

# Diameters and Heights of Trees with Cavities: Their Implications to Management<sup>1</sup>

Fred L. Bunnell,<sup>2</sup> Elke Wind,<sup>3</sup> Mark Boyland,<sup>4</sup> and Isabelle Houde<sup>4</sup>

## Abstract

Primary cavity nesters select larger trees when nesting in conifers than when nesting in hardwoods. Larger birds use larger nest trees, but the trend is more weakly expressed in hardwoods, as is expected if rot governs nest tree selection. Birds select larger nest trees in more productive coastal forests than in inland forests. Actual nest heights are much shorter than nest tree heights, but species-specific averages are rarely below 5 meters. Larger mammals require older, larger trees where rot is advanced. Bats also use larger trees, particularly when roosting in conifers. Sustaining all cavity users requires sustained provision of a range of diameters of decaying and dead trees, including some trees at least 50 cm dbh (smaller in less productive forests).

## Introduction

Dying and dead trees are common in unmanaged forests, and cavity users typically represent 25 to 30 percent of the terrestrial vertebrate fauna in forests of the Pacific Northwest (Bunnell and others 1999, Thomas and others 1979). Proportions are less where trees are smaller, as in the spruce-willow-birch zone of British Columbia (Bunnell and others 1999). Forest practices reduce cavity sites by reducing amounts of moribund and dead wood and by reducing the size of trees compared to that formerly present. As a result, lack of cavity sites is the most frequently reported threat to forest-dwelling species, including 28 taxa designated “at risk” in the Pacific Northwest (Bunnell and others 1999).

The only compelling way of selecting goals for what we should retain or produce as nest and den trees is to evaluate patterns that the animals exhibit in their selection. We first review cavity-using species and broad factors governing snag use. We then examine patterns of selection among available trees and as a function of the size of bird. From these patterns we derive management implications. We treat both birds and mammals, but focus on primary excavators of the Pacific Northwest,

---

<sup>1</sup> An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

<sup>2</sup> Professor, Center for Applied Conservation Research, University of British Columbia, 3004-2424 Main Mall, Vancouver, British Columbia, V6T 1Z4 (e-mail: fbunnell@interchange.ubc.ca)

<sup>3</sup> Research Technician, E. Wind Consulting, 1-2817 Glenayr Dr., Nanaimo, British Columbia, Canada V9S-3S7 (e-mail: ewind@telus.net)

<sup>4</sup> Ph.D. Candidate and Research Technician, respectively, Center for Applied Conservation Research, University of British Columbia, 3004-2424 Main Mall, Vancouver, British Columbia, V6T 1Z4 (e-mail: markbo@interchange.ubc.ca and houde@intergate.ca)

including Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California.

## Species Using Cavities

In the Pacific Northwest, 69 vertebrate species consistently use cavities and more species make opportunistic use (Bunnell and others 2002). Birds (48 species) and bats (13 species) represent 88 percent of the species consistently using cavities. More bird than mammal species use cavities, but the proportion of mammalian users is higher, ranging in size from long-legged myotis (*Myotis volans*) to black bears (*Ursus americanus*) (Bunnell and Chan-McLeod 1997, Cannings and Harcombe 1990, Peterson and others 1993, Whitaker 1993). Other than some bats and squirrels, mammal use of cavities is more opportunistic than it is for birds. Amphibians and reptiles also use snags and stumps opportunistically (Bunnell and Dupuis 1995, Stelmock and Harestad 1979).

Cavity users can be divided into three groups: species that excavate their own cavities (primary cavity nesters such as woodpeckers); species that use holes excavated by primary cavity nesters (secondary cavity users such as buffleheads [*Bucephala albeola*]<sup>5</sup> and flying squirrels [*Glaucomys* sp.]); and species that use other types of cavities (e.g., Vaux's swifts [*Chaetura vauxi*] and black bears) (Bunnell and others 2002). Most woodpeckers are strong primary cavity nesters, especially adapted for excavating (Spring 1965), and forage primarily by drilling in trees or snags. Weak primary cavity nesters, such as chickadees and nuthatches, are less well adapted for excavation and sometimes modify existing cavities rather than make their own (McClelland and others 1979). Strong excavators are generally large birds, while weak excavators are mainly smaller species. Exceptions to these generalizations include some larger species that are relatively weak excavators (e.g., Lewis's woodpecker [*Melanerpes lewis*], white-headed woodpecker [*Picoides albolarvatus*], and northern flicker [*Colaptes auratus*]).

If habitat requirements of the primary excavators are not met, secondary cavity users also may be lost (Daily and others 1993, Dobkin and others 1995). Larger woodpeckers and the northern flicker thus play a key role in forest ecosystems, providing nest holes for other cavity-nesting birds and roosts or dens for other birds and mammals (Bull and others 1986). Similarly, the sapwells of sapsucker create feeding opportunities for at least 23 bird species, 6 mammal species, and 9 Orders and 22 Families of arthropods (Foster and Tate 1996, Miller and Nero 1983, Sutherland and others 1982). Moreover, woodpeckers can constrain abundance of forest "pest" insects (Holmes 1990, and Thomas and others 1979). Because of these contributions, strong excavators have been termed "keystone species" (e.g., Dailey and others 1993), whose loss would substantially alter forest ecosystems. In the Pacific Northwest, only 10 of the 69 cavity-using species present are strong enough excavators to create habitat for other vertebrates. We emphasize primary cavity nesters because of the role they play in supporting other species.

---

<sup>5</sup> Unpublished data on file, Center for Applied Conservation Research, University of British Columbia, Vancouver, BC, Canada.

## A General Model of Cavity Use

Cavity-nesting birds benefit from the protection from predators that cavities provide their young, as well as shelter and insulation of the nest or roost (Miller and Miller 1980, O'Connor 1978). Size of cavity may affect productivity. Eriksson (1979) reported greater productivity of common goldeneyes (*Bucephala clangula*) in larger nest boxes. The cost for primary cavity-nesters is the time and energy required to excavate the cavity: about 20 days for hairy woodpeckers (*Picoides villosus*) (Ehrlich and others 1988). Ideally, a cavity nest is located where the outer wood is hard, to prevent predators from tearing open the nest, but the inner wood is soft, to allow easy excavation. Soft inner wood is preferred due to the mechanics of chiseling wood in an enclosed space. Heart rots, whether extensive or local, are of prime importance. Generally, all primary excavators seek decayed heartwood, although the strongest excavators do not require it (Bunnell and Allaye-Chan 1984, Kilham 1971, Shigo and Kilham 1968). For weak primary cavity-nesters, harder outer wood remains desirable to reduce predation, but these species cannot excavate hard wood. They must either compromise with softened sapwood, or find existing holes in hard outer wood, such as those created at dead branch stubs.

The ideal cavity nest also should be high in a tree to avoid terrestrial nest predators. The bole where the nest is located must be wide enough to allow a cavity large enough to contain nestlings. These factors promote preference for large-diameter trees, in which the stem is a suitable width well above the ground. The importance of softened heartwood also promotes preference for larger stems, because large stems are usually older stems that have developed heart rot. These needs for soft or hardwood, appropriate stem diameter at the nest, and height above the ground explain many of the preferences researchers have observed among cavity nesters. Most recommendations for snag management derive from these same considerations.

Unlike primary cavity-nesters, secondary cavity-users “take what they can get,” with certain limitations. The most obvious limitation is that nest holes must be big enough. Mountain bluebirds [*Sialia currucoides*], for example, rely primarily on nests made by flickers rather than those of smaller woodpeckers or sapsuckers (Dobkin and others 1995). The nest also needs to be near appropriate habitat, which is not the forest for many secondary users (e.g., cavity-nesting ducks, swallows, bluebirds, and American kestrels [*Falco sparverius*]). Because secondary users are relatively abundant compared to primary excavators, competition for cavities is often intense (Bock and others 1992, von Haartman 1957). Some secondary users, however, show strong preferences among cavity sites. For example, because of their high energy demands and temperature sensitivity, bats often select cavities with favorable microclimates (Kalcounis and Brigham 1998, Lewis 1995).

In the Pacific Northwest there are 23 primary cavity nesters and 40 secondary cavity users. Another six species use dying and dead trees differently. Some cavity users (raccoons [*Procyon lotor*], American martens [*Martes Americana*], fishers [*Martes pennanti*], black bears) are too large to use cavities excavated by woodpeckers. They must rely on large cavities formed by decay or fire. These cavities are uncommon, because old, large trees are uncommon. Vaux's swifts nest and roost in hollow snags large enough that they can fly up and down the hollow chamber (Baldwin and Zaczkowski 1963). Brown creepers [*Certhia Americana*] nest under slabs of loose bark on snags and old trees (Davis 1978). Some bats do as well, but also use cavities. Requirements of these six species can be considered individually during management.

## Diameters

Larger diameter trees or snags are clearly preferred by cavity-nesting birds (tables 1, 2). Nest tree diameters must be large enough to accommodate a cavity with room for an adult bird and nestlings, but sizes usually exceed that requirement. The selection of trees larger than the size of cavity required likely reflects age and the size at which heart rot develops. Flammulated owls [*Otus flammeolus*], for example, are only slightly larger than a sparrow, but nested in ponderosa pine [*Pinus ponderosa*], averaging 57.7 centimeters in diameter at breast height (dbh) on southern aspects and 71.7 centimeters on northern aspects (data of van Woudenberg 1992). The difference reflects greater rates of growth on north aspects, and thus size at the age when rot appears.

**Table 1**—Selection of nest tree diameter within different tree species by cavity-nesting birds of the Pacific Northwest (assessed by relative diameter).<sup>1</sup> Highest value in bold.

Tree species <sup>2</sup>	P <sup>3</sup>	S	All	P	S	P	S
TA	1.15	1.38				2.15	2.11
PB						1.57	2.29
BCo							
DF	3.32	3.93					
SPR	1.03		1.29	1.32	1.32		2.81
WRC				2.36		1.97	1.40
PP			1.08			2.59	2.18
LP		1.81	1.38			1.34	1.59
WL				1.36	1.49	2.22	1.61
WP					1.94		
SF			1.57	1.08			
WH				0.81			
GF							
Source and Comments	K. Martin <sup>4</sup>	(trees & snags > 12 cm dbh)	Scott and others 1980 (snags > 11 cm dbh; PP > 14 cm)	McClellan d 1977	(trees > 22 cm dbh)	C. Steeger <sup>5</sup>	(trees > 7 cm dbh)

<sup>1</sup> Relative diameter = mean diameter used/mean diameter available.

<sup>2</sup> Tree Species Codes: TA = Trembling aspen; PB = Paper birch (*Betula papyrifera*); BCo = Black cottonwood (*Populus balsamifera* ssp. *Trichocarpa*); DF = Douglas-fir; SPR = Spruce (*Picea* spp.); WRC = Western redcedar (*Thuja plicata*); PP = Ponderosa pine; LP = Lodgepole pine (*Pinus contorta*); WL = Western larch (*Larix occidentalis*); WP = White pine (*Pinus monitcola*); SF = Subalpine fir; WH = Western hemlock (*Tsuga heterophylla*); GF = Grand fir. (Sources of tree names are Crittenden 1992, Pojar and MacKinnon 1994, and Parish and others 1996.)

<sup>3</sup> All = all cavity nesters, P = Primary cavity nesters, S = Secondary cavity nesters.

<sup>4</sup> Unpublished data of K. Martin, Center for Applied Conservation Research, Faculty of Forestry, University of British Columbia, Vancouver, BC.

<sup>5</sup> Unpublished data of C. Steeger; Nelson, British Columbia.

**Table 2**—Selection of nest tree diameter by diameter class in old-growth and second-growth stands. Selection is measured by Chesson's alpha (Chesson 1983).

	Diameter class (cm)						Source and Notes
	Second-growth			Old-growth			
	10-19	20-49	>50	10-19	20-49	>50	
<b>P</b>	0.00	0.10	0.90	0.00	0.23	0.77	Lundquist and Mariani 1991 (snags & trees)
<b>All</b>	10-19 0.01	20-49 0.09		50-99 0.25	>99 0.66		Nelson 1988 (snags)
<b>All</b>	15-23 0.03	23-38 0.09	28-53 0.15	>53 0.73			Madsen 1985 (snags)
<b>P</b>	15-19 0.02	20-24 0.07	25-29 0.18	30-34 0.23	35-39 0.22	>40 0.27	Harestad and Keisker 1989 (trees)
<b>All</b>	15-27 0.05	28-52 0.20		53-77 0.17	78-102 0.22	103-127 0.19	>128 0.16 Schreiber and deCalesta 1992 (snags)

We collated data from Pacific Northwest forests relating nest tree diameter to size of bird when nesting in either hardwoods or coniferous trees, and found 162 estimates for 19 bird species (*fig. 1*). The same bird species selected smaller trees when nesting in hardwoods than when nesting in conifers (*fig. 1*).

For example, mean dbh of nest trees of pileated woodpeckers (*Dryocopus pileatus*) nesting in ponderosa pine was 84 centimeters, but only 40.0 and 46.6 centimeters when nesting in trembling aspen (*Populus tremuloides*). When nesting in hardwoods or inland conifers, there is a significant trend for larger birds to use larger trees but not in coastal conifers. The latter observation suggests that coastal conifers attain large sizes before even small pockets of rot develop. The same bird species selected larger conifers in coastal forests than in inland forests (*fig. 1b*). Hardwood data were combined because we had only seven coastal samples. The trend to select larger trees with increasing bird length is more weakly expressed in hardwoods. Each finding is expected if rot governs selection of nest trees. In the Pacific Northwest, hardwoods generally rot at younger ages and smaller sizes than do conifers (Bunnell and others 1999, Cline 1977). Because there is little relationship between degree of decay and size of hardwood trees, larger primary excavators need not consistently seek larger hardwoods. More time is required for heart rot to develop in conifers, and

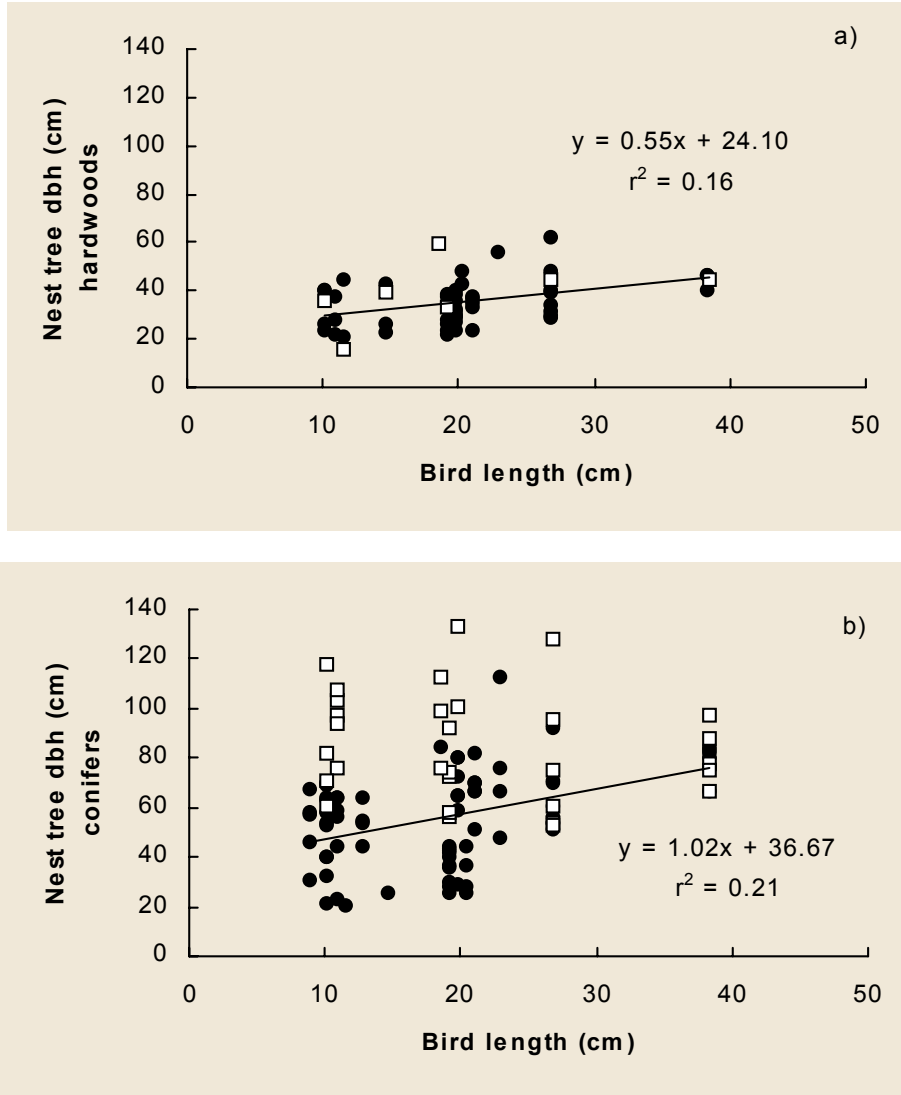
trees are larger before sizeable decay pockets accrue. Thus, larger bird species seeking larger pockets of heart rot seek older and larger conifers.

Milling efficiency constrains the sizes of trees grown in managed forests. Optimal milling efficiency varies with mill configuration, but for many sawmills in the Pacific Northwest the preferred maximum log diameter is < 46 to 50 centimeters (Bunnell and others 1997). Primary cavity nesters for which mean diameters of conifer trees consistently exceeded 50 centimeters dbh in inland forests include red-breasted, yellow-bellied and Williamson's sapsuckers [*Sphyrapicus thyroideus*], white-headed and pileated woodpeckers, and the northern flicker (fig. 1). Three of these 6 species are designated "at risk" in the Pacific Northwest. In coastal forests, some small birds (chestnut backed chickadee [*Poecile rufescens*], red-breasted nuthatch [*Sitta canadensis*]) consistently selected nest trees with a mean dbh > 50 centimeters, indicating the dominant role of decay in nest site selection. For inland forests, McClelland (1977) suggested that trees must be at least 23 centimeters dbh before providing a nesting site. Smaller mean values have been reported for black-capped and mountain chickadees [*Poecile gambeli*], red-breasted nuthatches, and downy woodpeckers [*Picoides pubescens*], especially when nesting in hardwoods (fig. 1).

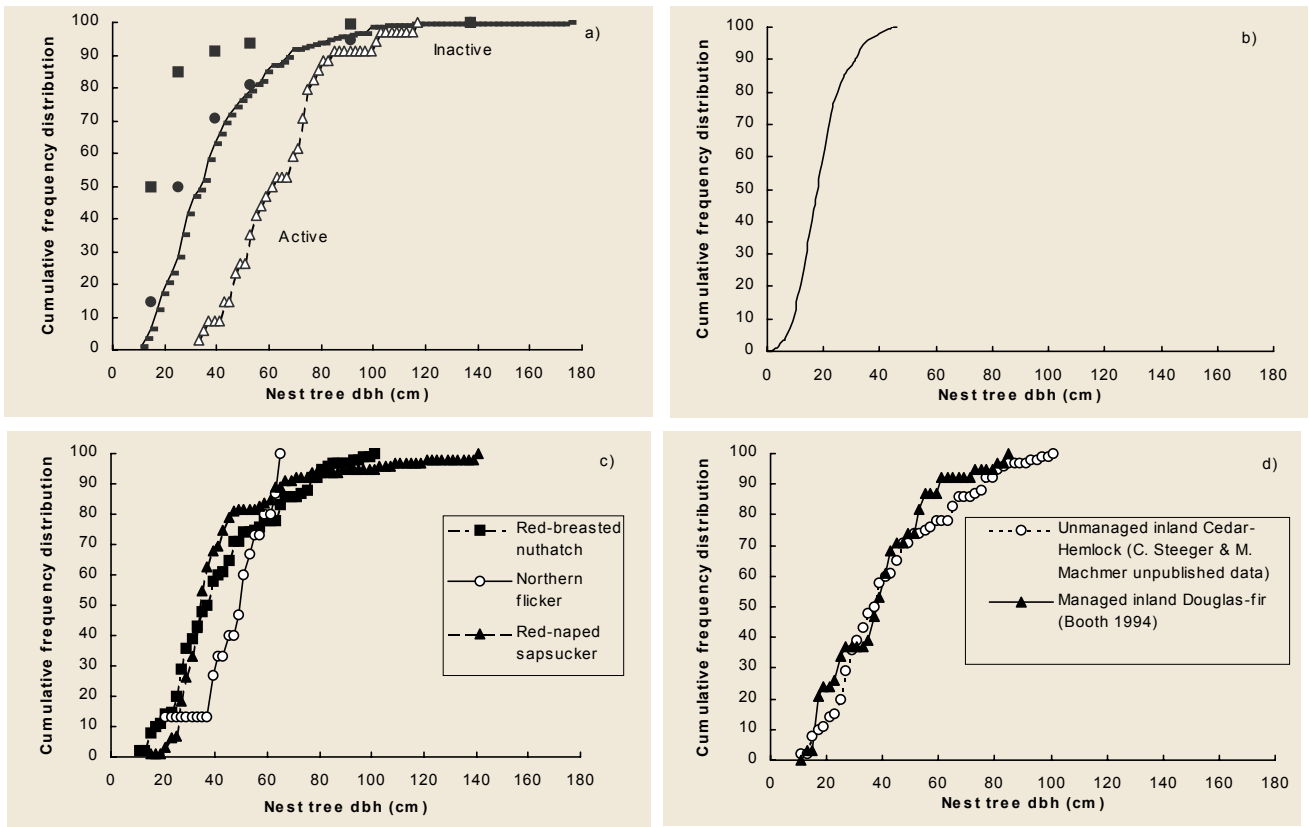
Shape of the diameter distribution is more important than the mean. Cumulative frequency distributions of diameters and heights of both "active" snags (used by birds for nesting) and "inactive" or unused snags tend to have a long tail of larger snags, although active snags are more normally distributed (fig. 2). Using non-parametric tests, Bunnell and Allaye-Chan (1984) found that active snags were larger (height and diameter) than inactive snags in old-growth areas ( $P < 0.05$ ); and that second-growth snags were smaller than either active or inactive old-growth snags ( $P < 0.01$ ). Only 10 to 17 percent of nest sites were located in snags < 46 centimeters dbh (fig. 2a). Figure 2b illustrates the cumulative frequency distribution of diameters of all aspen nest trees on 21 sites (a range of about 15 to 75 centimeters dbh).<sup>4</sup> Somewhat more than 50 percent of the nests were in trees < 30 centimeters dbh, and the central tendency was located around 30 centimeters dbh. Of 17 cavity nesting species nesting in aspen, four had mean nest tree diameters > 30 centimeters dbh (northern flicker, pileated woodpecker, American kestrel, and European starling [*Sturnus vulgaris*]).<sup>4</sup> The long tail of the distribution to the right elevates calculated mean diameters for most species (fig. 2). That pattern also is evident in data of Steeger and Machmer<sup>6</sup> (fig. 2c). Most data on snag use are collected from unmanaged forests. Figure 2d compares nest trees selected by red-breasted nuthatches in managed and unmanaged forests of different tree species. The similarity of snag sizes selected suggests some governing relationship within the two disparate forest types.

---

<sup>6</sup> Unpublished data on file, Pandion Ecological Research Ltd., Nelson, British Columbia, Canada.



**Figure 1**—Mean dbh of primary excavator nest trees or snags as a function of bird length (bill to tail length) in inland (●) and coastal (□) forests of the Pacific Northwest: a) nesting in hardwoods; b) nesting in conifer trees. All lengths from DeGraaf and others 1991. Other sources: B. Booth (unpublished); Bull 1987; Bull and others 1986; Bull and others 1992; Conway and Martin 1993; Cunningham and others 1980; Galen 1989; Harris 1982; Keisker 1987; Linder 1994; McClelland and others 1979; Peterson and Gauthier 1985; Putnam 1983; Schreiber and deCalesta 1992; Tashiro-Veirling 1994; Zarnowitz and Manuwal 1985; plus the following that are common with *figure 3*: K. Aubry and R. Raley (unpublished) from Bull 1980; Bull and Jackson 1995; Crockett and Hadow 1975; Dixon 1995a; Dixon 1995b; Dobkin and others 1995; Goggans and others 1989; Kelleher 1963; W. Klenner and D. Huggard (unpublished); Li and Martin 1991; Lundquist and Mariani 1991; M. Machmer and C. Steeger (unpublished); Madsen 1985; Mannan 1982; Mannan and others 1980; K. Martin (unpublished); McClelland 1977; McEllin 1979; Mellen 1987; Milne and Hejl 1989; Nelson 1988; Raphael and White 1984; Scott and others 1980; Sedgwick and Knopf 1990; Steeger and Hitchcock 1998; Steeger and others 1996.



**Figure 2**—Cumulative frequency distributions (percent) of snag and nest tree measurements: a) dbh of old growth snags without cavities (inactive), old growth snags with cavities (active), and snags in younger stands, 70 (■) and 100 (●) years of age (all inactive; data of Cline 1977:33 and Bunnell and Allaye-Chan 1984:361-362 for the Coastal Western Hemlock zone); b) dbh of aspen nest trees in the Cariboo (data of K. Martin); c) dbh of nest trees used by three species in unmanaged Interior Cedar-Hemlock (data of C. Steeger and M. Machmer unpublished data); d) dbh of nest trees used by red-breasted nuthatches.

We derive three points from (fig. 2). First, birds show a central tendency in nest tree selection, even across different forest types (see also Connor 1976, Connor and others 1975). Second, because of the long tails to distributions, this tendency is better reflected by medians (which typically are smaller than means). Unfortunately, means are more often reported. Third, minimum nest tree diameter is a poor management target, because it ignores the central tendency.<sup>4</sup> A more appropriate management target would be to provide trees larger than the median diameter at which heart rot commonly accrues in that forest type.

Roost trees, as well as nest trees, tend to be large. Unlike nests, which often are excavated anew each year, roosts usually are sought in natural cavities. Bull and others (1992) reported that the average diameter of 123 pileated woodpecker roost

trees was 71 centimeters. Most of these were grand fir (*Abies grandis*) extensively decayed by Indian paint fungus (*Echinodotium tinctorium*). Pygmy nuthatches (*Sitta pygmaea*) use communal roosts housing up to 100 birds during winter (Sydeman and Guntert 1983). In Arizona, these roost sites averaged 73.2 centimeters dbh (Hay and Guntert 1983). Similarly, the hollow trees or snags used by Vaux's swift must be large enough to allow the swift to fly up and down. Bull and Collins (1993) reported the mean dbh of 50 nest trees of Vaux's swift to be 68 centimeters.

Mammals also select large trees for cavity sites (*table 3*). In some instances, the trees are uncommonly large. Along the coast, from Vancouver Island south through Oregon, most black bear's dens are in large dead or dying trees and downed wood (Bunnell and others 1997, Davis 1996). In drier, inland forests where soil moisture favors earth dens, Bull and others (1996) reported that 41 percent (24/59) of black bear dens were in wooden structures.<sup>5</sup> Mean dbh of hollow, black bear den trees is > 100 centimeters in both coastal (Davis 1996) and inland forests (Bull and others 1996). Bats also use larger trees (*table 3*) because they often use either natural hollows or cavities excavated by woodpeckers. The difference between hardwoods and conifers persists. Diameters of bat roost trees in southeastern British Columbia, averaged 52.5 centimeters dbh in Douglas-fir (*Pseudotsuga menziesii*), but only 42.1 centimeters in trembling aspen (Steeger and Machmer 1996). Four species in *table 3* that use trees or snags > 50 centimeters dbh contain taxa listed as "sensitive" or "at risk" in the Pacific Northwest (northern long-eared myotis [*Myotis septentrionalis*], black bear, fisher, and American marten).

Most cavity-using birds and mammals of the Pacific Northwest seek large trees as cavity sites. Eight species "at risk" use trees or snags averaging > 50 centimeters dbh, which is greater than optimal milling diameter of most sawmills. Intensive fiber production is incompatible with sustaining habitat for these species.

## Heights

The fact that dbh of trees used for nesting may be much larger than the size of cavity sought by birds reflects the benefits of nesting high in trees to afford greater protection from mammalian predators (Nilsson 1984). Mean nest heights of all species but black-capped chickadee (*Poecile atricapillus*) are well above 5 meters (*fig. 3b*). In *tables 4-5* we collate data on nest heights by tree species and compare them to availability. The average height of nest trees is not consistently higher than the average height of trees in the stand (*table 4*), because many nests were in snags with broken tops. For example, in interior Douglas-fir of British Columbia, 14 of 20 nests of red-breasted nuthatches were within 2 meters of the top of decay class 4 Douglas-fir snags with broken tops (Thomas and others 1979); 21 of 22 nests in Englemann spruce-subalpine fir forest were in similar class 4 subalpine fir (*Abies lasiocarpa*) snags, broken off by wind and heart rot.<sup>7</sup> Small, weak excavators seek soft substrate, commonly found in short, broken-topped snags or stumps. That tendency is more apparent among chickadees than nuthatches, and accounts for some of the short nest tree heights in *figure 3a*. Some mid-sized, weak excavators, also seek out well-rotted substrates in older, broken-topped snags or stumps (e.g., downy, black-backed, three-toed, and Lewis's woodpeckers; *fig. 3b*).

<sup>7</sup> Unpublished data on file, British Columbia Ministry of Forests, Kamloops, British Columbia, Canada.

Table 3—Dimensions of trees and snags used as denning and roosting sites by mammals, weighted means by species.

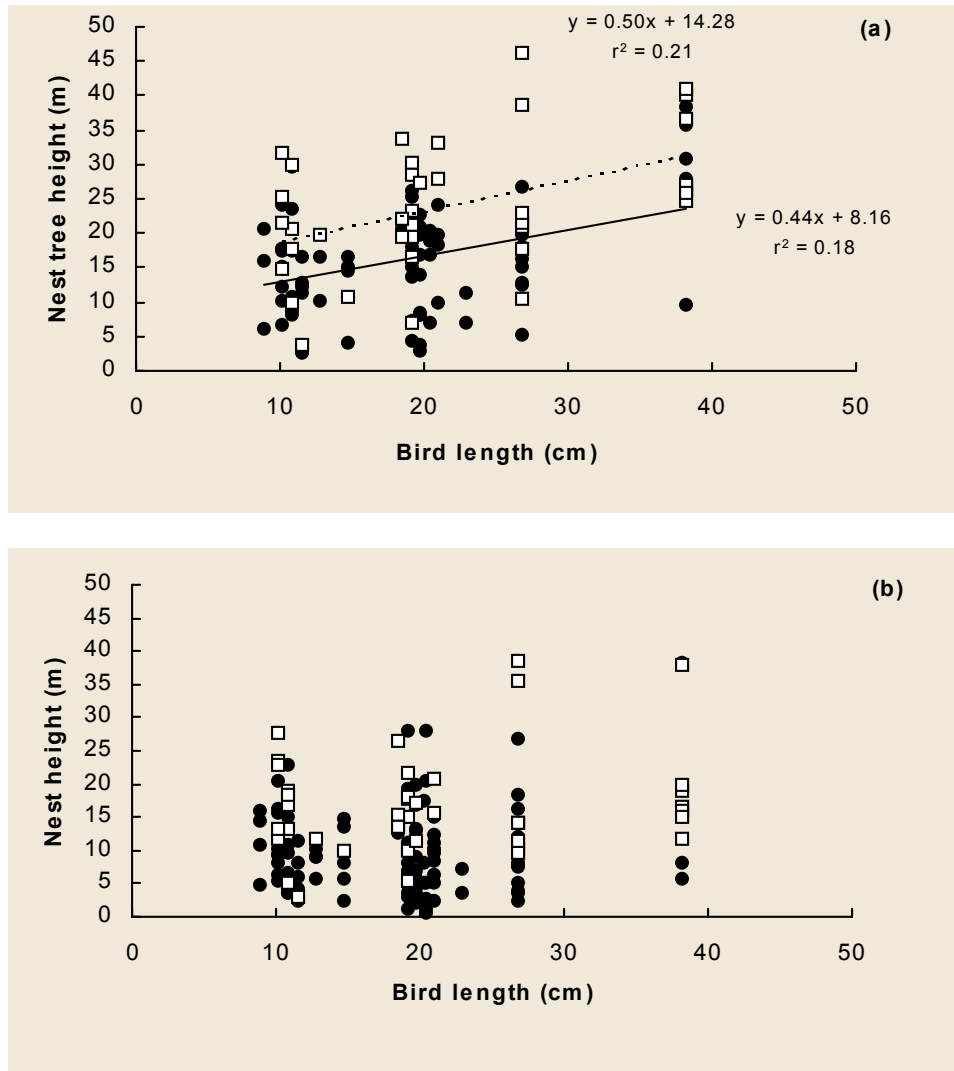
Species	Trees			Snags			Trees & Snags Pooled			Source
	dbh (cm)	height (m)	n	dbh (cm)	height (m)	n	dbh (cm)	height (m)	n	
<b>BATS</b>										
Big brown bat	44.6	24.6	13	54.8	25.8	8	76.3		4	Betts 1996, Rasheed & Holroyd 1995, Vonhof 1996
<i>Eptesicus fuscus</i>										Brigham and others 1997, Grindal 1997, Vonhof 1996
California myotis	34.0		2	55.5	26.6	23				Crampton & Barclay 1995, Grindal 1997, Rasheed & Holroyd 1995
<i>Myotis californicus</i>										Ormsbee & McComb 1998, Rasheed & Holroyd 1995
Little brown myotis	68.5	21.4	16	40.3	11.2	3	41.4		4	Caceres 1997
<i>Myotis lucifugus</i>										Betts 1996, Campbell and others 1996, Crampton & Barclay 1995, Rasheed & Holroyd 1995, Vonhof
Long-legged myotis		40.0	4	95.5	37.5	37	100.0			Caceres 1997
Northern long-eared myotis	102.2	35.5	4	67.7	30.5	3			25	Betts 1996, Campbell and others 1996, Crampton & Barclay 1995, Rasheed & Holroyd 1995, Vonhof
Silver-haired bat	37.1	24.3	18	39.0	15.5	8	45.1			Caceres 1997
<i>Lasionycteris noctivagans</i>										
Western long-eared myotis	72.7	49.0	2							
<i>Myotis evotis</i>										
Big brown and Silver-haired bat							68.0	22.0	6	Bull and others 1996
Big brown, Silver haired, California myotis							46.0	24.0	31	Steeger & Machmer 1996
<b>RODENTS</b>										
Flying squirrel	62.7	33.3	445	61.0	13.9	190	31.5		66	Carey and others 1997 <sup>1</sup> , Mowrey & Zasada 1984, C. Steeger <sup>2</sup>
Red squirrel		18.3	10				33.2		24	K. Martin <sup>3</sup> , C. Steeger <sup>2</sup>
<i>Tamiasciurus hudsonicus</i>										Meiselman & Doyle 1996 <sup>1</sup>
Red tree vole	99.4	24.3	78							
<i>Phenacomys longicaudus</i>										
<b>CARNIVORES</b>										
Black bear	161.8		5	114.0	19.0	16	152.1		43	Akenson 1994, Bull and others 1996, Davis 1996, Lindzey & Meslow 1976, Noble and others 1990
Fisher	71.3		28							Anon. 1996, Weir 1995
American marten	84.0		218	84.1	10.6	152	78.9	23.0	36	Martin & Barrett 1991, Raphael & Jones 1997, Spencer 1987

<sup>1</sup> Includes old-growth and second-growth/mature/young sites.

<sup>2</sup> Unpublished data on file, Pandion Ecological Research Ltd., Nelson, BC, Canada.

<sup>3</sup> Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

Although larger birds use taller trees and snags ( $P < 0.001$ ), there is great variability due to broken tops (*fig. 3a*). The same species tended to use taller trees in coastal forests than in the less productive inland forests, and the slope of the relationship is greater ( $P < 0.01$ ). Actual nest height shows no relation with size of the bird (*fig. 3b*;  $r^2 < 0.05$ ). The lack of relationship between bird size and nest height is expected, because the stem taper means that their larger cavities cannot be as near the top of the tree as those of smaller birds. Taller trees often are selected by cavity-nesting birds, but primarily because birds are seeking a large diameter tree with a nest site well above the ground. Management targets can be based on diameters alone.



**Figure 3**—Mean height of primary excavator nest trees or snags (a) and nests (b) as a function of bird length (bill to tail) in inland (●) and coastal (□) forests of the Pacific Northwest. All lengths from DeGraaf and others 1991. Other sources: Franzreb 1975, Hooge and others 1999, Mannan 1977, Manuwal 1981, Medin 1985, Miller and Bock 1972, Troetschler 1976, Western Foundation of Vertebrate Zoology in Garrett and others 1996, plus those common with *figure 1*.

**Table 4**—Selection of nest tree heights within different tree species by cavity nesting birds of the Pacific Northwest (assessed by relative height).<sup>1</sup>

Tree species <sup>3</sup>	Group <sup>2</sup>		P	S
	P	S		
TA	RH	RH	RH	RH
PB	n/a <sup>4</sup>		1.90	1.79
BCo	n/a	0.89	1.09	1.25
DF	n/a		0.99	0.56
SPR	0.48	0.78		1.41
WL	0.72		1.35	1.42
WRC	0.77		1.54	1.41
PP	1.36		0.90	n/a
SF	n/a			1.10
WH	0.31		1.29	
LP	0.68			
GF				
Source and Notes	McClelland 1977	(Avail. = trees > 22 cm dbh)	C. Steeger <sup>5</sup>	(Avail. = trees > 20 cm dbh)

<sup>1</sup> RH = relative height; mean height used/mean height available.

<sup>2</sup> Mean tree height of nests or nest trees/snags for all cavity nesters (P), and secondary cavity nesters (S).

<sup>3</sup> Tree Species Codes: TA = Trembling aspen; PB = Paper birch; BCo = Black cottonwood; DF = Douglas-fir; SPR = Spruce; WL = Western larch; WRC = Western red cedar; PP = Ponderosa pine; SF = Subalpine fir; WH = Western hemlock; LP = Lodgepole pine; GF = Grand fir; WP = White pine.

<sup>4</sup> Tree species used for nesting, but mean height available data were not provided.

<sup>5</sup> Unpublished data on file, Pandion Ecological Research, Nelson, British Columbia, Canada.

**Table 5**—Selection of nest tree heights by height class. Selection is measured by Chesson's alpha (Chesson 1983).

Height class (m)						Source and Notes
2-10	11-20	21-30	31-40	> 40		
0.00	0.02	0.07	0.14	0.76		Nelson 1988 (snags)
< 6	6-12	12-18	18-24	> 24		Madsen 1985 (snags)
0.05	0.25	0.18	0.14	0.37		Schreiber & deCalesta 1992 (snags)
1.8-3.3	3.4-6.3	6.4-9.3	9.4-12.3	12.4-15.2	> 15.3	
0.01	0.06	0.08	0.18	0.36	0.32	

## Implications to Management

There are several ways to create either cavities or snags, but it is more practical to sustain them than to create them (Bunnell and others 1999). Creating high stumps produces snags that are used (Bennett 1994), but these are well below the heights sought by most birds and may encourage high rates of depredation. Although diameter appears a more reliable basis of management targets than height, there is no simple diameter limit. We offer two broad recommendations:

- *Sustain a range of diameters of decaying and dead trees.*

This recommendation follows from the range of diameters selected by cavity using species (*fig. 1*). Smaller snags provide some nesting opportunities, but, more importantly, they provide foraging sites (Bull and others 1986, Bunnell and others 2002). Many more foraging sites are needed than nesting sites.

- *Maintain some conifer snags of at least 50 centimeters diameter (30 centimeters in less productive forests).*

Because trees grown to provide cavities must rot and are not harvested, there is economic incentive to retain small trees. Earlier workers suggested minimum values derived from active snags as guidelines for snag retention (e.g., Connor and others 1975, Thomas and others 1979). Minimum values imply that most individuals are equally successful at nesting and reproducing at the lower ends of size distributions as those nesting at middle and high portions of the distribution. Available data suggest otherwise: while individual species nest in a wide range of tree or snag sizes, they tend to select larger ones when available (*tables 2, 3*). Cavity-nesters appear to select median sizes at which heart rot develops. The appropriate diameter is likely to be a function of tree species composition, species-specific rot patterns, and site.

Target diameters for nest trees should not be less than documented median diameters for the largest bird species present (*fig. 1*). Conifer trees must exceed 50 centimeters dbh to support all bird species (*fig. 1a*). Hardwood trees can be about 10 cm smaller (*fig. 1b*). Because studies have concentrated on forest types where trees are larger and more valuable, existing data overestimate requirements for areas where trees are smaller. A diameter > 30 centimeters likely will accommodate most bird species occurring in less productive forest types, but not the pileated woodpecker. A few mammals require still larger trees or snags (e.g., American marten, black bear), but need fewer of them than are required to sustain bird populations. Large trees and snags also have the advantage of standing longer than small snags (Graham 1981, Morrison and Raphael 1993).

## Acknowledgments

Our research and synthesis was supported by Forest Renewal British Columbia, Lignum, MacMillan Bloedel, and Western Forest Products. The manuscript benefited from reviews by E. Bull and A. Harestad. We thank B. Booth, D. Huggard, W. Klenner, M. Machmer, K. Martin, and C. Steeger for unpublished data. This is Publication No. R-37 of the Centre of Applied Conservation Biology, University of British Columbia.

## References

- Akenson, James J. 1994. **Black bear den summary NE Region—interim progress report.** Starkey Bear Study, 1994 February. La Grande, OR: Oregon Department of Fish and Game; 3 p.
- Anonymous. 1996. **Ecological characteristics of fishers in southwestern Oregon.** Progress Report, June 1996. Olympia, WA: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 7 p.
- Baldwin, Paul H.; Zaczkowski, Nick K. 1963. **Breeding biology of the Vaux Swift.** Condor 65(5): 400-406.
- Bennett, Stephen N. 1994. **Initiatives in wildlife tree management: an evaluation of the high-cut stumping technique.** School of Resource and Environmental Management Report No. 152. Burnaby, BC: Simon Fraser University; 75 p.
- Betts, Burr J. 1996. **Roosting behaviour of silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*) in northeast Oregon.** In: Barclay, R. M. R.; Brigham, R. M., editors. Proceedings of the symposium on bats and forests; 1995 October 19-21; Victoria, BC: BC Ministry of Forests; 55-61.
- Bock, Carl E.; Cruz, Alexander Jr.; Grant, Michael C.; Aid, Charles S.; Strong, Thomas R. 1992. **Field experimental evidence for diffuse competition among southwestern riparian birds.** American Naturalist 140: 815-828.
- Booth, Barry. **Personal communication.** Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.
- Brigham, R. Mark; Vonhof, Maarten J.; Barclay, Robert M.R.; Gwilliam, John C. 1997. **Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*).** Journal of Mammalogy 78: 1231-1239.
- Bull, Evelyn L. 1980. **Resource partitioning among woodpeckers in northeastern Oregon.** Moscow, ID: University of Idaho; 109 p. Ph.D. dissertation.
- Bull, Evelyn L. 1987. **Ecology of the pileated woodpecker in northeastern Oregon.** Journal of Wildlife Management 51: 472-481.
- Bull, Evelyn L.; Collins, Charles T. 1993. **Vaux's swift (*Chaetura vauxi*).** In: Poole, A.; Gill, F., editors. The Birds of North America No. 77. Washington, DC: The Academy of Natural Sciences. 12 p.
- Bull, Evelyn L.; Jackson, Jerome A. 1995. **Pileated woodpecker (*Dryocopus pileatus*).** The Birds of North America, No. 148; 20 p.
- Bull, Evelyn L.; Meslow, E. Charles. 1977. **Habitat requirements of the pileated woodpecker in northeastern Oregon.** Journal of Forestry 75: 335-337.
- Bull, Evelyn L.; Holthausen, Richard S.; Henjum, Mark G. 1992. **Roost trees used by pileated woodpeckers in northeastern Oregon.** Journal of Wildlife Management 56: 786-793.
- Bull, Evelyn L.; Akenson, J. J.; Betts, Burr J.; Torgensen, T. R. 1996. **The interdependence of wildlife and old-growth forests.** In: Bradford, P.; Manning, T.; I'Anson, B., editors. Proceedings of the workshop on wildlife tree/stand-level biodiversity; October 17-18, 1995, Victoria, B.C.; Victoria, BC: British Columbia Ministry of Environment, Lands, and Parks, and Ministry of Forests; 71-75.
- Bull, Evelyn L.; Peterson, Steven R.; Thomas, Jack W. 1986. **Resource partitioning among woodpeckers in northeastern Oregon.** Res. Note PNW-RN-44. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 19 p.

- Bunnell, Fred L.; Allaye-Chan, Ann C. 1984. **Potential of ungulate winter-range reserves as habitat for cavity-nesting birds.** In: Meehan, W. R.; Merrell, T. R.; Hanley, T. A., editors. Proceedings of the symposium on fish and wildlife relationships in old-growth forests; 1982 April 12-15; Juneau, Alaska; Morehead City, NC: American Institute of Fishery Research Biologists; 357-365.
- Bunnell, Fred L.; Chan-McLeod, Ann C. 1997. **Terrestrial vertebrates.** In: Schoonmaker, P. K.; von Hagen, B.; Wolf, E.C., editors. The rain forests of home. Profile of a North American bioregion. Washington, D.C.: Island Press; 103–130.
- Bunnell, Fred L.; Dupuis, Linda A. 1995. **Riparian habitats in British Columbia: their nature and role.** In: Morgan, K. H.; Lashmar, M. A., editors. Proceedings of the riparian habitat management and research workshop, 1993 May 4-5; Kamloops, BC. Fraser River Action Plan special publication. Delta, BC: Canadian Wildlife Service; 7-21.
- Bunnell, Fred L.; Houde, Isabelle; Johnston, Barb; Wind, Elke 2002. **How dead trees sustain live organisms in western forests.** In: Laudenslayer, William F., Jr.; Shea, Patrick J.; Valentine, Bradley E.; Weatherspoon, C. Phillip; Lisle, Thomas E., technical coordinators. Proceedings of the symposium on the ecology and management of dead wood in western forests. 1999 November 2-4; Reno, NV. Gen. Tech. Rep. PSW-GTR-181. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; [this volume].
- Bunnell, Fred L.; Kremsater, Laurie L.; Wells, Ralph W. 1997. **Likely consequences of forest management on terrestrial, forest-dwelling vertebrates in Oregon.** Portland, OR: Oregon Forest Resources Institute; 130 p.
- Bunnell, Fred L.; Kremsater, Laurie L.; Wind, Elke. 1999. **Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands.** Environmental Reviews 7: 97-146.
- Caceres, Carolina. 1997. **Columbia Basin Fish and Wildlife Compensation Program.** Progress report number 014. Nelson, BC: BC Hydro and BC Environment; 21 p.
- Campbell, Lori A.; Hallett, James G.; O'Connell, Margaret A. 1996. **Conservation of bats in managed forests: use of roosts by *Lasionycteris noctivagans*.** Journal of Mammalogy 77: 976-984.
- Cannings, Richard A.; Harcombe, Andrew. P. 1990. **The vertebrates of British Columbia. Scientific and English names.** Heritage Record No.20, Victoria, BC: Royal British Columbia Museum; 110 p.
- Carey, Andrew B.; Wilson, Todd M.; Maguire, Christine C.; Biswell, Brian L. 1997. **Dens of northern flying squirrels in the Pacific Northwest.** Journal of Wildlife Management 61: 684-699.
- Chesson, Jean. 1983. **The estimation and analysis of preference and its relationship to foraging models.** Ecology 64(5): 1297-1304.
- Cline, Steven P. 1977. **The characteristics and dynamics of snags in Douglas-fir forests of the Oregon Coast Range.** Corvallis, OR: Oregon State University; 106 p. Ph.D. dissertation.
- Conner, Richard N. 1976. **Nesting habitat for red-headed woodpeckers in southwestern Virginia.** Bird-Banding 47: 40–43.
- Conner, Richard N.; Hooper, Robert G.; Crawford, Hewlette S.; Mosby, Henry S. 1975. **Woodpecker nesting habitat in cut and uncut woodlands in Virginia.** Journal of Wildlife Management 39: 144-150.
- Conway, Courtney J.; Martin, Thomas E. 1993. **Habitat suitability for Williamson's Sapsuckers in mixed-conifer forests.** Journal of Wildlife Management 57: 322-328.

- Crampton, Lisa H.; Barclay, Robert M.R. 1995. **Relationships between bats and stand age and structure in aspen mixedwood forests in Alberta.** In: Stelfox, J. B., editor. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Jointly published; Vegreville, AB: Alberta Environmental Centre (AECV95-R1). Edmonton, AB: Canadian Forest Service (Project No. 0001A); 211-225.
- Crittenden, Mabel. 1992. **Trees of the west.** Hancock House Publishers. Surrey, BC; 220 p.
- Crockett, Allen B.; Hadow, Harlo H. 1975. **Nest site selection by Williamson's and Red-naped Sapsuckers.** Condor 77: 365-368.
- Cunningham, James B.; Balda, Russell P.; Gaud, William S. 1980. **Selection and use of snags by secondary and cavity-nesting birds of the ponderosa pine forest.** Res. Pap. RM-RP-222. Fort Collins, CO: Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture; 15 p.
- Dailey, Gretchen C.; Ehrlich, Paul R.; Haddad, Nick M. 1993. **Double keystone bird in a keystone species complex.** Proceedings of the National Academy of Science USA 90: 592-594.
- Davis, Cheyleen M. 1978. **A nesting study of the Brown Creeper.** Living Bird 17: 237-263.
- Davis, Helen. 1996. **Characteristics and selection of winter dens by black bears in coastal British Columbia.** Burnaby, BC: Simon Fraser university; 147 p. M.Sc. thesis.
- DeGraaf, Richard M.; Scott, Virgil E.; Hamre, R. H.; Ernst, Liz; Anderson, Stanley H. 1991. **Forest and rangeland birds of the United States. Natural history and habitat use.** Agric. Handb. 688. Washington DC: Forest Service, U.S. Department of Agriculture; 625 p.
- Dixon, Rita D. 1995a. **Density, nest-site and roost-site characteristics, home-range, habitat-use, and behavior of White-headed woodpeckers: Deschutes and Winema National Forests, Oregon.** Nongame Report 93-3-01. Portland, OR: Oregon Department of Fish and Wildlife; 90 p.
- Dixon, Rita D. 1995b. **Ecology of white-headed woodpeckers in the central Oregon Cascades.** Boise, ID: University of Idaho, 142 p M.Sc. thesis.
- Dobkin, David S.; Rich, Adam C.; Pretare, Jennifer A.; Pyle, William H. 1995. **Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin.** Condor 97: 694-707.
- Ehrlich, Paul R.; Dobkin, David S.; Wheye, Darryl. 1988. **The birders handbook: a field guide to the natural history of North American birds.** New York: Simon and Schuster Inc.; 785 p.
- Eriksson, Mats O.G. 1979. **Clutch size and incubation efficiency in relation to nest-box size among goldeneyes *Bucephala clangula*.** Ibis 121(1): 107-109.
- Foster, William L.; Tate, James, Jr. 1966. **The activities and coactions of animals at sapsucker trees.** Living Bird 5: 87-113.
- Franzreb, Kathleen. 1975. **The effects of timber harvesting on an avian community in a mixed-coniferous forest.** White Mountains, Arizona. Tempe, AZ: Arizona State University; 205 p. Ph.D. dissertation.
- Galen, Christie. 1989. **A preliminary assessment of the status of Lewis' woodpecker in Wasco County, Oregon.** Nongame Project No. 88-3-0. Report to Oregon Dept. Fish & Wildlife; (original not seen; cited from Marshall and others 1996).
- Garrett, Kimball L.; Raphael, Martin G.; Dixon, Rita D. 1996. **White-Headed woodpecker (*Picoides albolarvatus*).** The birds of North America, No. 252: 1-22.

- Goggans, Rebecca; Dixon, Rita D.; Seminara, L.C. 1989. **Habitat use by three-toed and black-backed woodpeckers, Deschutes National Forest.** Technical Report no. 87-3-02. Portland, OR: Oregon Department of Fish and Wildlife; 50 p.
- Graham, Robin Lee L. 1981. **Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range.** Corvallis, OR: Oregon State University; 152 p. Ph.D. dissertation.
- Grindal, Scott. 1997. **Upper Kootenay River bat survey.** Athlmer, BC: Columbia Basin Fish and Wildlife Compensation Program. 60 p.
- Harestad, Alton S.; Keisker, Dagmar G. 1989. **Nest tree use by primary cavity-nesting birds in south central British Columbia.** Canadian Journal of Zoology. 67: 1067-1073.
- Harris, Mary A. 1982. **Habitat use among woodpeckers in forest burns.** Missoula, MT: University of Montana; 63 p. M.Sc. thesis.
- Hay, Douglas B.; Güntert, Marcel. 1983. **Seasonal selection of tree cavities by pygmy nuthatches based on cavity characteristics.** In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., editors. Proceedings of the symposium snag habitat management; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-GTR-99. Fort Collins, CO: Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture; 117-120.
- Holmes, Richard T. 1990. **Ecological and evolutionary impacts of bird predation on forest insects: an overview.** Studies in Avian Biology 13: 6-13.
- Hooge, Philip N.; Stanback, Mark T.; Koenig, Walter D. 1999. **Nest-site selection in the acorn woodpecker.** Auk 116: 45-54.
- Kalcounis, Matina C.; Brigham, R. Mark. 1998. **Secondary use of aspen cavities by tree-roosting big brown bats.** Journal of Wildlife Management 62: 603-611.
- Keisker, Dagmar G. 1987. **Nest tree selection by primary cavity-nesting birds in south-central British Columbia.** Wildlife Report Number R-13. Victoria, BC: British Columbia Ministry of Environment, Lands, and Parks; 67 p.
- Kelleher, Kevin E. 1963. **A study of hole-nesting avifauna of southwest British Columbia.** Vancouver, BC: University of British Columbia; 169 p. M.Sc. thesis.
- Kilham, Lawrence. 1971. **Reproductive behavior of yellow-bellied sapsuckers. I. Preference for nesting in *Fomes* infested aspens and nest hole interrelations with flying squirrels, raccoons, and other animals.** Wilson Bulletin 83: 159-171.
- Klenner, Walter, and David Huggard. BC Ministry of Forests, Kamloops, BC, Canada. [Personal communication].
- Lewis, Susan E. 1995. **Roost fidelity of bats: a review.** Journal of Mammalogy 76: 481-496.
- Li, Pingjun.; Martin, Thomas E. 1991. **Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages.** Auk 108: 405-418.
- Linder, Kathleen A. 1994. **Habitat utilization and behavior of nesting Lewis' woodpeckers (*Melanerpes lewis*) in the Laramie range, southeast Wyoming.** Laramie, WY: University of Wyoming; 98 p. M.Sc. thesis.
- Lindzey, Frederick G.; Meslow, Charles. 1976. **Characteristics of black bear dens on Long Island, Washington.** Northwest Science 50: 236-242.
- Lundquist, Richard W.; Mariani, Jina M. 1991. **Nesting habitat and abundance of snag-dependent birds in the southern Washington Cascade Range.** In: Ruggiero, L. F.; Aubry, K. B.; Carey, A. B.; Huff, M. F., editors. Wildlife and vegetation of unmanaged Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-285. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 221-240.

- Machmer, Machmer; Steeger, Chris. Pandion Ecological Research Ltd., Nelson, BC, Canada. [Personal communication].
- Madsen, Sarah J. 1985. **Habitat use by cavity-nesting birds in the Okanogan National Forest, Washington.** Seattle, WA: University of Washington; 112 p. M.Sc. thesis.
- Mannan, Robert W. 1977. **Use of snags by birds, Douglas-fir Region, western Oregon.** Corvallis, OR: Oregon State University. M.Sc. thesis.
- Mannan, Robert W. 1982. **Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon.** Corvallis, OR: Oregon State University; 114 p. Ph.D. dissertation.
- Mannan, Robert W.; Meslow, E. Charles; Wright, Howard M. 1980. **Use of snags by birds in Douglas-fir forests, Western Oregon.** Journal of Wildlife Management 44: 787-797.
- Manuwal, David A. 1981. **Cavity nesting birds of the Olympic National Forest Washington.** Seattle, WA: Wildlife Science Group, College of Forest Resources, University of Washington; 144 p.
- Marshall, David B.; Chilcote, Mark W.; Weeks, Hal. 1996. **Species at risk. Sensitive, threatened, and endangered vertebrates of Oregon.** Portland, OR: Oregon Department of Fish and Wildlife; unnumbered.
- Martin, Kathy. Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada. [Personal communication].
- Martin, S.K.; Barrett, R.H. 1991. **Resting site selection by marten at Sagehen Creek, California.** Northwest Naturalist 72: 37-42.
- McClelland, B. Riley 1977. **Relationships between hole-nesting birds, forest snags, and decay in western larch and Douglas-fir forests of the northern Rockies.** Missoula, MT: University of Montana; 469 p. Ph.D. dissertation.
- McClelland, B. Riley; Frissle, Sidney S.; Fischer, William C.; Halvorson, Curtis H. 1979. **Habitat management for hole-nesting birds in forests of western larch and Douglas-fir.** Journal of Forestry 77: 480-483.
- McEllin, Shaun M. 1979. **Nest sites and population demographics of white-breasted and pygmy nuthatches in Colorado.** Condor 81: 348-352.
- Medin, Dean E. 1985. **Densities and nesting heights of breeding birds in an Idaho Douglas-fir forest.** Northwest Science 59: 45-52.
- Meiselman, N.; Doyle, Arlene T. 1996. **Habitat and microhabitat use by the red tree vole (*Phenacomys longicaudus*).** American Midland Naturalist 135: 33-42.
- Mellen, Teresa K. 1987. **Home range and habitat use of pileated woodpeckers, western Oregon.** Corvallis, OR: Oregon State University; 96 p. M.Sc. thesis.
- Miller, Alden H.; Bock, Carl E. 1972. **Natural History of the Nuttall woodpecker at the Hastings Reservation.** The Condor 74: 284-294.
- Miller, Eileen; Miller, Donald R. 1980. **Snag use by birds.** In: DeGraaf, R. M., editor. Management of western forests and grasslands for nongame birds. Gen. Tech. Rep. INT-GTR-86. Logan, UT: Interior Research Station, Forest Service, U.S. Department of Agriculture; 337-356.
- Miller, Richard S.; Nero, Robert W. 1983. **Hummingbird-sapsucker associations in northern climates.** Canadian Journal of Zoology 61: 1540-1546.
- Milne, Kathleen A.; Hejl, Sallie J. 1989. **Nest-site characteristics of white-headed woodpeckers.** Journal of Wildlife Management 53: 50-55.

- Morrison, Michael L.; Raphael, Martin G. 1993. **Modeling the dynamics of snags.** Ecological Applications 3: 322-330.
- Mowrey, Robert A.; Zasada, John C. 1984. **Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management.** In: Meehan, W. R.; Merrel, T. R.; Hanley, T. A., editors. Proceedings of a symposium on fish and wildlife relationships in old-growth forests. 1982 April 12-15; Juneau, Alaska. Moorhead City, NC: American Institute of Fishery Research Biologists; 351-356.
- Nelson, S. Kim. 1988. **Habitat use and densities of cavity-nesting birds in the Oregon coast ranges.** Corvallis, OR: Oregon State University; 156 p. M.Sc. thesis.
- Nilsson, Sven G. 1984. **The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition.** Ornis Scandinavica 15(3): 167-175.
- Noble, William O.; Meslow, E. Charles; Pope, Michael D. 1990. **Denning habits of black bears in the central Coast Range of Oregon.** Corvallis, OR: Department of Fisheries and Wildlife, Oregon State University; 28 p.
- O'Conner, Roslyn J. 1978. **Nest-box insulation and the timing of laying in the Wytham Woods population of great tits *Parus major*.** Ibis 120: 534-537.
- Ormsbee, Patricia C.; McComb, William C. 1998. **Selection of day roosts by female long-eared myotis in the central Oregon Cascade Range.** Journal of Wildlife Management 62: 596-603.
- Parish, Roberta; Coupé, Ray; Lloyd, Dennis, editors. 1996. **Plants of Southern Interior British Columbia.** Vancouver, BC: Lone Pine Publishers; 462 p.
- Parsons, Gary L.; Cassis, Gerasimos; Moldenke, Andrew R.; Lattin, John D.; Norman, Neville H.; Miller, Jeffrey C.; Hammond, Paul C.; Schowalter, Timothy D. 1991. **Invertebrates of the H. J. Andrews Experimental Forest, Western Cascades Range, Oregon. V: An annotated list of insects and other arthropods.** Gen. Tech. Rep. PNW-GTR-290. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 168 p.
- Peterson, Barbara; Gauthier, Gilles. 1985. **Nest site use by cavity-nesting birds of the caribou parkland, British Columbia.** Wilson Bulletin 97: 319-331.
- Peterson, Roger T.; Mountford, Guy; Hollom, P.A.D. 1993. **The Audubon Society field guide to birds of Britain and Europe.** Boston, MA: Houghton Lifflin; 261 p.
- Pojar, Jim; MacKinnon, Andy, editors/compiler. 1994. **Plants of coastal British Columbia.** Vancouver, BC: Lone Pine Publishers; 526 p.
- Putnam, Betsy J. 1983. **Songbird responses of precommercially thinned and unthinned stands in east-central Washington.** Corvallis, OR: Oregon State University; 58 p. M.Sc. thesis.
- Raphael, Martin G.; Jones, Lawrence L.C. 1997. **Characteristics of resting and denning sites of American martens in central Oregon and western Washington.** In: Proulx, G.; Bryant, H. N.; Woodward, P. M., editors. Martens: taxonomy, ecology, techniques and management. Edmonton, AB: Provincial Museum of Alberta; 146-165.
- Raphael, Martin G.; White, Marshall. 1984. **Use of snags by cavity-nesting birds in the Sierra Nevada.** Wildlife Monographs 86: 1-66.
- Rasheed, Sadig A.; Holroyd, Susan L. 1995. **Roosting habitat assessment and inventory of bats in the Mica Wildlife Compensation Area.** Columbian Basin Fish and Wildlife Compensation Program. Nelson, BC: BC Hydro and BC Environment; 77 p.
- Schreiber, Barry; deCalesta, David S. 1992. **The relationship between cavity-nesting birds and snags on clearcuts in western Oregon.** Forest Ecology and Management 50: 299-316.

- Scott, Virgil E.; Whelan, Jill A.; Svoboda, Paul L. 1980. **Cavity-nesting birds and forest management**. In: DeGraff, R.M., technical coordinator. Proceedings of a workshop on management of western forests and grasslands for nongame birds. 1980 February 11-14; Salt Lake City, UT. Gen. Tech. Rep. INT-86. Fort Collins, CO: Intermountain Research Station, Forest Service, U.S. Department of Agriculture; 311-324.
- Sedgwick, James A.; Knopf, Fritz L. 1990. **Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains**. Journal of Wildlife Management 54: 112-124.
- Shigo, Alex L.; Kilham, Lawrence. 1968. **Sapsuckers and *Fomes ignarius* var. *populinus***. Res. Note NE-RN-84. Saint Paul: Northeast Research Station, Forest Service, U.S. Department of Agriculture; 2 p.
- Spencer, Wayne D. 1987. **Seasonal rest-site preferences of pine martens in the northern Sierra Nevada**. Journal of Wildlife Management 51: 616-621.
- Spring, Lowell W. 1965. **Climbing and pecking adaptations in some North American woodpeckers**. Condor 67: 457-488.
- Steeger, Cristoph; Hitchcock, Christine L. 1998. **Influence of forest structure and diseases on nesting habitat selection by red-breasted nuthatches**. Journal of Wildlife Management 62: 1349-1358.
- Steeger, Cristoph; Machmer, Marlene M. 1996. **Use of trees by cavity nesters in managed and unmanaged Interior Cedar—Hemlock stands of southern British Columbia**. In: Bradford, P.; Manning, T.; I'Anson, B., editors. Proceedings of the Workshop on Wildlife Tree/Stand-level Biodiversity. Proceedings of the workshop on wildlife tree/stand-level biodiversity; October 17-18, 1995, Victoria, BC; Victoria, BC: British Columbia Ministry of Environment, Lands, and Parks, and Ministry of Forests; 45-54.
- Steeger, Cristoph ; Machmer, Marlene M.; Walters, Eric. 1996. **Ecology and management of woodpeckers and wildlife trees in British Columbia**. Delta, BC: Environment Canada, Fraser River Action Plan, Canadian Wildlife Service; 23 p.
- Stelmock, James J.; Harestad, Alton S. 1979. **Food habits and life history of the clouded salamander (*Aneides ferreus*) on northern Vancouver Island**. Syesis 12: 71-75.
- Sutherland, Glenn D.; Gass, Clifton Lee; Thompson, Peter A.; Lertzman, Kenneth. P. 1982. **Feeding territoriality in migrant rufous hummingbirds: defense of yellow-bellied sapsucker feeding sites**. Canadian Journal of Zoology 60: 2046-2050.
- Sydean, William J.; Guntert, Marcel. 1983. **Winter communal roosting in the pygmy nuthatch**. In: Davis, J. W.; Goodwin, G. A.; Ockenfels, R. A., technical coordinators. Snag habitat management. Gen. Tech. Rep. RM-99. Fort Collins, CO: Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture; 121-124.
- Tashiro-Vierling, K.Y. 1994. **Population trends and ecology of the Lewis' woodpecker (*Melanerpes lewis*) in southeastern Colorado**. Boulder, CO: University of Colorado; 73 p. M.A. thesis.
- Thomas, Jack W.; Anderson, R. G.; Maser, Chris; Bull, Evelyn L. 1979. **Snags**. In: Thomas, J. W., editor. Wildlife habitats in managed forests. the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, D.C.: Forest Service, U.S. Department of Agriculture; 60-77.
- Troetschler, Ruth G. 1976. **Acorn woodpecker breeding strategy as affected by starling nest-hole competition**. Condor 78: 151-165.
- van Woudenberg, Astrid M. 1992. **Integrated management of flammulated owl breeding habitat and timber harvest in British Columbia**. Vancouver, BC: University of British Columbia. M.Sc. thesis; 56 p.

- von Haartman, Lars. 1957. **Adaptation in hole-nesting birds**. *Evolution* 11: 339-347.
- Vonhof, Maarten J. 1996. **A survey of the abundance, diversity, and roost-site preferences of bats in the Pend d'Oreille valley, British Columbia**. The Columbia Basin Fish and Wildlife Compensation Program. Nelson, BC: BC Hydro and BC Environment; 69 p.
- Weir, Richard 1995. **Diet, spatial organization, and habitat relationships of fishers in south-central British Columbia**. Burnaby, BC: Simon Fraser University; 139 p. M.Sc. thesis.
- Whitaker, John O. 1993. **The Audubon Society field guide to North American mammals**. Toronto, ON: Random House; 745 p.
- Zarnowitz, Jill E.; Manuwal, David A. 1985. **The effects of forest management on cavity-nesting birds in northwestern Washington**. *Journal of Wildlife Management* 49: 255-262.