Characteristics and densities of Williamson's Sapsucker nest trees in British Columbia

L.W. Gyug, C. Steeger, and I. Ohanjanian

Abstract: We characterized Williamson's Sapsucker (*Sphyrapicus thyroideus* (Cassin, 1852)) nest trees in southern British Columbia from 1995 to 2008 to determine the nesting requirements of this endangered species in Canada. In the East Kootenay (n = 32) and the Okanagan (n = 157) regions where western larch (*Larix occidentalis* Nutt.) occurred, 81% and 75% of the nest trees were western larch, respectively. In regions west of the Okanagan Valley where western larch did not occur (n = 73), 77% of the nest trees were trembling aspen (*Populus tremuloides* Michx.). Conifer nest trees were larger (72 cm DBH), on average, than broad-leaved nest trees (35 cm DBH), and this pattern was consistent across the breeding range of Williamson's Sapsucker. Live western larch >67 cm DBH with either broken or dead tops were the trees with the highest frequency (20%) among the trees estimated to be suitable for nesting, primarily because these larch tended to be infected with heart rots. Based on observed densities, targets should be 1.36 suitable nest trees/ha in managed stands, although in many instances such as aspen patches, this target will only be met in portions of the nesting territories. The recommended stand structure for long-term maintenance of high nest-tree density in western larch stands is for ≥20 trees/ha with DBHs >57 cm and 60–150 trees/ha with DBHs >22 cm.

Résumé : De 1995 à 2008, nous avons caractérisé les arbres utilisés pour la nidification par le pic de Williamson (*Sphyrapicus thyroideus* (Cassin, 1852)) dans le sud de la Colombie-Britannique afin de déterminer les exigences de nidification de cette espèce en voie de disparition au Canada. Dans les régions de East Kootenay (n = 32) et de l'Okanagan (n = 157), où l'on trouve du mélèze de l'Ouest (*Larix occidentalis* Nutt.), respectivement 81 et 75 % des arbres utilisés pour la nidification étaient des mélèzes de l'Ouest. Dans les régions situées à l'ouest de la vallée de l'Okanagan où il n'y a pas de mélèze de l'Ouest, 77 % des arbres utilisés (n = 73) étaient des peupliers faux-trembles (*Populus tremuloides* Michx.). Parmi les arbres utilisés pour la nidification, les conifères étaient en moyenne plus gros (DHP = 72 cm) que les feuillus (DHP = 35 cm) partout dans l'aire de nidification du pic de Williamson. Les mélèzes vivants avec un DHP >67 cm et dont la tête était cassée ou morte avaient la fréquence la plus élevée (20 %) parmi les arbres jugés adéquats pour la nidification, essentiellement parce qu'ils avaient tendance à être infectés par des caries de cœur. Sur la base des densités que nous avons observées, l'objectif devrait être de 1,36 arbres/ha adéquats pour la nidification dans les peuplements aménagés bien que dans plusieurs cas, notamment dans les bouquets de peuplier, cette cible sera atteinte seulement dans certaines parties des territoires de nidification. Pour assurer le maintien à long terme d'une forte densité d'arbres adéquats pour la nidification dans les peuplements de mélèze de l'Ouest, nous recommandons une structure de peuplement caractérisée par au moins 20 arbres/ha avec un DHP >57 cm et 60–150 arbres/ha avec un DHP >22 cm.

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Introduction

Williamson's Sapsucker (*Sphyrapicus thyroideus* (Cassin, 1852)) is a medium-sized woodpecker specialized for feeding on tree sap. It breeds in mixed-conifer forests of the mountains of western North America. In Canada, it is restricted to the southern interior of British Columbia, where in 2005, the population was listed as endangered based largely on small estimated population sizes and the rate of habitat loss of mature western larch (*Larix occidentalis* Nutt.) forests owing to land clearing and timber harvesting (COSEWIC 2005).

Williamson's Sapsucker nests exclusively in cavities excavated in standing live trees or standing dead trees (snags). The first summary of nest-tree use was by Crockett (1975), who summarized most of the available published records (n = 44) of Williamson's Sapsucker nests. The majority of nests in the southern Rocky Mountains were in trembling aspen (*Populus tremuloides* Michx.), with ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) infrequently used. The majority of nests in California were in Sierra-Cascade lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *murrayana* Balf.), with other conifers used less frequently. None of Crockett's (1975) cited records were from British Columbia, and up to that date, there had been no published nest studies of Williamson's Sapsuckers in western larch forests. Campbell et al. (1990) published records for 28 Williamson's Sapsucker nests in British Columbia, of which 43% were in western larch. Since 1975 other studies have provided detailed data on Williamson's Sapsucker nest trees in the United States, including Bull et al. (1986), Crockett and Hadow (1975), Conway and Martin

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(1993), Dobbs et al. (1997), McClelland (1977), Nielsen-Pincus and Garton (2007), and Raphael and White (1984). These studies found that Williamson's Sapsucker nested primarily in trembling aspen in the southern Rocky Mountains and primarily in conifers elsewhere.

Up until 1954, all records of Williamson's Sapsucker in British Columbia were from western larch forests, but thereafter, the species underwent a westward range expansion into ponderosa pine and mixed ponderosa pine – Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – trembling aspen forests (Gyug et al. 2007). Because Williamson's Sapsucker was found in two very different forest types in different regions of British Columbia after its range expansion, it was impossible to formulate a single definition of the species' breeding habitat using only stand characteristics.

Targets to meet nest-tree requirements for Williamson's Sapsucker in managed forests have previously been estimated in terms of providing an adequate density of suitable snags for nesting (Thomas et al. 1979; Raphael and White 1984; Conway and Martin 1993), and in terms of the densities of both snags and the live trees from which those snags develop (Bull et al. 1980). However, none of these recommendations recognized the contribution of live trees as suitable nest trees for Williamson's Sapsucker, even though about half or more of nest trees used were live in the studies of both Raphael and White (1984) and Bull et al. (1980). The characteristics of suitable nest trees and the density and dispersion of these trees had yet to be determined for Williamson's Sapsucker in British Columbia.

Studies (e.g., Gyug et al. 2007, 2009) began in British Columbia in 1996 to locate Williamson's Sapsucker nests and were expanded in 2006 to better describe and define the species' habitat requirements, and to provide recommendations for timber harvesting prescriptions that could mitigate losses of nest trees and other habitat features. Here we describe the characteristics of Williamson's Sapsucker nest trees and quantify their densities and frequencies of occurrence among different tree species, sizes, and condition classes within 225 m of nests. These results are intended to guide the development of a management plan for this endangered species in British Columbia.

Materials and methods

The study area was the southern interior of British Columbia within the breeding range of Williamson's Sapsucker (Gyug et al. 2007). This area included three geographical regions: the East Kootenay near Cranbrook; the Okanagan, east of the Okanagan Valley to Grand Forks; and the western region, west of the Okanagan Valley near Merritt and Princeton (Fig. 1). In the East Kootenay and Okanagan, Williamson's Sapsuckers are associated primarily with mixed-conifer forests that include western larch, while in the western region, they are associated primarily with mixed forests of ponderosa pine, Douglas-fir, and trembling aspen.

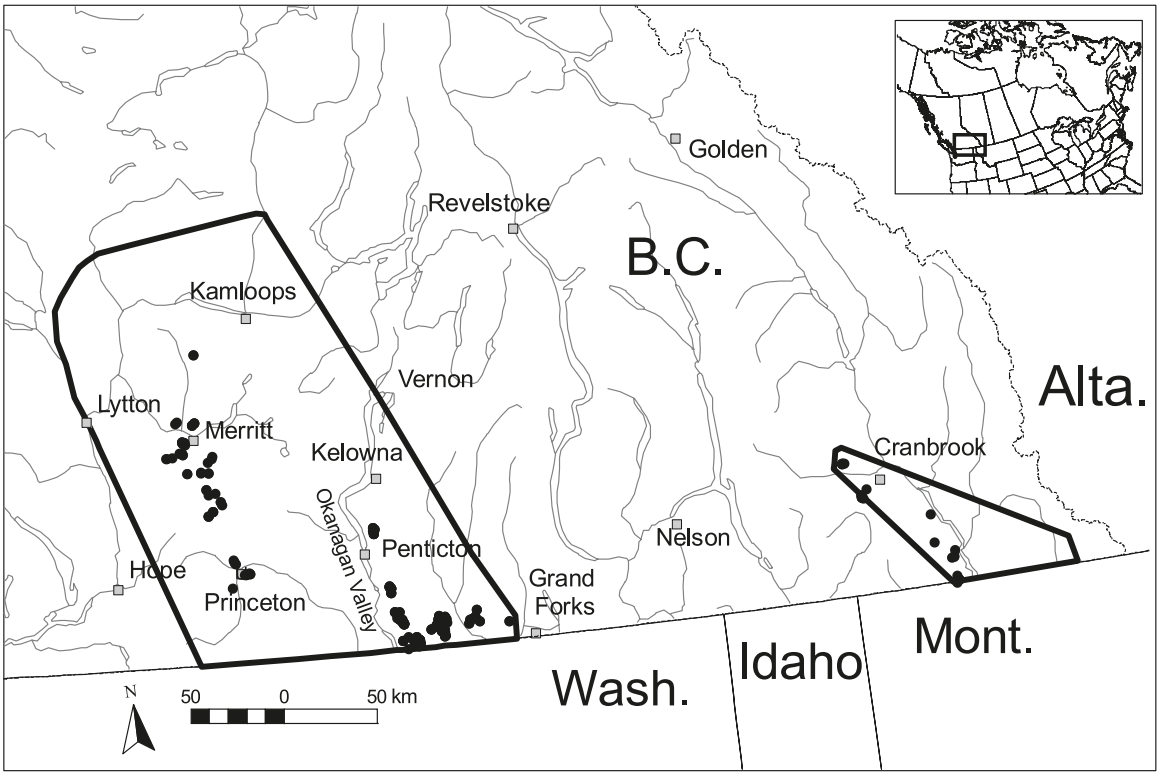
From 1996 to 2008, Williamson's Sapsucker nests were primarily located by following up on detections made during wide-ranging-call and drum-playback surveys, as described in Gyug et al. (2007). These surveys were intended to, first, determine the areas occupied by Williamson's Sapsucker in British Columbia (Gyug et al. 2007), and then, second, sample all types of habitats within that occupied area for nest occurrence (L. Gyug, C. Steeger, I. Ohanjanian, unpublished results, 2004–2009). Some additional nests were located during preliminary studies in 1995. Measurements made at most nest trees included tree species, diameter at breast height (DBH), tree height, nest entrance height, nest entrance aspect, tree condition using wildlife tree classification (WTC) code, and a qualitative description of the type of decay if any was apparent. The WTC code used was from Resources Inventory Standards Committee (2004) based on Thomas et al. (1979), with the following condition classes: 1, live, healthy; 2, live, unhealthy; 3, recently dead; 4 to 7, progressively more decayed; 8, dead, soft, and less than one-third of the original height.

A 225 m radius around each nest (16 ha) was chosen as the sampling area because this area was assumed to approximate the minimum breeding territory size based on mean nearest-neighbor nest distances of 450 m in the Okanagan and East Kootenay (Gyug et al. 2007). Sampling areas were centered on 41 nests in the western region, 68 nests in the Okanagan, and 28 nests in the East Kootenay (Fig. 1). Data were collected to determine the densities of suitable Williamson's Sapsucker nest trees and the frequencies of occurrence of suitable nest trees among different tree species, sizes, and condition classes. Suitable nest trees included the known nest trees around which the plots were centered, as well as any trees occurring in the sample plots that were either known to be used for nesting by Williamson's Sapsucker in a previous year or had both older and recently excavated nest cavities with entrances in the size range made and used by sapsuckers (3–5 cm diameter). We found (this study) that almost all Williamson's Sapsucker nest trees had both old and new holes, so we did not consider trees that only had very recent or fresh cavities as possible Williamson's Sapsucker nest trees, as these holes were most likely excavated by Red-naped Sapsuckers (*Sphyrapicus nuchalis*) or by other woodpeckers.

Vegetation sampling for standing live and dead trees was based on the protocol of the Birds and Burns Network (2005) using 50 m transects. For each 50 m transect, sampled widths from each side of the centerline were 1 m for small trees 8–22 cm DBH, 3 m for large live trees 23–57 cm DBH, and 10 m for both large dead standing trees ≥23 cm DBH and ≥1.4 m in height and very large live trees ≥58 cm DBH. Plot sizes were 0.01, 0.03, and 0.1 ha for the three size classes, respectively. For plots sampled in 2006 and 2007, 50 m transects were used, but for plots sampled in 2008 located between 60 and 225 m from the nest tree, circular fixed-radius plots of equivalent sizes were used: 5.64 m radius for 0.01 ha plots, 9.77 m radius for 0.03 ha plots, and 17.84 m radius for 0.1 ha plots. Recorded for each live or dead standing tree within a plot were the following: species, DBH within 5 cm classes, tree condition using WTC code, whether the tree was a known Williamson's Sapsucker nest tree, and the presence of recent and old nest cavities in the tree.

The 225 m radius was divided into two strata based on distance from the nest. Based on the Birds and Burns Network (2005) protocol, the area within 60 m of the nest tree was sampled using four 50 m transects laid out in cardinal directions. The north and south transects began at the nest

Fig. 1. Location of 139 Williamson's Sapsucker nests (black dots) in the southern interior of British Columbia for which vegetation data was collected from 2004 to 2008. The map shows the extent of occurrence (heavy black line), a minimum convex polygon around all known and suspected breeding locations in British Columbia (Gyug et al. 2007).



tree, and the east and west transects began 10 m from the nest tree. The area within 60–225 m from the nest tree (about 15 ha) was sampled by 15 plots placed randomly. The sampling intensity was lower in this area (1 plot/ha) than within 60 m from the nest tree (4 plots/ha) because available funds did not permit such intensive sampling over the larger area.

The frequency of suitable nest trees within a single species, size, or condition class was calculated from the tally of suitable nest trees divided by the total tally of trees in the class. The known nest trees at the center of the plots were sampled by design (probability of inclusion in the sample = 1) and therefore could not be included in the tallies of suitable nest trees (where probability of inclusion in the sample is less 1) without adjusting for probability of inclusion in the sample. The tally for each central nest tree was multiplied by the probability of its encounter within any plot in the 16 ha area before inclusion in the calculation of frequency. For example, any large snag would have a probability of inclusion in the sample of 0.119 (4 × 0.1 ha plots at the nest tree plus 15 × 0.1 ha plots in the remainder of the 16 ha area = 11.9% of total area).

Densities of suitable nest trees would be biased upward if the nest trees around which the plots were centered were included in the density calculations. Therefore densities of suitable nest trees were estimated without including the central nest tree, and the densities were contrasted in a two-factor ANOVA using the distance strata (0–60 and 60–225 m from the nest tree) and geographical region within British Columbia as the factors.

Throughout the text, the term tree refers to both live trees and standing dead trees. Where reference is only to live trees or only to standing dead trees, also called snags, then one or the other is specified. Means were presented in text and tables along with the standard error of the mean (SE) and sample size (n). ANOVA was used to test for significant differences in nest-tree characteristics due to different factors at the $\alpha = 0.05$ level. Factors included tree species, region, and tree status (live or dead). Different tree species were used as nest trees in different regions within British Columbia, thereby making some comparisons impossible because of missing cells within the study design, or because some cells had very small sample sizes requiring grouping of some data for analyses. Analysis of covariance (ANCOVA) was used to test for differences due to factors in nest-tree characteristics where these were correlated. Nest trees were only used once in the analyses, even if they were known to be used for a number of years. Where more than one nest hole was known to be used in a tree, the mean within-tree nest height was used as the nest height for each tree. F statistics are presented with numerator and denominator degrees of freedom as subscripts. Scheffé's test was used to test for differences among several means when the ANOVA showed a significant difference among several groups. Chi-square tests were used to test for differences in proportions among groups.

Results

Nest-tree characteristics

Western larch was the species most frequently used as a

nest tree by Williamson's Sapsucker in the East Kootenay and Okanagan regions of British Columbia (81% and 75%, respectively, Table 1). Six other infrequent nest-tree species (Table 1) were found, including water birch (*Betula occidentalis* Hook.), which had not been previously reported as a Williamson's Sapsucker nest tree. West of the Okanagan, where western larch is almost entirely absent from areas inhabited by Williamson's Sapsucker, trembling aspen was the most frequently used (77%, Table 1) nest tree.

The mean (±SE) DBH of coniferous nest trees (72.4 ± 1.9 cm; $N = 172$) was significantly larger ($F_{[1,257]} = 178.4$, $p < 0.001$) than that of broad-leaved nest trees (35.4 ± 1.1 cm; $N = 87$). The only exception to this finding was the single black cottonwood (*Populus trichocarpa* Torr. & Gray) nest tree (Table 1), which was 37 cm larger in diameter than the next largest broad-leaved nest tree. The maximum DBH attainable by trembling aspen and water birch in the study area is lower than the mean DBH of the coniferous nest trees. Clearly, tree size alone is not the only characteristic used by Williamson's Sapsucker to select nest trees, and any analysis of nest-tree characteristics must separate the effect of tree size from the effect of tree species or species group.

The mean diameter of western larch nest trees was significantly greater in the Okanagan than in the East Kootenay, and was significantly greater for live trees than for dead trees (Tables 1 and 2). Other coniferous nest trees including Douglas-fir, ponderosa pine, and hybrid spruce (*Picea glauca* × *Picea engelmannii*) were grouped for contrasts because of small sample sizes. For this group of conifers, there were significant differences in mean DBH among the three regions, with a smaller mean DBH in the East Kootenay than in either the western region or the Okanagan, but no significant difference in mean DBH by tree status (live or dead, Tables 1 and 2). The mean DBH of trembling aspen nest trees varied significantly by region, with larger trees used in the Okanagan than in the western region (Tables 1 and 2). Water birch as a nest tree was only found in the Okanagan (Table 1), and these trees had a significantly smaller ($F_{[1,27]} = 4.89$, $p = 0.036$) mean DBH than trembling aspen nest trees in the same region (Table 1).

Nest-tree height was significantly correlated with DBH ($r = 0.67$, $F_{[1,238]} = 194.2$, $p < 0.001$), so this variable was analyzed as a covariate of DBH. Factors examined included tree species (western larch, other conifers grouped, and trembling aspen) and tree status (live or dead). Nest-tree height varied significantly with tree status ($F_{[1,223]} = 8.64$, $p = 0.004$), with dead nest trees shorter than live nest trees. There was no significant variation in nest-tree height among species or species group that was not already accounted for by significant differences in DBH ($F_{[2,223]} = 0.95$, $p = 0.39$).

Nest height was significantly correlated with both DBH ($r = 0.73$, $F_{[1,243]} = 272.2$, $p < 0.001$) and tree height ($r = 0.77$, $F_{[1,235]} = 332.8$, $p < 0.001$). Analyzing nest height as a covariate of DBH and tree height showed that it did not vary significantly with tree status (live or dead) ($F_{[1,219]} = 0.20$, $p = 0.65$) or by species – species group (western larch, other conifers, and trembling aspen) ($F_{[2,219]} = 0.04$, $p = 0.96$). Mean nest height as a percentage of tree height was significantly lower ($F_{[2,\ 313]} = 18.34$, $p < 0.001$) for trembling aspen (41.9% ± 2.3%, $n = 86$) than for western larch (56.8% ± 1.4%, $n = 202$) and for other conifers (60.4% ± 4.0%, $n = 28$).

Nests were found at heights from 1 to 44 m above ground, covering almost the entire possible range of tree heights available (Table 1). We recorded renesting in 65 trees, with some trees observed to be used for up to 5 years. For trees that had renesting, mean within-tree standard deviation (SD) of nest height (1.6, $n = 65$) was much lower than the among-tree SD of nest height (7.9, $n = 245$) for all nest trees. For species with >10 trees that had renesting, and only including the trees in which there was renesting, mean within-tree SD of nest height was lower than the among-tree SD both for trembling aspen (0.6 vs. 4.4, $n = 13$) and for western larch (1.9 vs. 7.3, $n = 45$). Nests were not being excavated randomly in nest trees but were placed consistently closer together than would be expected based on the variation of the overall nest height sample.

The majority of western larch, trembling aspen, and Douglas-fir nest trees were alive rather than standing dead (Table 1). The percentage of western larch nest trees <55 cm DBH that were alive (64%, $n = 33$) was significantly lower ($\chi^2 = 13.67$, $p < 0.001$) than the percentage of western larch ≥55 cm DBH that were alive (92%, $n = 108$). For other coniferous trees as a group, the percentage of nest trees <55 cm DBH that were alive (25%, $n = 16$) was lower (but not significantly, $\chi^2 = 3.23$, $p = 0.07$) than the percentage of conifers ≥55 cm DBH that were alive (56%, $n = 16$). The percentage of coniferous nest trees that were alive increased with increasing tree diameter because dead nest trees tended to be smaller in diameter than live nest trees (Table 1). For trembling aspen, the percentage of live nest trees did not vary with tree diameter but was the same (71.4%) for both small (<40 cm DBH, $N = 56$) and large (≥40 cm DBH, $N = 21$) nest trees ($\chi^2 < 0.001$, $p > 0.999$).

The majority of live western larch ($n = 117$) nest trees had either broken tops (54%) or dead tops (21%). Fire or other injury scars that had penetrated through the bark into the wood were found on 33% of the live western larch nest trees. Only 15% of trees did not show signs of any of these three conditions. However, all live western larch nest trees would have been infected with internal decay or heartwood rots, even though the infection was not always outwardly evident, because otherwise the tree would not have been suitable for nest excavation, as is true for most woodpeckers species (Jackson and Jackson 2004). The majority of dead western larch ($n = 17$) nest trees had broken tops (65%).

Only one nest tree was found where the only nest hole in the tree was the active nest. All other nest trees had one or more old nest holes. While many of these were probably old Williamson's Sapsucker nest holes, our counts included all nest holes, many of which may have been excavated by other cavity-nesting birds. There were significant differences in numbers of old nest holes per tree among tree species groups ($F_{[2,140]} = 5.68$, $p = 0.004$; Fig. 2). Aspen and birch nest trees had significantly fewer previous nest holes (5.7 ± 0.1, $N = 43$) than western larch nest trees (16.5 ± 0.2, $N = 85$). The number of holes in ponderosa pine – Douglas-fir – black cottonwood nest trees as a group (15.7 ± 1.4, $N = 15$), while more similar to that of western larch, was not significantly different from the number of nest holes in both other

Table 1. Williamson's Sapsucker nest-tree DBH and height and nest height grouped by species or species group, region, and tree status (live or dead) for nest trees sampled in British Columbia from 1995 to 2008.

		Nest-tree DBH (cm)				Nest-tree height (m)				Nest height (m)			
Tree species and region	Status	n^a	Mean	SE	Range	n^a	Mean	SE	Range	n^a	Mean	SE	Range
Western larch													
Okanagan	Live	102	78.5	2.4	29–163	100	30.1	0.7	15–49	102	17.9	0.8	3–44
	Dead	15	64.0	5.1	34–109	15	18.9	2.7	7–34	15	10.0	1.5	3–23
East Kootenay	Live	21	64.0	4.8	38–104	20	25.5	1.4	15–35	21	12.4	1.2	4–20
	Dead	5	46.2	11.8	27–92	4	17.7	10.4	1–46	5	10.2	7.5	2–40
Other conifers (grouped)[b]													
Okanagan													
Py, 1; Fd, 1; Sx, 1	Live	3	65.0	3.6	60–72	3	23.0	3.5	19–30	3	14.2	1.4	12–16
Py, 3; Fd, 2; Sx-2	Dead	7	55.3	6.3	42–86	7	17.6	3.8	5–32	7	12.6	3.0	5–26
West													
Py, 3; Fd, 4	Live	7	84.9	10.1	35–120	4	25.8	3.8	15–32	6	17.8	3.8	2–30
Py, 8; Fd, 2	Dead	10	66.7	8.2	39–114	10	22.7	3.8	6–40	9	12.8	2.2	3–23
East Kootenay													
Fd, 3	Live	3	36.7	3.8	30–43	3	14.6	3.3	8–19	3	6.2	0.8	5–7
Py, 1; Fd, 1	Dead	2	48.5	3.5	45–52	2	24.5	7.5	17–32	2	13.0	4.0	9–17
Trembling aspen													
Okanagan	Live	12	42.3	3.4	26–59	12	25.9	1.2	20–32	12	12.8	1.5	2–20
	Dead	8	37.1	2.9	25–41	8	16.9	2.1	9–25	8	8.4	1.4	3–13
West	Live	42	33.1	1.2	22–54	42	18.4	0.8	9–31	42	7.4	0.9	1–36
	Dead	14	33.4	1.6	23–46	13	15.2	1.6	6–26	14	6.3	0.5	4–10
East Kootenay	Live	1	27.5	—	—	1	21.0	—	—	1	9.7	—	—
Water birch													
Okanagan	Live	3	37.0	3.2	32–43	3	13.0	1.7	10–16	3	5.7	1.9	2–8
	Dead	6	29.3	1.6	24–33	6	13.0	2.0	8–20	6	6.3	1.0	3–10
Black cottonwood													
Okanagan	Live	1	96.0	—	—	1	25.0	—	—	1	16.5	—	—

[a]Nest trees used for >1 year were only included once. Sample size (n) may differ because tree and nest height were not available for all nest trees. Where renesting was found in a single tree over a number of years, the mean nest height was used.

[b]For grouped conifers, the numbers of each tree species are given under the region using the following two-letter codes: Py, ponderosa pine; Fd, Douglas-fir; Sx, hybrid white spruce.

Table 2. Statistics of the analysis of variance (ANOVA) comparing the DBH of Williamson's Sapsucker nest trees by tree species, region, and tree status (live or dead).

	ANOVA statistics		
Factors	df[a]	*F*	*p*
Within tree species: western larch			
Region (Okanagan and East Kootenay)	1,139	5.93	0.016
Status	1,139	5.89	0.017
Region × status	1,139	0.06	0.81
Within tree species group: other conifers			
Region	2,26	4.79	0.017
Status	1,26	0.35	0.56
Region × status	1,26	0.90	0.42
Within tree species: trembling aspen			
Region (Okanagan and western region)	1,75	8.18	0.006
Status	1,75	1.16	0.28
Region × status	1,75	1.50	0.22
Within tree species: water birch			
Status	1,7	5.99	0.044

[a]Degrees of freedom of the numerator followed by denominator.

species groups. There did not appear to be any favoured nest entrance orientation. There were almost identical proportions of active nest holes facing each quadrant: 25% facing north, 24% east, 26% south, and 24% west ($N = 290$).

Nest-tree frequency and density

The 16 675 live trees and 3038 standing dead trees tallied in our sampling included 196 trees with nest evidence, 21% of which ($n = 42$) we considered to be suitable nest trees for Williamson's Sapsucker (Table 3). Unhealthy, live western larches with dead or broken tops ≥68 cm DBH were three times and 53–67 cm DBH were two times more suitable for nesting than trees of any other species, condition, or size class (Table 3). The next trees most frequently suitable for nesting were dead western larches from decay classes 3–7, and large (≥38 cm DBH) live broad-leaved trees and dead large (≥23 cm DBH) broad-leaved trees in decay classes 3–7, including trembling aspen, water birch, and black cottonwood. Only one nest was found in trees <22.5 cm DBH (a dead aspen of 22.1 cm DBH). No nests were found in lodgepole pines (*Pinus contorta* Dougl. ex Loud.) (Table 3).

Densities of suitable nest trees were significantly greater within 60 m of the known nest tree ($F_{[1,270]} = 5.73$, $p = 0.017$), even when the known nest tree was not included in the sample, i.e., the density was underestimated within that area (Table 4). If the density of the known nest tree, i.e., 1/ha, was added to the estimated density of other suitable nest trees, then there were an estimated 1.36 suitable nest trees/ha within 60 m of known nest trees, which was much greater than the estimated 0.14/ha >60 m from known nest trees. Clearly, suitable nest trees appeared to be clumped and not spread evenly across the breeding territories. There were no significant differences among regions ($F_{[2,270]} = 0.97$, $p = 0.38$).

Discussion

Nest-tree size and age

In British Columbia the frequency of suitable nest trees was lower as tree DBH decreased within each tree species or species group. Western larch nest trees were smaller, on average, in the East Kootenay than in the Okanagan. Relative densities of Williamson's Sapsucker in the East Kootenay were lower than those in the Okanagan (Gyug et al. 2007) — this finding may be related to nest-tree suitability or availability. We cannot therefore use mean nest-tree size from one region alone as a baseline for setting minimum tree-size targets without a better understanding of the history and dynamics of the stands, the factors that make individual trees suitable in different stands, and the responses of Williamson's Sapsucker populations to the availability of this resource.

The lower size limit on Williamson's Sapsucker nest trees in British Columbia was 22.0 cm DBH, with trees smaller than that considered unsuitable. However, this limit would not hold for every locality; for example, in Rocky Mountain National Park in Colorado mean aspen nest-tree DBH was 23.5 cm, about 10 cm smaller than that in British Columbia, and nesting occurred in trees with a DBH as small as 18 cm (Crockett 1975). Aspen nest trees in our study sites were in the 90–130 year range (L. Gyug, unpublished results for four nest trees, 2008), but the age of nest trees or stands elsewhere has not been reported for Williamson's Sapsucker. Winternitz and Cahn (1983) also found aspen nest trees (for other cavity nesters) impossible to age reliably because of internal decay, but their research showed that it took about 100 years for aspen in Colorado to reach a DBH of 18 cm, making them large enough for nesting.

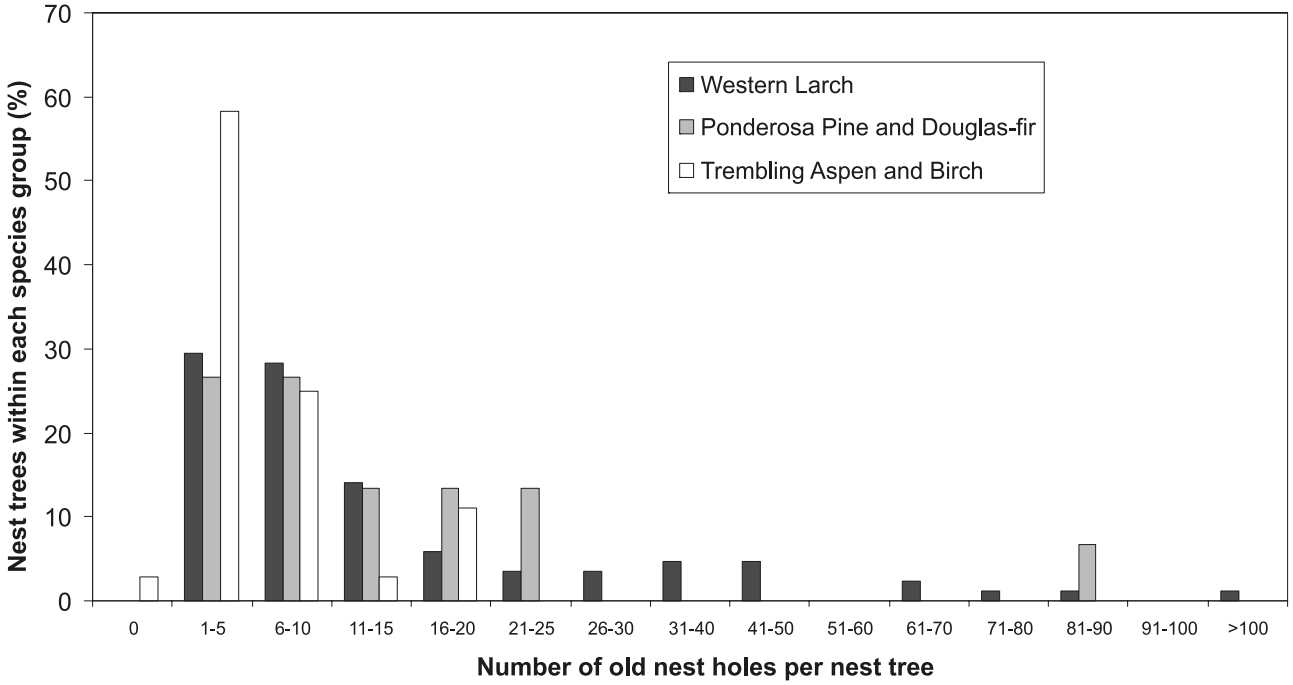
In western larch, heartwood rots are relatively rare in young trees and uncommon until trees reach an "overmature" state (Carlson et al. 1995), usually >200 years old (McClelland and McClelland 2000). Large veteran larch >70 cm DBH were typically found to be 350–500 years old in northwestern Montana (Lanner 1995). The only western larch nest tree that we aged was 543 years (based on annual ring counts from the stump of a nest tree cut down for firewood), placing it into a very old class of trees similar to those of veteran western larch nest trees found elsewhere. In the relatively small live larches were we found nesting, heartwood rots had typically entered the tree through trunk injuries from logging >20 years prior to our study.

Nest-tree characteristics were relatively consistent across the North American breeding range of Williamson's Sapsucker (Table 5). Coniferous nest trees were consistently larger, averaging >60 cm DBH in most localities, than trembling aspen nest trees, which averaged <40 cm DBH. The majority of western larch nest trees (74%–100%) were alive, but the proportion of living trees was much smaller (6%–60%) for other conifers. The proportion of aspen nest trees that were alive varied considerably from 14% to 73% among study localities. Tree decay characteristics and the pattern of development of this decay were likely more important than the simple status of the nest trees as alive or dead.

Nest-tree suitability

While, in general, nest height was correlated with tree

Fig. 2. Frequency of the number of old nest holes (of any bird species) per Williamson's Sapsucker nest tree grouped by tree species, British Columbia, 1996–2006.



DBH and height, there was a considerable amount of variation. Year-to-year variation in nest height was also larger among trees than within trees, indicating that the suitable internal decay conditions for nesting may occur at almost any height on a tree, but that in any given tree, nest excavation was concentrated in local areas of decay. The lack of any apparent choice of particular direction for nest entrance orientation may indicate that decay characteristics and position of that decay in the tree are more important, or that nest entrance orientation is simply not a significant factor.

Other than that the tree must contain some internal decay, adequate definitions of nest-tree suitability based only on the physical properties or the state of decay of the wood have yet to be developed. Williamson's Sapsuckers excavated nests in aspen with internal decay that were softer, on average, than those used by Hairy Woodpeckers (*Picoides villosus*) and Red-naped Sapsuckers, and similar in hardness to those used by the Downy Woodpecker (*Picoides pubescens*) (Schepps et al. 1999). However, this observation may be an oversimplification based on only one species of nest tree and would not explain the observed behaviour of Williamson's Sapsuckers drilling through extremely hard western larch sapwood to reach internal decay in the heartwood. Downy Woodpeckers appear to be incapable of such a feat, and we suspect that if the methods of Schepps et al. (1999) were to be repeated over a wider range of tree species, Williamson's Sapsucker would not be classified as a weak excavator on par with the Downy Woodpecker.

Williamson's Sapsucker may use the same western larch nest trees for many years if these trees are relatively rare and little choice is available. However, the tendency to use the same aspen nest trees for many years (Fig. 2) may indicate that they are choosing trees with extensive internal decay that are relatively softer than the trees selected by the Red-naped Sapsucker, which in British Columbia will often excavate nest holes in aspen trees that have no previous holes (Kathy Martin, personal communication, 2009).

Trembling aspen and water birch are shorter lived, reach senescence earlier, and have a smaller maximum diameter than western larch, ponderosa pine, and Douglas-fir. The conifers generally remain sound until they reach diameters much larger than aspen and birch are capable of reaching. Therefore, suitable nesting conditions occur in smaller and younger aspen and birch but in larger and older coniferous species. Hence, tree diameter and age were not the most significant factors determining which tree species would be used for nesting, but these were important in determining suitability within each tree species.

Decay patterns differ among conifer species, and this difference is reflected in the relatively high frequency of nest evidence in western larch, and the species apparently higher suitability compared with that of most other conifers. The sapwood of western larch is more resistant to decay than that of most other conifers. When heartwood rots do infect the tree, making it suitable for cavity nests, the solid sapwood may keep the tree standing much longer than any other conifers (McClelland 1995; McClelland and McClelland 2000), often for centuries (Arno et al. 1997; Fiedler and Harrington 2004). The primary heartwood rot affecting western larch in Williamson's Sapsucker nest trees in the Okanagan region appeared to be *Fomitopsis officinalis* (Todd Manning, B.C. Ministry of Forests and Range, personal communication, 2008), although western larch may be affected by other trunk or heartwood rots as well (Carlson et al. 1995).

Western larch will likely persist in a suitable state for cavity nesting longer than will pines, Douglas-fir, or true firs. For Williamson's Sapsucker, these other conifers tend

Table 3. Frequency of suitable Williamson's Sapsucker nest trees and frequency of other trees with cavity nests within tree species, status, and DBH class.

Tree species and status[a]	DBH range (cm)	Total live trees, *n*	Trees within class, *n*	Known nest trees, *n*	Other suitable nest trees		Other trees with nest cavities		Total suitable-nest-tree frequency (%)
					n	%	*n*	%	
Western larch									
Live (2, other)	23–37	996	198	4	0	0	3	1.5	0.1
	38–52	480	126	5	0	0	4	3.2	0.1
	53–67	227	116	4	1	0.9	6	5.2	1.1
	≥68	236	138	10	2	1.4	1	0.7	2.3
Live (2, with broken or dead tops)	38–52	480	8	5	0	0	0	0.0	2.2
	53–67	227	12	7	1	8.3	2	16.7	13.7
	≥68	188	48	29	7	14.6	7	14.6	20.3
Dead (3–7)	23–37		95	2	3	3.2	12	12.6	3.4
	38–52		58	3	4	6.9	9	15.5	7.5
	53–67		32	2	1	3.1	3	9.4	3.8
	≥68		19	3	1	5.3	7	36.8	7.0
Dead (8)	≥23		46	0	0	0	2	4.3	0.0
Broad-leaved trees									
Live (2)	18–22	137	75	0	0	0	0	0	0.0
	23–37	464	251	20	1	0.4	2	0.8	0.7
	≥38	66	44	11	2	4.5	2	4.5	5.6
Dead (3–7)	18–22		35	1	0	0	0	0	<0.1
	23–37		209	7	7	3.3	11	5.3	3.7
	≥38		41	5	2	4.9	3	7.3	6.2
Dead (8)	≥23		15	0	0	0	3	20.0	0.0
Lodgepole pine									
Live (2)	≥23	254	106	0	0	0	0	0.0	0.0
Dead (3–7)	≥23		212	0	0	0	1	0.5	0.0
Other conifers									
Live (2)	23–37	3938	506	3	0	0	2	0.4	<0.1
	38–57	1833	290	1	0	0	0	0.0	<0.1
	≥58	711	258	3	3	1.2	6	2.3	1.3
Dead (3–7)	23–37		687	0	1	0.1	29	4.2	0.2
	38–57		300	8	3	1.0	6	2.0	1.3
	≥58		115	5	3	2.7	8	7.0	3.1
Dead (8)	23–57		195	0	0	0	18	9.2	0.0
	≥58		95	0	0	0	3	3.2	0.0
Small conifers									
Live (2)	8–22	7333	1758	0	0	0	1	0.1	0.0
Dead (3–7)	8–22		889	0	0	0	3	0.3	0.0

[a]Status is indicated by live or dead followed by the wildlife tree class code (2, live, unhealthy; 3–8, dead and progressively more decayed).

to become suitable for cavity nesting after tree death, and consequently they would not be available for nesting for long periods. Pines tend to have relatively high fall-over rates, with the majority of trees falling over within 10 years of death (see review by Bull et al. 1997; Conner and Saenz 2005). Everett et al. (1999) found that the relatively short time that ponderosa pine remained standing after death was shorter than the time required for the snags to soften enough to be used by cavity-nesting birds. Only very large and old ponderosa pines >100 cm DBH had a tendency to remain standing for long periods after death (Keen 1955). Dead Douglas-fir and true firs of all sizes tend to remain standing longer than pines (Raphael and Morrison 1987). Everett et al. (1999) found that 40% of Douglas-fir >40 cm DBH persisted for 80 years after being killed by fire, a period long enough for the snags to soften and become suitable for cavity-nesting birds.

Nest-tree species

The species of nest trees used by Williamson's Sapsucker in British Columbia depended on the local tree species available. Where both Williamson's Sapsucker and western larch occurred, larch was their primary nest tree. Where Williamson's Sapsucker occurred outside of the range of

Table 4. Williamson's Sapsucker mean density of suitable nest trees per hectare and standard error (SE) by geographical region within British Columbia, 2004–2008, not including the known nest tree around which plots were centered.

		Distance from nest tree			
		0–60 m		60–225 m	
Region	n^a	Mean	SE	Mean	SE
Western region	41	0.49	0.18	0.05	0.03
Okanagan	68	0.26	0.09	0.14	0.08
East Kootenay	28	0.45	0.18	0.29	0.11
Overall total	137	0.36	0.08	0.14	0.05

[a]Nests used for >1 year, or where alternate nest trees were used in subsequent years within 60 m of previous nest tree, were only included once in the data presented here.

western larch, trembling aspen was the primary nest tree. These patterns in British Columbia were similar to those found elsewhere in the breeding range.

In the northern Rocky Mountains in Montana, McClelland (1977) found western larch to be the preferred nest tree not only of Williamson's Sapsuckers but of all the primary cavity nesters in his study area. Western larch was used 20 times more commonly for cavity nesting than was Douglas-fir, even though Douglas-fir was five times more abundant than western larch. In northeastern Oregon the most common nest tree was western larch in 1976–1978 (Bull et al. 1986), but 25 years later, Douglas-fir and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) were the preferred nest trees (Nielsen-Pincus and Garton 2007). This shift was due to unprecedented levels of standing dead trees (>50/ha) from spruce budworm (*Choristoneura fumiferana*) and tussock moth (*Orgyia pseudotsugata*) infestations in the 1980s. However, these trees would be expected to decay and fall relatively quickly compared with long-lived western larch, suggesting that sometime in the future, western larch might again be the most prominent Williamson's Sapsucker nest tree in northeastern Oregon.

In the southern Rocky Mountains (Colorado, Wyoming, and Arizona, see Table 5) where trembling aspen was abundant and western larch absent, trembling aspen was the primary Williamson's Sapsucker nest tree. However, where suitable trembling aspen were not available, nesting usually took place in ponderosa pine (Crockett 1975; Dobbs et al. 1997), as observed in the western region of British Columbia. The association of Williamson's Sapsucker with aspen nest trees in the southern Rocky Mountains has sometimes been assumed to be a characteristic trait of the Rocky Mountain subspecies (*Sphyrapicus thyroideus nataliae* (see Dobbs et al. 1997). However, in British Columbia, the Rocky Mountain subspecies occurs in the East Kootenay (Cowan 1938), where it nested primarily in western larch, and the nominate subspecies occurred elsewhere, nesting primarily in western larch in the Okanagan and in trembling aspen west of the Okanagan. Nest-tree choice appeared to depend only on which tree species were suitable and available and was not a characteristic trait of either subspecies.

There has been only one published study on nest-tree characteristics in the mountains of California, Nevada, and southern Oregon (Raphael and White 1984, see Table 5), although there are a number of other sources reporting nest-tree species (Bendire 1895; Barlow 1901; Dixon 1905; Keyes 1905; Grinnell 1908; Ray 1918; Dawson 1923; Michael 1935; Rowley 1939; McAllister and Marshal 1945; Russell 1947; Farner 1952; Johnson 1965). The predominant nest tree appeared to be the Sierra-Cascades subspecies of lodgepole pine; however white fir (*Abies concolor*), red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), ponderosa pine, and trembling aspen were also used a nest trees.

Nest-tree targets for habitat management

Suitable Williamson's Sapsucker nest trees were found to be relatively scarce, and individual nest trees tended to be used for many years based on the numbers of nest holes found in each nest tree. Mean numbers of holes per Williamson's Sapsucker nest tree were much higher in this study (5.7 for aspen and 16.4 for conifers) than the numbers observed for Red-naped Sapsuckers in aspens in central British Columbia (2.4; Martin et al. 2004) and in paper birch (*Betula papyrifera*) (2) and western larch (4) in Montana (McClelland and McClelland 2000). The relative scarcity of suitable nest trees for Williamson's Sapsucker in British Columbia may be resulting in more annual reuse of nest trees than otherwise expected, but there are no published data on Williamson's Sapsucker for either density of suitable nest trees or numbers of holes in nest trees for comparison.

We found no suitable nest trees, other than the known nest trees around which the plots were centered, in the sampling plots at 103 of the 137 nests. This resulted in a skewed distribution typical of count data of rare events and meant we could not distinguish on an individual-site basis between sites that had no other suitable nest trees and sites where they were simply uncommon. Further sampling has shown us that where suitable nest tree densities averaged 0.15/ha, plots totaling 20 ha were required to detect at least one suitable nest tree within each set of plots (L. Gyug, unpublished results, 2009). Within our 16 ha sampling areas around nests, complete censuses would have been required to accurately and reliably estimate suitable nest-tree density at each site, and this sampling intensity would not have been possible with the available budgets.

Densities of suitable nest trees averaged 1.36/ha in the area nearest to the nest and were much lower >60 m from the known nest tree. If the areas nearest to the nests were considered optimal nesting habitat, and most of the areas around the nest trees were considered suboptimal nesting habitat (although it may be relatively good foraging habitat), then this known density should be set as the target level for densities of suitable nest trees. However, it was clear that in most sites, this density may not be obtainable on the short term throughout breeding territories given the current scarcity of suitable trees.

Maintenance of suitable nest trees in patches would apply particularly in the western region, where nesting tended to be in relatively small (<1 ha) aspen clumps. Suitable nest-tree densities outside the nest patches (>60 m from the nest) in the surrounding matrix of coniferous forests were very low (Table 4). Similarly, in Arizona, small, isolated aspen patches within ponderosa pine forests were significant to both Williamson's Sapsucker and other cavity-nesting birds (Griffis-Kyle and Beier 2003).

Maintenance of nesting habitat will require average den-

Table 5. Summary of available data on Williamson's Sapsucker nest-tree species including percentage of nest trees of each species or species group that were alive, and mean DBH (with standard error in parentheses).

		Coniferous nest trees				Broad-leaved nest trees			
Study location	Source	Tree species[a]	*n*	% trees live	DBH (cm)	Tree species[a]	*n*	% trees live	DBH (cm)
British Columbia	This study	Lw	119	86	75.0 (2.2)	At western region	37	73	34.0 (1.2)
		Py, Fd, Sxw	27	33	63.0 (4.6)	At Okanagan region	17	59	40.4 (2.7)
						Ew	9	33	31.9 (1.9)
						Ac	1	100	96 (—)
Northwestern Montana	McClelland 1977	Lw	4	100	66.5 (12.5)		0		
Northeastern Oregon									
1976–1978	Bull et al. 1986	Lw, Py, Fd, Bg	86	—	70 (2.8)		0		
		Lw	35	74	—				
		Py, Fd, Bg	51	30	—				
2003–2004	Nielsen-Pincus and Garton 2007	Fd, Bg, Lw, Py	69	6	60.9 (2.2)		0		
Sierra Nevada, Calif.	Raphael and White 1984	Pl, Bw, Br, Pj	50	60	82 (—)	At	1[b]	—	—
Colorado	Crockett 1975	Py	8	0	50.9 (—)	At	40	83	23.5 (—)
Wyoming	Loose and Anderson 1995	Any conifer	0			At	3	100	28.7 (—)
Arizona	Li and Martin 1991	Py	3[b]	—	—	At	36	14	38.1 (8.9)
Arizona	Conway and Martin 1993	Any conifer	0			At	29	21	37.7 (—)

[a]Nest-tree species listed in decreasing abundance at each study location using the following codes: Ac, black cottonwood; At, trembling aspen; Bg, grand fir; Bw, white fir; Br, red fir; Ew, water birch; Fd, Douglas-fir; Lw, western larch; Py, ponderosa pine; Pl, lodgepole pine, Pj, Jeffrey pine; Sxw, hybrid white spruce.

[b]The DBH for this species was grouped with that of the more abundant tree species group for that study location in the original source.

sities of suitable nest trees at or above 1.36/ha. Achievement of these targets can be verified by directly counting suitable nest trees or by estimating the density of tree classes that most frequently give rise to suitable nest trees (see Table 3). Estimating the densities of suitable nest trees based on counts will require almost complete censuses for any areas <20 ha in size, and subsampling totaling 20 ha in size for larger areas. The second method would provide targets for the tree classes from which suitable nest trees are recruited. For example, to provide just one suitable Williamson's Sapsucker nest tree per 16 ha territory from among very large (≥68 cm DBH) western larches with broken or dead tops, an average of 5 such trees need to be maintained because the probability that any one will be suitable is about 20% (Table 3). To meet the recommended target of 1.36 suitable nest trees/ha would require at least 7 trees/ha in that tree class. Nest-tree targets would not normally be met from only one tree species, status, or size class but by summing the contributions from several different classes depending on local conditions.

Others have attempted to estimate the number of snags required for nesting for Williamson's Sapsuckers and for other cavity-nesting birds (see review by Raphael and White 1984). Since Williamson's Sapsucker nest in living trees as well as snags, management for provision of nest trees should not be based on snag density alone. Using our Table 3 of nesting frequencies should allow us to predict nest suitability for any given tree from its species, condition, and size class, and develop nest tree targets based on all trees rather than just snags.

Long-term approaches to habitat management

Managing timber harvest entries in the short term to meet target densities of suitable nest trees will consist of retaining either all known nest trees and trees considered to be suitable nest trees or a sufficient number of trees within classes of trees assumed to provide suitable nesting opportunities based on estimated frequencies (Table 3). However, this management approach may not ensure the long-term recruitment of suitable nest trees and may not meet foraging requirements. Most current timber harvesting regimes result in a reduction of suitable nest trees, since such trees are felled because they are considered hazardous or unhealthy and nonmerchantable.

Integrating foraging requirements with nest-tree requirements into habitat targets for management may result in complex matrices of desired tree densities in different classes that may be difficult to apply to any particular managed stand. Habitat requirements may be more simply met by specifying desired stand structure to be left after timber harvesting if that structure will result in meeting short-term needs and long-term recruitment of all habitat elements required. Because of industrial forestry activities, most stands occupied by Williamson's Sapsucker in British Columbia exhibit unnatural structural conditions in terms of patchiness, stocking densities, and distribution of suitable habitat trees. The best guidance on desired stand structure for Williamson's Sapsucker may come from the two sites where we found high nest densities (Gyug et al. 2007; L. Gyug, unpublished results, 2008) and from analyses of the disturbance regimes that gave rise to those stand structures. Where we observed the highest densities of Williamson's Sapsucker in British Columbia (Gyug et al. 2007), densities of very large (>57 cm DBH) western larch and Douglas-fir were relatively high (35/ha), and overall the density of trees >22 cm DBH was 143/ha. These tree densities occurred over areas >60 m from the nest trees, i.e., these were not very small isolated patches.

In the areas where it occurs, western larch is clearly the single most important nest-tree species for Williamson's Sapsucker in British Columbia. Western larch is the most fire-resistant conifer in western North America and the most shade intolerant (Fiedler and Lloyd 1995). As such, fire is required for western larch to persist, and the species survives under three different fire regimes: (1) infrequent stand-replacing fire regime, (2) a mixed-severity fire regime, and (3) frequent surface fire regime that does not generally replace stands (Arno and Fisher 1995). Stands occupied by Williamson's Sapsucker in the Okanagan region in British Columbia, which is the only region where Williamson's Sapsucker has been known to occur consistently over the past 100 years within British Columbia (Gyug et al. 2007), appear to be primarily of the frequent or mixed-intensity fire regimes, where veteran western larch trees >57 cm DBH are relatively abundant. Williamson's Sapsucker does not occur in the Interior Cedar–Hemlock biogeoclimatic zone wet-belt western larch stands in British Columbia (Gyug et al. 2007), which are characterized by infrequent stand-replacing fires.

Published descriptions of western larch stands characterized by frequent fire regimes are rare. Two such stands with mean fire return intervals of 27 and 24 years, respectively, prior to fire exclusion around 1900 were both characterized by an open park-like appearance, with densities of trees >22 cm DBH (reconstructed to 1900) of about 150 and 60/ha and densities of trees >57 cm DBH of about 11 and 27/ha (Arno et al. 1997). In the 1990s these same stands each had about 35 trees/ha with DBHs >57 cm. We could find only one published record of ecological restoration in a western larch stand with a frequent fire regime that referred to one of the same stands cited above (Fiedler and Harrington 2004). After thinning and reintroduction of surface fires, the older veteran trees of the stand were able to regain some vigour (Fiedler and Harrington 2004), whereas in the absence of such restoration, the large, old western larch trees would predictably be out-competed for nutrients and water by a dense undergrowth of shade-tolerant conifers and die prematurely (Carlson et al. 1995). In addition, without fire, the old western larches would eventually be replaced by shade-tolerant conifers because of the limited reproduction of western larch in the absence of fire (Carlson et al. 1995). Some sort of ecological restoration, whether by prescribed burning alone or by burning after partial timber harvesting, would appear to be necessary to maintain western larches in the stands, and especially to maintain the large, old western larches that are the primary nest trees of Williamson's Sapsucker.

Ecological restoration of dry-belt western larch stands in British Columbia may be the simplest method for long-term maintenance or for restoration of Williamson's Sapsucker breeding habitat in regions where these stands occur. Structure of these stands would be typified by a relatively high

density (≥20/ha) of large trees (>57 cm DBH), as compared with the structure of most managed stands, and by moderate densities of trees >22 cm DBH (60–150/ha), by comparison with either the low densities of heavily cut stands or the densely stocked stands regenerating after intense fire events. This stand structure should be spread over areas larger than just an immediate nest area (<60 m from a nest). This structure would also meet the needs of other species occurring in this type of habitat and would be less complex than setting habitat targets to meet separate foraging and breeding requirements of Williamson's Sapsucker. While this study has shown that nest-tree targets can be set for managing stands used by Williamson's Sapsucker, we advocate an approach based on a desired stand structure that would replicate the effects of the natural disturbance regimes that have created and maintained old-seral stands of western larch. In regions where Williamson's Sapsucker nests in aspen patches or in ponderosa pine stands within ponderosa pine – Douglas-fir forests, desired stand structures have yet to be determined and will likely be more complex than those in western larch stands because of the heavy reliance on aspen stands within a coniferous forest matrix.

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