of the nonexcavated cavities) were ≥ 10 cm in diameter. Cavities suitable for larger species such as Virginia opossum (Didelphus virginianus) (McComb and Noble 1980) were found only in large-diameter remnant open-form Oregon white oaks.

Cavity densities were greater in the oak (excluding small-diameter patches) than in the mixed and Douglas-fir types of stands ($P < 0.01$, Table 4, Figure 7), but cavity densities are highly influenced by the presence of large open-form trees within the stands. Hence this discussion is restricted to the 30 sampled stands. Inferences should not be made to other stands with different diameter distributions and frequencies of open-form trees.

Remnant open-form oak ≥ 50 cm dbh (the most cavity-prone type of oak) comprised only 1.3% of the stems in the small-diameter patches (Figure 4), and this lack of large, remnant oak undoubtedly reduced cavity abundance in the small-diameter patches. Conversely, large, remnant open-form oak constituted > 8% of the stems in all other types of oak stands. The relatively high proportions of remnant trees among these 5 types of stands probably helped equalize their cavity abundances. Mixed Oregon white oak/Douglas-fir stands had fewer cavities ($P \leq 0.01$, Table 4) than the oak and the Douglas-fir stands.

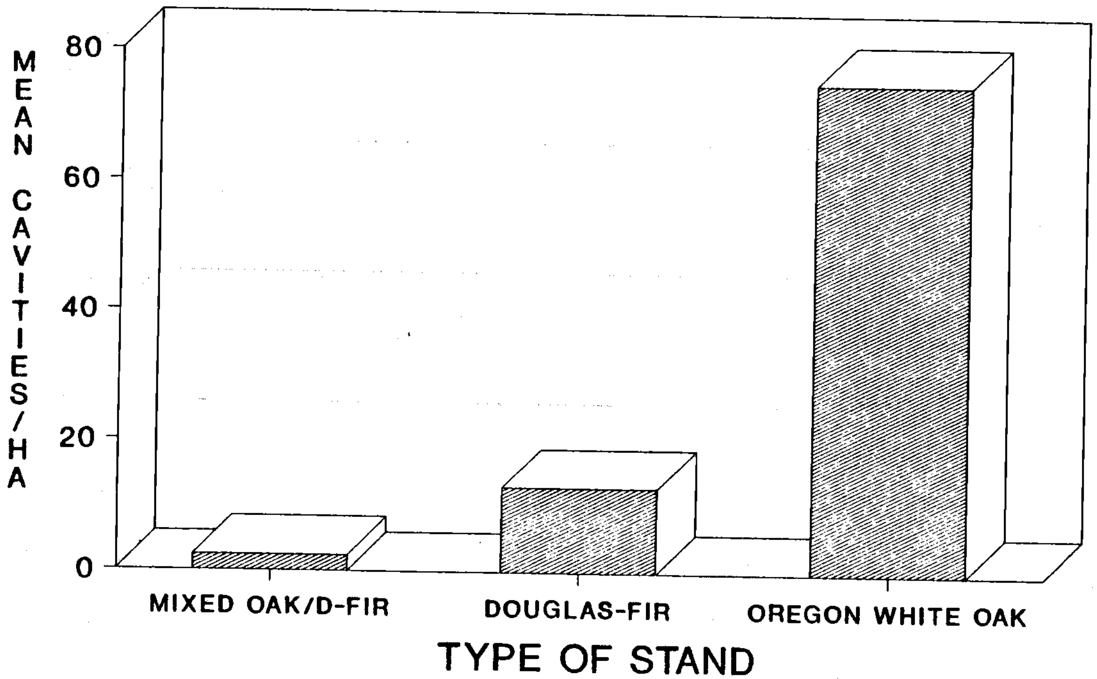
Table 4. Densities of cavities (≥ 2.5 cm entrance diameter) in 10 types of stands in the mid-Willamette Valley, Oregon ($\underline{n}$ = 30).

Type of Stand	Density* (cavities/ha)	Range
Oregon white oak grove ≤ 4 ha		
20.0-34.9 cm dbh	4.5A	0.0-8.2
35.0-49.9 cm dbh	22.9B	0.8-51.6
50.0 + cm dbh	36.4B	0.7-104.4
Oregon white oak stand > 4 ha		
20.0-34.9 cm dbh	8.6B	0.8-20.9
35.0-49.9 cm dbh	16.1B	2.4-34.4
50.0 + cm dbh	13.6B	3.5-39.5
Douglas-fir stand > 4 ha		
20.0-34.9 cm dbh	3.3A	1.6-4.9
35.0-49.9 cm dbh	2.1A	1.4-2.8
50.0 + cm dbh	3.9A	0.3-6.7
Mixed Oregon oak/Douglas-fir stand > 4 ha		
35.0-49.9 cm dbh	2.9A	0.4-6.9

*Densities with different letters differ (Kruskal-Wallis test, $P < 0.01$).

Figure 7. Densities of cavities (cavities/ha, $P < 0.01$) for Oregon white oak, Douglas-fir and mixed Douglas-fir/Oregon white oak stands in the mid-Willamette Valley, Oregon.

Figure 7.


MEAN CAVITIES/HA
80
60
40
20
0
MIXED OAK/D-FIR
DOUGLAS-FIR
OREGON WHITE OAK
TYPE OF STAND

Predicting availability of cavities among stands for cavity-nesters. While estimating cavity densities among various types of stands provides needed information, efforts to effectively manage the stands may be ineffective without knowledge of how vertebrate wildlife species might use cavities in these stands. But delineating how cavity resources are partitioned within and among habitats and vertebrate species is difficult without long-term, species-specific studies (Carey 1983). Without such studies any predictions regarding use of cavities by species must be made cautiously and remain tentative.

For example, some woodpeckers typically have several roost cavities and frequently shift to different roost cavities throughout the year (Hoyt 1957, Stickel 1964). White-breasted nuthatches (Sitta carolinensis) commonly use more than one cavity in the mid-Willamette Valley, and this behavior may be governed by efforts to avoid predation (Conner et al. 1983) and/or obtain a suitable microclimate (Gumtow-Farrior, unpub. data). Conner et al. (1983) has stated that adult woodpeckers need at least 4 cavities throughout the year (one for nesting and 3 for roosting) and that young of the year also require roost cavities for their first winter. Young European nuthatches

(Sitta europa) typically remain in their parent's territory for up to a year after fledging (Matthijsen and Dhondt 1983), thus habitat-quality assessments for cavity-using species should probably include numerous cavities for each individual and for each breeding pair and their offspring. Not all cavities capable of being used by vertebrates are used. For example, parasite levels in a frequently used nest cavity can build to intolerable levels, or cavities may simply be positioned at improper heights relative to use by a species (Bull 1986).

Given these constraints, I will make generalized inferences about potential roost or nest-cavity availability for species in the 30 stands that I sampled based on: a) documented habitat associations; b) recorded use of excavated or nonexcavated cavities by species; c) no consideration of competition for cavities among species; d) that each pair uses 4 cavities/year for roosting and nesting (Conner et al. 1983, Nietro et al. 1985), and e) assumptions that cavities with entrances large enough to admit a species are suitable for use by that species. Raphael and White (1984) reported a high correlation ($r = 0.73$) between cavity entrance diameter and internal cavity size (i.e., internal diameter and depth) for 526 cavities (15% nonexcavated, 85% excavated).

Gysel (1961) found that the amount of vertical cavity development was approximately proportional to the inner diameter in nonexcavated cavities. Estimates of the maximum percentages of pairs of selected primary and secondary cavity-nesting species potentially supported by the cavity resources among the 30 stands that I sampled are shown in Tables 5 and 6, respectively. Given that most woodpecker species create new nest cavities each year and use existing cavities only for roosting (Lewis' woodpecker is an exception, see Galen 1989), it is possible to assess only roost cavity availability for woodpeckers.

Densities of cavities reported in Tables 5 and 6 generally support the observations that most habitats with large-diameter Oregon white oak would probably have more than adequate cavity resources to support maximum population levels of most cavity-using species and some Douglas-fir habitats (with their lower cavity resources) could have significantly lower population levels of cavity-users. However, stands with different representations of large and/or open-form trees would have different cavity availability.

The Oregon white oak stands that I sampled provided cavities with entrances 2.5-4.9 cm diameter in excess of that needed to support maximum roosting densities of most

Table 5. Maximum percentages of roosting pairs of woodpeckers potentially supported among 10 types of stands ($n=30$) in the mid-Willamette Valley, Oregon, as determined by densities of excavated cavities with appropriate entry diameters.

	Bird Density[1] (D) pairs/ha		Cavities excavated/ pair/year[2]	Cavities used[3]	Cavities/ha needed for D[4]		Maximum percentage by type of stand and dbh class (cm)					
							Oregon white oak ≤ 4 ha			Oregon white oak > 4 ha		
	oak	D-fir			oak	D-fir	20.0-34.9	35.0-49.9	50.0+	20.0-34.9	35.0-49.9	50.0+
Cavities/ha (2.5- to 4.9-cm)							4.8	38.5	72.8	17.1	22.3	8.3
Species												
downy woodpecker (*Picoides pubescens*)	0.1	0.05	2	4	0.8	0.4	600	4,813	9,100	2,138	2,788	1038
hairy woodpecker (*Picoides villosus*)	0.20	0.40	3	4	2.4	4.8	200	1,604	3,033	713	929	346
northern flicker (*Colaptes auratus*)	0.10	0.30	1	4	0.4	1.2	1,200	9,625	18,200	4,275	5,575	2075
acorn woodpecker (*Melanerpes formicivorus*)	0.09	0.09	5	4	1.8	1.8	267	2,139	4,044	950	1,239	461
Cavities/ha (5.0- to 7.4-cm)							4.8	0.8	7.2	3.5	2.4	5.3
Species												
Lewis' woodpecker (*Melanerpes lewis*)	0.30		1	4	1.2		400	67	600	292	200	442
pileated woodpecker (*Dryocopus pileatus*)	0.02	0.01	3	4	0.24	0.12	2,000	333	3,000	1,458	1,000	2208

Table 5. Continued.

	Bird Density (D) pairs/ha		Cavities excavated/ pair/year (C)	Cavities used	Cavities/ha needed for D		Maximum percentage by type of stand and dbh class (cm)			
							Douglas-fir stands > 4 ha			Mixed Oregon white oak/Douglas-fir > 4 ha
	oak	D-fir			oak	D-fir	20.0-34.9	35.0-49.9	50.0+	35.0-49.9
Cavities/ha (2.5- to 4.9-cm)							4.9	1.4	1.9	2.8
Species										
downy woodpecker (Picoides pubescens)	0.10	0.05	2	4	0.8	0.4	1225	350	475	700
hairy woodpecker (Picoides villosus)	0.20	0.40	3	4	2.4	4.8	102	29	40	58
northern flicker (Colaptes auratus)	0.10	0.30	1	4	0.4	1.2	408	117	158	233
acorn woodpecker (Melanerpes formicivorus)	0.10		5	4	1.8	1.8				156
Cavities/ha (5.0- to 7.4-cm)							0	0	0.3	1.5
Species										
Lewis' woodpecker (Melanerpes lewis)	0.30		1	4	1.2		0	0	25	125
pileated woodpecker (Dryocopus pileatus)	0.02	0.01	3	4	0.24	0.12	0	0	250	1,250

Table 5. Continued.

---

[1]Maximum densities are derived from Anderson (1970) and Nietro et al. (1985); [2]estimates of cavities excavated/pair/year from Nietro et al. (1985); [3]estimates of cavities used/pair from Nietro et al. (1985).

Maximum percentages obtained by using the formula: (cavities/ha)/(4), where (4)=(1)(2)(3).

Table 6. Maximum percentages of pairs of facultative and secondary-nesting species potentially supported by the cavity resources among 10 types of stands (n=30) in the mid-Willamette Valley, Oregon.

	Bird Density[1] (D) pairs/ha	Cavities excavated/ pair/year[2]	Cavities used[3]/ pair	Maximum percentage by type of stand and dbh class (cm)					
				Oregon white oak grove ≤ 4 ha			Oregon white oak stand > 4 ha		
				20.0-34.9	35.0-49.9	50.0 +	20.0-34.9	35.0-49.9	50.0 +
Excavated Cavities/ha (2.5-4.9 cm)				4.8	38.5	72.8	17.1	22.3	8.3
Facultative Excavator Species									
red-breasted nuthatch (Sitta canadensis)	0.10	1	4	1200	9,625	18,200	4,275	5,575	2,500
Excavated and nonexcavated cavities/ha (2.5-4.9 cm)				13.0	90.1	177.2	38.0	56.7	47.8
Species									
white-breasted nuthatch (Sitta carolinensis)	0.20	1	4	1,625	11,263	22,150	4,750	7,088	5,975
black-capped chickadee (Parus atricapillus)	0.50	1	4	650	4,505	8,860	1,900	2,835	2,390
Nonexcavated cavities/ha (2.5-4.9 cm)				8.2	51.6	104.4	20.9	34.4	59.5
Nonexcavators									
brown creeper (Certhia americana)	0.15	0	4	1,367	8,600	17,400	3,483	5,733	6,583

Table 6. Continued.

	Bird Density pairs/ha	Cavities excavated/ pair/year	Cavities used/ pair	Maximum percentage by type of stand and dbh class (cm): Oregon white oak grove ≤ 4 ha 20.0-34.9	35.0-49.9	50.0+	Oregon white oak stand > 4 ha 20.0-34.9	35.0-49.9	50.0+
western bluebird (<u>Sialia</u> <u>mexicana</u>)	0.25	0	4	820	5,160	10,440	2,090	3,440	3,950
Bewicks's wren (<u>Thryomanes</u> <u>bewickii</u>)	0.20	0	4	1,025	6,450	13,050	2,613	4,300	4,938
winter wren (<u>Troglodytes</u> <u>troglodytes</u>)	0.05	0	4	4,100	25,800	52,200	10,450	17,200	19,750
house finch (<u>Carpodacus</u> <u>mexicanus</u>)	0.40	0	4	513	3,225	6,525	1,306	2,150	2,469
Nonexcavated 5.0 + cm cavities				0.0	23.6	34.3	10.0	21.3	14.7
great horned owl (<u>Bubo</u> <u>virginianus</u>)	0.01	0	4	0	59,000	85,750	25,000	53,250	36,750

Table 6. Continued.

	Bird Density pairs/ha	Cavities excavated/ pair/year	Cavities used/ pair	Maximum percentage by type of stand and dbh class (cm): Douglas-fir stands > 4 ha, 20.0-34.9	Douglas-fir stands > 4 ha, 35.0-49.9	Douglas-fir stands > 4 ha, 50.0 +	Mixed Oregon oak/Douglas-fir > 4 ha, 35.0-49.9
Excavated Cavities/ha (2.5-4.9 cm)				4.9	1.4	1.9	2.8
Facultative Excavator Species							
red-breasted nuthatch	0.10	1	4	1,225	350	475	700
(*Sitta canadensis*)							
Excavated and nonexcavated cavities/ha (2.5-4.9 cm)				4.9	4.2	8.3	9.7
Species							
white-breasted nuthatch	0.20	1	4	613	525	1,038	1,213
(*Sitta carolinensis*)							
black-capped chickadee	0.50	1	4	245	210	415	485
(*Parus atricapillus*)							
Nonexcavated cavities/ha (2.5-4.9 cm)				0	2.8	6.4	6.9
Nonexcavators							
brown creeper	0.15	0	4	0	467	1,067	1,150
(*Certhia americana*)							

Table 6. Continued.

	Bird Density pairs/ha	Cavities excavated/ pairs/year	Cavities used/ pair	Maximum percentage by type of stand and dbh class (cm) — Douglas-fir stands > 4 ha: 20.0-34.9	35.0-49.9	50.0+	Mixed Oregon oak/Douglas-fir stand > 4 ha: 35.0-49.9
western bluebird* (Sialia mexicana)	0.25	0	4	---	---	---	690
Bewicks's wren* (Thryomanes bewickii)	0.20	0	4	---	---	---	863
winter wren (Troglodytes troglodytes)	0.05	0	4	0	1400	3200	3,450
house finch* (Carpodacus mexicanus)	0.40	0	4	---	---	---	431
Nonexcavated 5.0 + cm cavities				1.6	0.0	11.1	4.4
great horned owl (Bubo virginianus)	0.01	0	4	2500	0	27,750	11,000

[1]Cavities/ha based on total cavities available by appropriate entry diameter and forest type to species that use either nonexcavated, excavated, or both types of cavities as listed in Appendix Maximum densities are derived from Anderson (1970); [2]assumed each pair of facultative excavators excavates 1 cavity/year; [3]assumed 4 cavities/pair are needed to support maximum densiti breeding pairs, as was done by Nietro et al. (1985). Maximum percentages for excavator species obtained by using the formula: (cavities/ha)/(4), where (4) = (1) x (2) x (3); maximum pen for nonexcavator species obtained by using the formula: (cavities/ha)/(4), where (4) = (1) x (3).

*Species not documented as occurring in Douglas-fir forests in western Oregon.

species of woodpeckers; the mid-diameter oak groves provided for only 67% of the maximum densities of Lewis' woodpeckers. All types of oak stands had trees (including large-diameter trees) whose dead branches obviously were more than adequate for excavation of 2.5- to 4.9-cm holes. The results of this study, however, do not indicate whether these cavities occurred predominantly in the few, larger open-formed trees or also occurred in the small, closed-form trees. While oak groves and stands that I sampled could apparently support roosting Lewis' woodpeckers and pileated woodpeckers, their densities would generally be lower than those of smaller woodpecker species.

The mid- and large-diameter Douglas-fir stands that I sampled supported < 40% of the roosting densities for hairy woodpeckers (<u>Picoides villosus</u>) and < 25% of the maximum roosting densities of Lewis' woodpeckers. The small- and mid-diameter Douglas-fir stands did not provide roost cavities for pileated woodpeckers. Mixed Oregon white oak/Douglas-fir stands supported < 60% of the roosting densities of hairy woodpeckers.

Many secondary cavity-using species have more cavities available to them than do similar-sized woodpeckers because the former can use both excavated and nonexcavated cavities (Appendix 1) for nesting and roosting. With only a few exceptions, cavity abundance among the 30 stands appeared to greatly exceed that required to support maximum pair densities of secondary cavity-using species (Table 6): small-diameter Douglas-fir stands did not provide cavities for brown creepers (Certhia americana) or winter wrens (Troglodytes troglodytes) and mid-diameter Douglas-fir stands did not provide cavities for great horned owls (Bubo virginianus).

Cavity abundance and stand dynamics

While tree structure, dbh, and presence of disease are integral components of excavated and nonexcavated cavity-forming processes, neither Oregon oak nor Douglas-fir stands in the mid-Willamette Valley are in successional climax (Franklin and Dyrness 1973). It is therefore important to be able to predict how ecological succession from Oregon white oak to Douglas-fir might alter the cavity resource.

Inferences regarding changes in cavity resources as mid-diameter oak stands are replaced by Douglas-fir can be made based on similarities of oak stems in the 2 types of stands: oaks in the mid-diameter oak stands and the mixed stands had similar proportions of their stems in each of the 3 diameter classes (Figure 4) and open- and closed-growth forms (32% vs. 29% open-form and 68% vs. 71% closed-form in the mid-diameter oak and mixed stands, respectively).

Without fire, grand fir (Abies grandis) will probably be the zonal climax tree species in the Willamette Valley (Fanklin and Dyrness 1973), but there is general agreement that the comparatively fast-growing Douglas-fir will have at least an intermediate role in some Oregon oak communities, especially those on drier sites (Thilenius 1968, Habeck 1961, Sprague and Hansen 1946, Stein, in press). While cessation of prairie fires in the last 150 years has fostered the development of oak forests, in many places it has also permitted young Douglas-fir to develop under established oak canopy and rapidly overtop and kill the oak (Franklin and Dyrness 1973).

The differential competitiveness of Oregon white oak and Douglas-fir is significant when considering cavity resources because Oregon oak is more cavity-prone than Douglas-fir. Oregon oak and Douglas-fir were equally sampled in the mixed stands (n= 300 oak and 300 Douglas-fir), yet Oregon oak in the mixed stands produced 98% of the cavities (Oregon oak = 55/56 cavities in the mixed stands, range = 97-100%). The tendency for hardwoods to produce more cavities than softwoods has also been noted in other studies (Table 1). In California oak woodlands, digger pine (Pinus sabiniana), 9% of the cavity trees, produced 6.9% of the cavities, while blue oak (Quercus douglasii) and valley live oak, 84.8% of the cavity trees, produced 91.7% of the cavities (Waters et al. 1990). Frequencies of cavities $\geq$ 2.5 cm increased in Florida and South Carolina pine types as the hardwood component of the stand increased (McComb et al. 1986).

While cavities/tree did not differ for oaks in the mid-diameter oak stands and the mixed stands ($P > 0.005$, Wilcoxon Rank-sum test), fewer cavities were present in the mixed stands than oak stands of comparable diameters. Presumably, this occurred because of the progressive replacement of Oregon white oak by the less cavity-prone Douglas-fir.

CONCLUSIONS

Oregon white oak, especially large-diameter open-form oak, is a valuable source of cavities in the mid-Willamette Valley, and managed Douglas-fir less so. Cavity densities are lower in Douglas-fir and mixed Oregon oak/Douglas-fir stands than in groves and stands of Oregon white oak. Deliberate management may be necessary to enhance or maintain Oregon oak as a cavity resource in this region.

MANAGEMENT RECOMMENDATIONS

If landowners wish to maintain Oregon white oak on their property and provide opportunity for cavity-using wildlife and/or timber then they should consider these management activities:

1) Retain decayed oak and Douglas-fir as existing or potential cavity resources;

2) As a possible measure for perpetuating Oregon oak as long-term cavity resources in mixed Oregon oak/Douglas-fir stands, initiate small patch cuts (e.g., 0.2- to 0.5-ha cuts) in mixed stands that periodically remove Douglas-fir; this practice would allow either existing open-form oak to persist in the middle of the cut or encourage extant oak to develop an open-form;

3) Manage hardwood stands containing Oregon white oak by establishing hardwood plantations following clearcutting and manipulating sprout stands; heart rot in young, regenerating Oregon oak stands designed for commercial use could be virtually eliminated by leaving stumps < 20 cm tall at the time of cutting (McDonald et al. 1983).

LITERATURE CITED

Anderson, S.H. 1970. The avifaunal composition of Oregon white oak stands. Condor 72:417-423.

Baumgartner, L.L. 1939. Fox squirrel dens. J. Mammal. 20(4):456-465.

Boyce, J.S. 1961. Forest Pathology. 3rd. ed. McGraw-Hill, New York. 572 pp.

Brown, E.R. 1985. Plant community descriptions. Pages 22-24 in Brown, E.R., ed. Management of wildlife and fish habitats in forests of western Oregon and Washington, Part II-Appendices. USDA For. Serv. 302pp.

Brush, T. 1983. Cavity use by secondary cavity-nesting birds and response to manipulations. Condor 85:461-466.

Bull, E. 1986. Ecological value of dead trees to cavity-nesting birds in northeastern Oregon. Oregon Birds 12(2):91-99.

Carey, A.B. 1983. Cavities in trees in hardwood forests. Pages 167-184 in J.W. Davis, G.A. Goodwin and R.A. Ockenfels, tech. coords. Snag habitat management; proceedings of the symposium. USDA For. Serv. Gen. Tech. Rep. RM-99.

Clark, J.W. 1957. Comparative decay resistance of some common pines, hemlock, spruce, and true fir. For. Sci. 3:314-320.

Cole, D. 1977. Ecosystem dynamics in the coniferous forest of the Willamette Valley, Oregon, U.S.A. J. of Biogeog. 4:181-192.

Conner, R.N., O.K. Miller, Jr. and C.S. Adkisson. 1976. Woodpecker dependendence on trees infected by fungal heartrots. Wilson Bull. 88:575-581.

Conner, R.N. 1978. Snag management for cavity nesting birds. Pages 120-128 in R.M. DeGraaf, tech. coord. Proceedings: management of southern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. SE-14.

Conner, R.N., J.C. Kroll and D.L. Dulhavy. 1983. The potential of girdled and 2,4-D-injected southern red oaks as woodpecker nesting and foraging sites. So. J. Appl. For. 7:125-128.

Cottam, G. and J.T. Curtis. 1956. The use of distance measures in phyto-sociological sampling. Ecology 37(3):451-460.

Cross, S.P. 1983. Techniques for locating natural roost sites of bats in the forests of Southwestern Oregon. Or. Dept. Fish and Wildlife Tech. Rep. #83-2-02A. 13pp.

Dalke, P.D. 1948. Some observations on den trees in the Missouri Ozarks. J. Wildl. Manage. 12:107-109.

Devore, J. and R. Peck. 1986. Statistics: The Exploration and Analysis of Data. West Publ. Co. 699p.

Fowells, H.A. 1965. Oregon white oak. Pages 596-599 in Silvics of Forest Trees of the United States. USDA Forest Service, Ag. Handbk. No. 271.

Franklin, J.F. 1979. Vegetation of the Douglas-fir region. Pages 93-112 in P.E. Heilman, H.W. Anderson and D.M. Baumgartner, eds. Forest Soils of the Douglas-Fir Region. Washington State Univ. Coop. Ext. Serv. Pullman, WA. 298pp.

Franklin, J.F. and C.T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon. 452pp.

Galen, C. 1989. A preliminary assessment of the status of the Lewis' woodpecker in Wasco county, Oregon. Oregon Dept. of Fish and Wildlife Tech. Rep. #88-3-01. 23pp.

Gedney, D.R., P.M. Bassett and M.A. Mei. 1986. Timber resource statistics for non-federal forest land in northwest Oregon. USDA For. Serv. Res. Bull. PNW-RB-140. 26pp.

Gedney, D.R., P.M. Bassett and M.A. Mei. 1987. Timber resource statistics for non-Federal forest land in west-central Oregon. USDA For. Serv. Res. Bull. PNW-RB-143. 26pp.

Gysel, L.W. 1961. An ecological study of tree cavities and ground burrows in forest stands. J. Wildl. Manage. 25(1):12-20.

Habeck, J.R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northwest Sci. 35:65-77.

Harestad, A.S. and D.G. Keisker. 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. Can. J. Zool. 67:1067-1073.

Highley, T.L. and T. K. Kirk. 1979. Mechanisms of wood decay and the unique features of heartrots. Phytopathology 69:1151-1157.

Hollander, M. and D.A. Wolfe. 1973. Nonparametric Statistical Methods. John Wiley and Sons Publ., New York. 503pp.

Hoyt, S.F. 1957. The ecology of the pileated woodpecker. Ecology 38(2):246-256.

Johannessen, C.L., W.A. Davenport, R. Millet and S. McWilliams. 1971. The vegetation of the Willamette Valley. Annal of the Assoc. of Am. Geographers 61(2):288-302.

Matthijsen, E. and A.A. Dhondt. 1983. Die Ansiedlung junger Kleiber (Sitta europaea) in Spatsommer und Herbst. J. Orn. 124:281-290.

McComb, W.C. and R.E. Noble. 1980. Effects of single-tree selection cutting upon snag and natural cavity characteristics in Connecticut. Proc. NE Sec. Wildl. Soc. pp50-57.

McComb, W.C., S.A. Bonney, R.M. Sheffield and N.D. Cost. 1986. Den tree characteristics and abundance in Florida and South Carolina. J. Wildl. Manage. 50(4):584-591.

McDonald, P.M., D. Minore and T. Atzet. 1983. Southwestern Oregon-northern California hardwoods. Pages 29-32, in R.M. Burns, tech. compiler. Silvical systems for the major forest types of the United States. USDA For. Serv. Agr. Handb. No. 445.

Miller, H.A. and S.H. Lamb. 1985. Oaks of North America. Naturegraph Publ., Inc. Happy Camp, CA.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species- a literature review. USDA For. Serv., Pacific Northwest Forest and Range Exper. Sta., Gen. Tech. Rep. PNW-87. 71pp.

Nelson, S.K. 1989. Habitat use and densities of cavity nesting birds in the Oregon Coast Ranges. M.S. Thesis. Oregon State Univ. 137pp.

Nietro, W., V.W. Binkley, S.P. Cline, R.W. Mannan, B.G. Marcot, D. Taylor, and F.F. Wagner. 1985. Snags: wildlife trees. Pages 126-169 in Brown, E.R., ed. Management of wildlife and fish habitats in forests of western Oregon and Washington, Part 1: chapter narratives. USDA For. Serv., Pacific Northwest Forest and Range Exper. Sta. Portland.

Peace, T.R. 1962. Pathology of Trees and Shrubs. Clarendon Press, Oxford. 694pp.

Popino, J.H. and D.R. Gedney. 1984. The hardwood resource in western Oregon. USDA For. Serv., Res. Bull. PNW-116. 26pp.

Raphael, M.G. and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs No. 86. 66pp.

Runde, D.E. and D.E. Capen. 1987. Characteristics of northern hardwood trees used by cavity-nesting birds. J. Wildl. Manage. 51(1):217-223.

Sabin, T. and S. Stafford. 1990. Assessing the need for transformation of response variables. Forest Research Lab., College of Forestry, Oregon State University, Corvallis. Special Publ. 20. 31pp.

SAS Institute, Inc. 1987. SAS/STAT guide for personal computers. Version 6 ed. SAS Institute, Inc. Cary, N.C. 1028pp.

Scott, V.E., K.E. Evans, D.R. Patton and C.P Stone. 1977. Cavity-nesting birds of North American forests. USDA For. Serv. Agr. Handb. No. 511. 112pp.

Sedgwick, J.A. and F.L. Knopf. 1986. Cavity-nesting birds and the cavity-tree resource in plains cottonwood bottomlands. J. Wildl. Manage. 50(2):247-252.

Shigo, A.S. 1976. A tree hurts, too. USDA For. Serv., Northeast Forest Exper. Sta. 27pp.

Silen, R.R. 1958. Silvical characteristics of Oregon white oak. USDA For. Serv. Pacific Northwest Forest and Range Exper. Sta. Silvical Series- No.10. 11pp.

Smith, D.M. 1986. The Practice of Silviculture. 8th Ed. John Wiley and Sons, Inc. 527pp.

Sprague, F.L. and H.I. Hansen. 1946. Forest succession in the McDonald forest, Willamette Valley, Oregon. Northwest Sci. 20(4):89-98.

Stein, W.I. in press. Quercus garryana Dougl. ex Hook: Oregon white oak in R.M. Burns and B.H. Honkala, tech coord. Silvics of North America. USDA For. Serv. Agr. Handb. 654. Volume 2: Hardwoods. USDA For. Serv. Pacific Northwest Forest and Range Exper. Sta., Portland, Oregon.

Stickel, D.W. 1964. Roosting habits of red-bellied woodpeckers. Wilson Bull. 76:382-383.

Thilenius, J.F. 1968. The Quercus garryana forest of the Willamette Valley, Oregon. Ecology 49:1124-1133.

Towle, J.C. 1982. Changing geography of the Willamette Valley woodlands. Oreg. Hist. Quarter. 83:66-88.

USDA. 1988. Wood Handbook: Wood as an Engineering Material. USDA For. Serv. Ag. Handb. 72. 448pp.

Waters, J.R. 1988. Population and habitat characteristics of cavity-nesting birds in a California oak woodland. M.S. Thesis, Humboldt State University. 100pp.

Waters, J.R., B.R. Noon and J. Verner. 1990. Lack of nest site limitation in a cavity-nesting bird community. J. Wildl. Manage. 54(2):239-245.

Wilkes, C. 1844. United States exploring expedition, 1838-1842. C. Sherman Pub., Philadelphia.

Winternitz, B.L. and H. Cahn. 1983. Nestholes in live and dead aspen. Pages 102-106 in J.W. Davis, G.A. Goodwin and R.A. Ockenfels, tech. coords. Snag habitat management; proceedings of the symposium. USDA For. Serv. Gen. Tech. Rep. RM-99.

APPENDICES

APPENDIX 1. Cavity features used by cavity-using species in upland Oregon white oak and Douglas-fir woodlands in the mid-Willamette Valley, Oregon. Information in this table is a composite from Anderson (1970), Brown (1985), Hoyt (1957), Cross (1983), Nelson (1989), Scott et al. (1977), Waters (1988), Gumtow-Farrior, unpub. data.

	Minimum			Type of cavities used	
Primary excavators	Hole	---Forest type---		Woodpecker	Decay
of sound wood	Diam (cm)	Oak	Douglas-fir	holes	holes
hairy woodpecker	3.1		X	X	
(Picoides pubescens)					
red-breasted sapsucker	3.8	X	X	X	
(Sphyrapicus ruber)					
acorn woodpecker	5.0	X		X	
(Melanerpes formicivorus)					
pileated woodpecker	7.0	X	X	X	
(Dryocopus pileatus)					
Primary excavators					
of soft wood					
chestnut-backed chickadee	2.0	X	X	X	X
(Parus rufescens)					
white-breasted nuthatch*	2.0	X		X	X
(Sitta carolinensis)					
red-breasted nuthatch	2.4	X	X	X	X
(Sitta canadensis)					
black capped chickadee	2.5	X	X	X	X
(Parus atricapillus)					
northern flicker	3.0	X	X	X	X
(Colaptes auratus)					

APPENDIX 1. Continued

Primary excavators of soft wood	Minimum Hole Diam (cm)	---- Forest type ---- Oak	Douglas-fir	Type of cavities used Woodpecker holes	Decay holes
downy woodpecker (Picoides pubescens)	3.1	X		X	
Lewis' woodpecker* (Melanerpes lewis)	6.2	X	X	X	X
Nonexcavator bird species					
brown creeper (Certhia americana)	2.0	X		X	
Western bluebird (Sialia mexicana)	3.8	X		X	
tree swallow (Tachycineta bicolor)	4.2	X		X	
violet-green swallow (Tachycineta thalassina)		X		X	
purple martin (Progne subis)		X		X	
house wren (Troglodytes aedon)	4.4	X		X	
European starling (Sturnus vulgaris)	5.0	X	X	X	
northern pygmy owl (Glaucidium gnoma)	5.0	X	X	X	

APPENDIX 1. Continued.

Nonexcavator bird species	Minimum Hole Diam (cm)	---Forest type--- Oak	Douglas-fir	Type of cavities used Woodpecker holes	Decay holes
Bewick's wren (Thryomanes bewickii)		X		X	
house sparrow (Passer domesticus)		X		X	
house finch (Carpodacus mexicanus)		X	X		
American kestrel (Falco sparverius)	6.7	X	X	X	X
great-horned owl (Bubo virginianus)		X	X	X	X
common barn owl (Tyto alba)		X	X	X	X
Mammals					
California myotis (Myotis californicus)		X	X		X
Keen's myotis (Myotis keenii)		X	X		X
little brown myotis (Myotis lucifugus)		X	X		X
big brown bat (Eptesicus fuscus)		X	X		X
pallid bat (Antrozonous pallidus)		X	X		X

APPENDIX 1. Continued.

	Minimum Hole Diam (cm)	---Forest type---		Types of cavities used	
		oak	D-fir	Woodpecker holes	Decay holes
Mammals					
deer mouse (Peryomyscus maniculatus		X	X	X	X
short-tailed weasel (Mustela erminea)		X	X		X
Northern flying squirrel (Glaucomys sabrinus	4.0	X	X		X
Douglas squirrel (Tamiasciurus douglasii)			X	X	X
Western gray squirrel (Sciurus griseus)		X	X	X	X
Virginia opossum (Didelphis virginiana)		X	X		X
raccoon (Procyon lotor)		X	X		X
bobcat (Lynx rufus)		X	X		X

* = species that uncommonly excavate their own cavities, and then usually only in extremely decayed substrate.

APPENDIX 2. Features of 10 types of stands (*n*=30) in the mid-Willamette Valley, Oregon.

Type of Stand	Stand	Ownership	History	Notes
Oregon white oak $\leq$ 4 ha				
20.0-34.9 cm dbh	1	Private	Unmanaged grove	Even-sized (dbh) stand.
	2	Private	Unmanaged grove	Cattle grazing on periphery.
	3	Private		Unmanaged grove. Grazed by sheep.
35.0-49.9 cm dbh	1	Federal	Unmanaged grove	On W. L. Finley National Wildlife Refuge (NWR), Corvallis, OR.
	2	State	Mostly unmanaged grove	A 1-lane dirt road runs through the grove; cattle are grazed in the grove.
	3	State	Unmanged grove	Located at E.E. Wilson Wildlife Area, Adair, Oregon.
50.0 + cm dbh	1	Federal & private	Mostly unmanaged groves	Comprised of 4 groves: 3 from W. L. Finley NWR and another private grove East of W. L. Finley NWR
	2	State & private	Managed and unmanaged groves	Comprised of 6 groves, including groves at Bald Hill and Walnut Park, Corvallis, Oregon; Oregon State University property, 1 privately-owned grove grazed by cattle.
	3	State & private	Managed and unmanged groves	Comprised of 4 groves: 1 private grove was grazed by sheep, oaks of another showed scarring from being used as fenceposts; remaining 2 groves were unmanaged.

APPENDIX 2. Continued.

Type of Stand	Stand	Ownership	History	Notes
Oregon white oak > 4 ha				
20.0-34.9 cm dbh	1	Federal	Unmanaged stand	Located at W.L. Finley NWR; some evidence of fire history.
	2	State	Unmanaged stands	Apparently a 2-aged stand; 2 perimeters grazed by sheep and llama along eastern and southern perimeters but not inside the stand; no evidence of fire history.
	3	Federal	Unmanaged	On old homestead now a part of Baskett Slough NWR, Rickreall, OR; no evidence of fire history seen.
35.0-49.9 cm dbh	1	Federal	Unmanaged	Located at W. L. Finley NWR; fire scars seen on some Oregon oak boles.
	2	Private	Unmanaged	Stand divided by a fence; southern portion of stand more densely wooded with generally smaller-diameter trees than northern portion of stand.
	3	Private	Unmanaged	A few Oregon oak removed for firewood from western perimeter of stand.
50.0 + cm dbh	1	Federal	Unmanaged	Also known as "Pigeon Butte Research Natural Area," W. L. Finley NWR; apparently a 2-aged stand; fire scars seen on several oak boles, especially those on the eastern perimeter of the stand. Pigeon Butte was once part of a farm and remnant fenceposts are still present.
	2	State	Partially managed	Western portion of "Witham Hill." A fence separates the stand into a western portion with a grass understory (grazed by sheep) and an eastern portion with a more complex understory. Some large-diameter trees were removed from this stand. This stand has the most prolific regeneration of Oregon white oak that I have seen in the mid-

APPENDIX 2. Continued

Type of Stand	Stand	Ownership	History	Notes
Oregon white oak > 4 ha				
				Willamette Valley.
	3	Private	Partially managed	Several oaks removed from the stand, but snags, diseased and apparently healthy trees were still distributed throughout the stand.
Douglas-fir stands > 4 ha				
20.0-34.9 cm dbh	1	Private	Unmanaged	Unthinned, naturally regenerated stand.
	2	State	Unmanaged	Unthinned, naturally regenerated stand.
	3	State	Managed	Commercially thinned in 1978.
35.0-49.9 cm dbh	1	Private	Unmanaged	Stand naturally regenerated on an abandoned homestead meadow.
	2	State	Unmanaged	Unthinned, naturally regenerated stand.
	3	State	Managed	Heavily thinned in 1978.
50.0 + cm dbh	1	Private	Unmanaged	Unthinned, a few Oregon white oak in the stand.
	2	State	Unmanaged	Remnant "old-growth" stand.
	3	State	Managed	Thinned in 1978.

APPENDIX 2. Continued.

Type of Stand	Stand	Ownership	History	Notes
Mixed Oregon white oak/Douglas-fir > 4 ha				
35.0-49.9 cm dbh	1	State	Unmanaged	Most Oregon white oak not yet suppressed by Douglas-fir.
	2	State	Unmanaged	Oregon white oak generally codominant in the canopy with Douglas-fir.
	3	State	Unmanaged	Oregon white oak generally suppressed by Douglas-fir.