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RESEARCH ARTICLE

Foraging ecology of the Williamson's Sapsucker: Implications for forest management

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ABSTRACT

Williamson's Sapsuckers (*Sphyrapicus thyroideus*) are montane woodpeckers threatened by widespread tree removal activities and climate change. Current forest management plans focus on nesting trees, but the incorporation of foraging trees would lead to a more effective management strategy to mitigate habitat loss for this species. We investigated the selection of foraging trees in forests managed for timber extraction and maintenance of wildlife values using foraging observations of 27 radio-tagged adult Williamson's Sapsuckers during the breeding season in 2 regions (Okanagan and Western) of their limited Canadian range. Characteristics of foraging trees (88% of observations on live trees, 11% on dead trees) differed with foraging mode. Large, live Douglas-firs (*Pseudotsuga menziesii*; ≥ 22.5 cm dbh) were used for gleaning and sap feeding on tree trunks in both regions, whereas trees used for trunk pecking were mostly large, senescent western larches (*Larix occidentalis*) in the Okanagan region and large, dead ponderosa pines (*Pinus ponderosa*) in the Western region (average dbh = 46 cm). For overall foraging activities, Williamson's Sapsuckers selected large, live Douglas-firs with signs of resin exudation and blistering (pitching), and avoided live lodgepole pines (*Pinus contorta*), quaking aspens (*Populus tremuloides*), and ponderosa pines. Larger trees and standing dead conifer trees were reused more often for foraging than smaller and live trees. The quality of Williamson's Sapsucker habitat could decrease over the long term if forest management practices reduce the overall size of trees or alter tree species composition to promote lodgepole pine. Forest management should focus on retaining and promoting large live Douglas-fir trees and large senescent or standing dead conifers (also used for nesting), which can be achieved by using thinning, prescribed fire, partial harvesting, and tree retention strategies.

Keywords: Foraging habitat, telemetry, *Sphyrapicus thyroideus*, resource selection function, woodpecker, large trees, *Pseudotsuga menziesii* var. *glauca*, montane forest

Écologie de L'alimentation du *Sphyrapicus thyroideus*: Implications pour la Gestion de la Forêt

RÉSUMÉ

Sphyrapicus thyroideus est une espèce de pic-bois menacée par la récolte d'arbres et les changements climatiques. Des pratiques efficaces de gestion de la forêt qui inclut les arbres d'alimentation pourraient servir comme outils pour atténuer la perte d'habitat. Nous avons évalué la sélection des arbres d'alimentation de 27 adultes en forêt aménagée, durant la période de reproduction dans 2 régions distinctes au Canada (Okanagan et Western). Les caractéristiques des arbres d'alimentation (88% des observations étaient sur des arbres vivants et 11% sur des chicots) différaient selon le mode d'alimentation. *Sphyrapicus thyroideus* utilisait les sapins de Douglas vivants de grande taille pour le glanage et l'alimentation de sève sur les troncs d'arbres, alors que lors de l'alimentation par excavation, il utilisait les mélèzes de l'ouest mourants de grande taille dans la région de l'Okanagan et les pins ponderosa morts de grande taille dans la région Western (46 cm dhp en moyenne pour les deux régions). *Sphyrapicus thyroideus* sélectionnait les sapins de Douglas vivants de grande taille qui présentaient des écoulements de sève ou de résine, tandis que les pins tordus, peupliers faux-tremble et pins ponderosa vivants étaient évités. Les arbres de plus grande taille et les chicots de conifères étaient réutilisés plus souvent pour l'alimentation. La qualité de l'habitat d'alimentation de *Sphyrapicus thyroideus* pourrait décroître si les activités d'aménagement forestier contribuent à réduire la taille des arbres et changent la composition en espèce d'arbres, de sortes à promouvoir les peuplements de pins tordus. Les plans d'aménagement forestier doivent préserver et promouvoir la croissance de sapin de Douglas vivants et les conifères morts ou sénescents, ce qui est possible en utilisant des techniques d'éclaircie, de feu contrôlé, de coupe partielle et de rétention.

Mots-clés : Habitat d'alimentation, télémétrie, *Sphyrapicus thyroideus*, fonction de sélection des ressources, picidae, *Pseudotsuga menziesii* var. *glauca*, forêts de montagnes

INTRODUCTION

Forest management practices that fail to accommodate wildlife values are often associated with negative effects on wildlife species that use dead or decaying trees for nesting and foraging, including bark-foraging and cavity-nesting birds. In forest ecosystems, large live or dead trees are important nesting and foraging substrates used by bark-foraging birds that feed on insects by gleaning or excavating (Tremblay et al. 2010). Tree removal during forest management operations can alter tree species composition and reduce the availability of large live trees and dead trees used by bark-foraging birds (Imbeau and Desrochers 2002). Effective forest management practices can be used as a conservation tool to maintain or create suitable habitat when combined with fine-scale knowledge of nesting and foraging habitat components. Traditional forest management practices tend to focus on nesting habitat requirements because nesting trees, which are more easily identified, are better described than foraging trees for most species of bark-foraging birds in North America. Bark-foraging birds may select trees with different characteristics for nesting and foraging activities; therefore, forest management plans that include overall habitat requirements may achieve better results for conservation (Nappi et al. 2015).

Foraging trees are fine-scale habitat components that are essential to the occupancy, fitness, and persistence of bark-foraging birds (Hall et al. 1997). Foraging tree characteristics (e.g., tree species, size, decay class, branches, and concealment properties) are measurable physical attributes, which can also fulfill secondary functions, such as communication and protection from the elements and predators (Huey and Pianka 1981, Wiley 1991, Liao et al. 2008). Foraging tree characteristics can be identified by quantifying selection patterns (use in relation to availability) using resource selection functions (Jones 2001, Lele et al. 2013). Some foraging tree characteristics may be suitable for several foraging modes, offering cumulative individual fitness benefits, whereas other foraging trees may only be used for a specific foraging mode (e.g., gleaning insects or feeding on sap; Klopfer and Ganzhorn 1985).

Sapsuckers (*Sphyrapicus* spp.) are a group of woodpeckers that forage mostly on the trunks of live trees. Their morphological adaptations (short tongue and weak pecking force) make them less efficient at extracting food from crevices of (mostly) dead trees than other arboreal woodpeckers (e.g., *Picoides*; Spring 1965). Instead, sapsuckers spend more time gleaning insects from bark or sap feeding on injured trees, but they may also consume bast (cambium), fruit, and seeds (Williams 1975, Raphael and White 1984, Walters 1996, Mancuso et al. 2014).

Williamson's Sapsuckers (*Sphyrapicus thyroideus*) breed in open coniferous and mixed coniferous–deciduous

montane forests in western North America from southern Canada to central New Mexico (Gyug et al. 2012). They have been listed as Endangered in Canada under the Species at Risk Act since 2006 (Species at Risk Public Registry 2017), Blue-listed in British Columbia (British Columbia Conservation Data Centre, <http://a100.gov.bc.ca/pub/eswp/>), and are on the federal list of birds of conservation concern in the United States (U.S. Fish and Wildlife Service 2008). The predicted effect of climate change on the montane forests in which Williamson's Sapsuckers breed could bring the species to near extinction by reducing its current range by 73–78% by the end of the century (van Riper et al. 2014). Intensive forestry activities also pose a potential threat to Williamson's Sapsucker populations as nesting and foraging trees are harvested. Forest management recommendations for nesting trees of Williamson's Sapsuckers are well established (Gyug et al. 2009a, Drever et al. 2015); however, few data are available for management of foraging trees. In Canada, one of the current objectives of the Species at Risk Recovery Strategy is to incorporate foraging habitat requirements into its definition of critical habitat, as the existing small populations of Williamson's Sapsucker occur in the managed forest landscape with ongoing forest harvest and other anthropogenic activities (Environment Canada 2014). Large forested areas where Williamson's Sapsuckers occur in Canada are being harvested with a rotation of 60–80 yr (1.3–1.7% of habitat harvested per year; B. Drobe personal communication), and local decreases in breeding density have been reported (CO-SEWIC 2005).

Adult Williamson's Sapsuckers mostly feed on sap early in the spring by drilling and maintaining sap wells—shallow holes that expose the sap from the phloem or xylem of trees (Eberhardt 2000). Williamson's Sapsuckers select coniferous trees for sap, chiefly Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*; 54% of sap trees in Colorado, USA: Crockett 1975; 85% in British Columbia, Canada: Gyug et al. 2009b). During the nestling stage, adult foraging behavior changes dramatically to gleaning for ants, mostly the *Formica rufa* group and *Camponotus* spp., which comprise 98% of the arthropods found in the fecal sacs of nestlings (Gyug et al. 2014a). In Colorado, pecking into a woody substrate for subcortical larvae was described as an uncommon foraging mode overall, but more frequent during periods of cold temperatures (Crockett 1975). In Canada, pecking represented 28% of the overall time spent foraging (St-Amand 2017). Opportunistic foraging behaviors, which are used intensively when prey are available, include aerial foraging (flycatching) and gleaning from the foliage of coniferous trees for defoliating insects such as spruce budworms (*Choristoneura* spp.; Crockett 1975, St-Amand 2017). Previous studies of Williamson's Sapsucker foraging tree

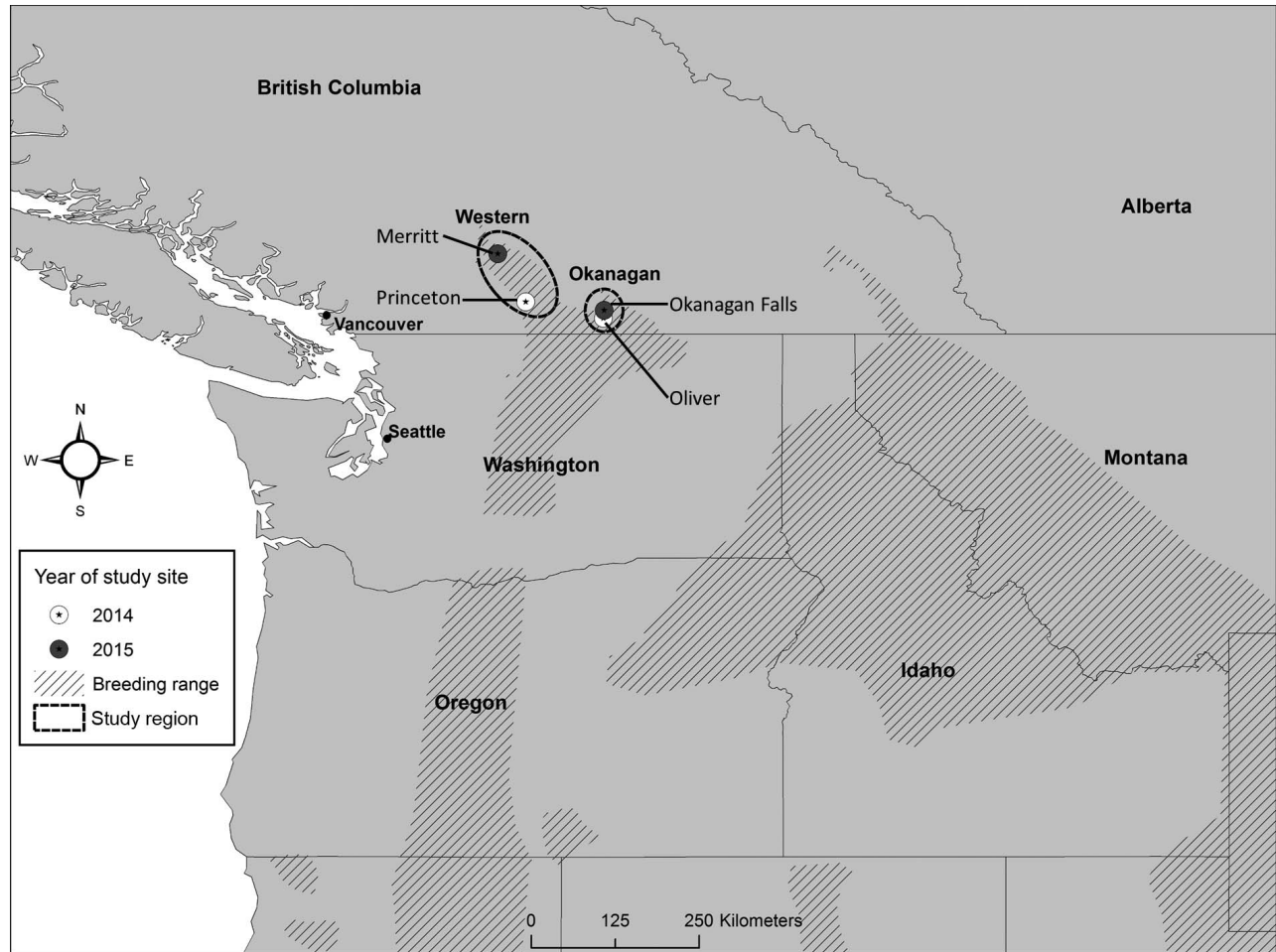


FIGURE 1. Study sites (Oliver and Princeton in 2014, Okanagan Falls and Merritt in 2015) within study regions in southern British Columbia, Canada, relative to the northwestern range of the Williamson's Sapsucker.

characteristics have been limited to opportunistic observations of sap trees and foraging observations near the nest, and thus are not representative of all foraging modes and resource use during the breeding season (Crockett 1975, Gyug et al. 2009b). Live mature coniferous trees could be required for sapsucker foraging during the breeding season, but these trees are also harvest priorities in montane forests within the range of Williamson's Sapsuckers. The suspected incompatibility of traditional forest management practices with Williamson's Sapsucker habitat maintenance is currently a source of conflict for multilateral land management partnerships.

Mediating the conflict between harvest priorities and conservation objectives requires the identification of fine-scale foraging habitat for all foraging modes used by Williamson's Sapsuckers during the breeding season. The inclusion of comprehensive foraging habitat requirements in forest management plans is key to locating and protecting habitat that will support Williamson's Sapsucker breeding in managed forests. Here, we describe the

foraging ecology of Williamson's Sapsuckers using observations of radio-tagged individuals to identify critical foraging habitat characteristics. We also evaluate how forest management can affect foraging trees in 2 regions in southern British Columbia, Canada (the Okanagan and Western regions; Figure 1). We address 3 objectives related to foraging at the tree level: (1) quantification of characteristics of foraging trees, including species, size, decay, and surrounding canopy cover in relation to availability; (2) determination of how foraging tree characteristics vary according to foraging mode; and (3) identification of forest management alternatives that best preserve Williamson's Sapsucker critical breeding habitat based on foraging and nesting requirements.

METHODS

Study Area

During April–July in 2014 and 2015, we monitored Williamson's Sapsucker foraging behavior at 4 study sites,

2 sites each in the Okanagan and Western regions, in British Columbia (Figure 1). After identifying clusters of breeding territories from Williamson's Sapsucker nest locations from 1994 to 2013, we selected study sites based on road access, breeding pair density, and proximity of nesting territories (4–28 sapsucker pairs detected per year in each of the 4 sites; Gyug et al. 2014b).

In the Okanagan region, we monitored a site near Oliver (49°10'N, 119°21'W; Figures 2A, 2B, and 3A) in 2014, and a second site near Okanagan Falls (49°19'N, 119°25'W; Figures 2C and 3B) in 2015. Both Okanagan sites were located in montane forest ranging from dry–mild Interior Douglas-fir to dry–mild Montane Spruce biogeoclimatic zones (British Columbia Vegetation Resources Inventory, www.for.gov.bc.ca/hts/vri/). Stands were dominated by Douglas-fir, western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and hybrid spruce (*Picea engelmannii* × *Picea glauca*), and contained small patches of quaking aspen (*Populus tremuloides*), water birch (*Betula occidentalis*), grand fir (*Abies grandis*), and subalpine fir (*Abies lasiocarpa*). Mature forest was the most abundant forest type; however, 2 of the 8 monitored Williamson's Sapsucker nests were located <100 m from a clear-cut (most trees <10 m in height), and 2 nests were located <100 m from a harvest with tree cluster retention. Elevation was 1,020–1,450 m at the Oliver site and 1,150–1,370 m at the Okanagan Falls site. The 2 sites in the Okanagan region were ~10 km apart but separated by a steep canyon.

In the Western region, we monitored one site near Princeton (49°25'N, 120°28'W; Figures 2D and 3C) in 2014, and a second site near Merritt (49°58'N, 120°42'W; Figures 2E and 3D) in 2015. Both sites were located in the very dry–hot Interior Douglas-fir biogeoclimatic zone (British Columbia Vegetation Resources Inventory, www.for.gov.bc.ca/hts/vri/), and were dominated by Douglas-fir and ponderosa pine (*Pinus ponderosa*), with some quaking aspen and black cottonwood (*Populus trichocarpa*) in wet areas. Stands of mature forest were common; none of the 8 monitored nests were <100 m from a clear-cut, although 7/8 were <100 m from open unforested areas, such as grasslands, pastures, and clearings for utility lines. Elevation was 800–950 m at the Princeton site, and 880–1,180 m at the Merritt site. The Merritt site was one of the northernmost clusters of Williamson's Sapsucker breeding territories in British Columbia, ~75 km north of the Princeton site.

Location and Capture of Williamson's Sapsuckers

We used playback of territorial Williamson's Sapsucker calls to find and confirm breeding territories. We attempted to catch both members of a pair using 3 different methods: (1) before the nestling stage, we lured adult territorial males into mist nets by using playbacks

and a male Williamson's Sapsucker decoy; (2) we caught males and females that were incubating eggs or feeding nestlings by affixing a dip net to the top of an extensible pole (up to 14 m) to block the entrance of the nest cavity when the bird was inside; and (3) when the nest cavity was not accessible with a dip net, we caught females by positioning aerial mist nets supported by poles (up to ~9 m high) to intercept them in flight. For each bird captured, we determined their sex and age, and fitted them with a numbered U.S. and Canadian Wildlife Service aluminum band, 3 colored plastic bands (maximum of 2 bands per leg), and a radio-transmitter (BD-2 or BD-2G, weighing 1.2 g; Holohil Systems, Carp, Ontario, Canada). The radio-transmitters, with an expected battery life of 56 days, were tail-mounted by suturing the radio-tag onto the 2 central rectrices following Tremblay et al. (2009), and were designed to drop off during the molt of the rectrices before migration (Pyle 1997).

Radio-tracking

We radio-tracked Williamson's Sapsuckers with an RA-2AK H-type antenna (Telonics, Mesa, Arizona, USA) and an R-1000 receiver (Communications Specialists, Orange, California, USA), using a homing protocol (i.e. trying to see the animal; Mech 1983) to monitor the foraging behavior of individual sapsuckers and to identify their foraging trees. We followed Williamson's Sapsuckers during telemetry sessions of 0.5–4.0 hr during morning, afternoon, and evening periods from early May to mid-July, until 5–6 days after the last fledgling left the last nest. We limited the maximum number of consecutive observations to 6 (generally 1–3), and we later excluded observations that were separated by <5 min to avoid the potential effect of temporal autocorrelation. We identified 35 additional foraging trees during behavioral observations of banded birds with depleted radio-transmitters within a 60-m radius of nests in 2015 (only 4.5% of foraging trees were identified from birds with depleted transmitters; 31 live and 4 dead trees in 5 nesting territories). These observations were used only to identify foraging trees.

Behavioral Observations

The observed foraging modes of Williamson's Sapsuckers were sap feeding (drilling to create sap wells, sipping sap), gleaning on wood (picking insects from the surface of a trunk or branch), gleaning on vegetation (feeding from coniferous needles while hanging on the branches), bark scaling (removing segments of bark from the trunk to uncover insects), pecking (hitting a woody surface to extract insects or subcortical larvae), and aerial foraging (catching insects in flight). Gleaning on wood and vegetation and bark scaling were combined for statistical analyses due to their similarity and the low frequency of observations. A behavioral observation started when the

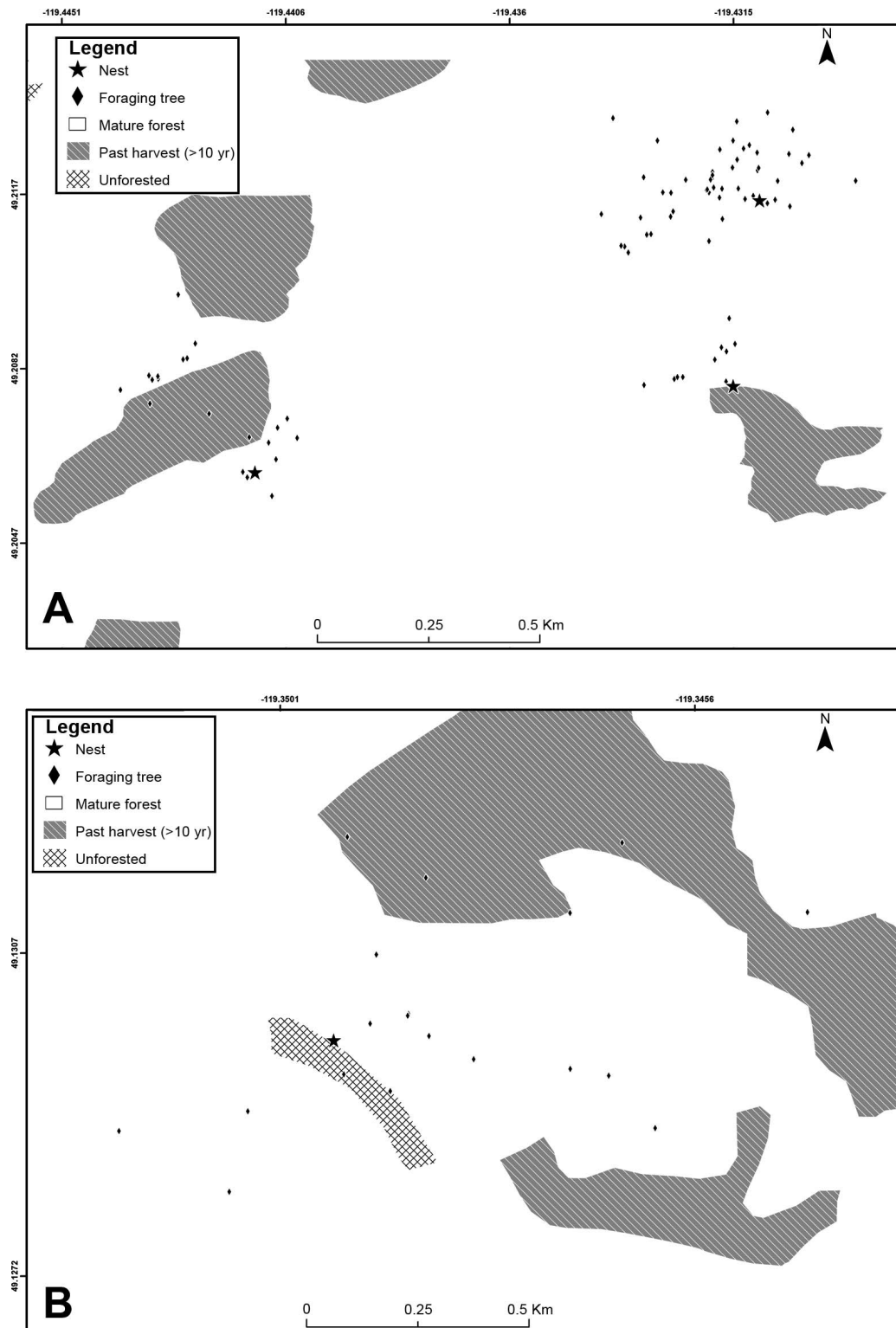


FIGURE 2. Locations of foraging and nesting trees used by Williamson's Sapsuckers at 4 sites in southern British Columbia, Canada, in 2014 and 2015: (A–B) Oliver (see Figure 1 for study site location). Forest polygons include mature forest (forest undisturbed by logging), areas that have been harvested in the past >10 yr ago = past harvest), and areas that have been recently harvested (≤ 10 yr ago = recent harvest; British Columbia Vegetation Resource Inventory, www.for.gov.bc.ca/hts/vri/). Harvest operations include clear-cutting and harvesting with tree cluster retention. Unforested areas include roads, utility lines, grasslands, and pastures.

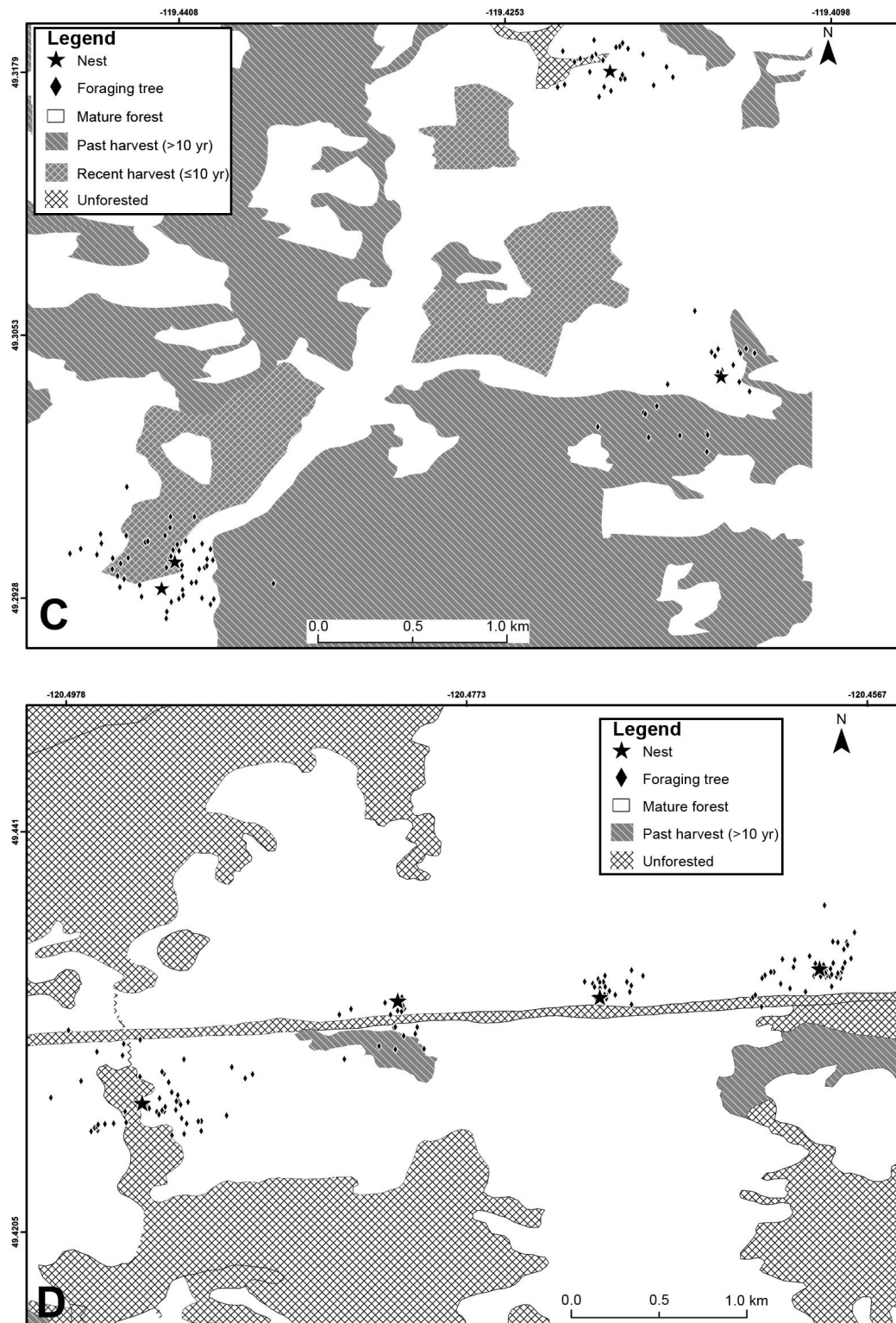


FIGURE 2. Continued. Locations of foraging and nesting trees used by Williamson's Sapsuckers at 4 sites in southern British Columbia, Canada, in 2014 and 2015: (C) Okanagan Falls, and (D) Princeton (see Figure 1 for study site location). Forest polygons include mature forest (forest undisturbed by logging), areas that have been harvested in the past (>10 yr ago = 'past harvest'; British Columbia Vegetation Resource Inventory, www.for.gov.bc.ca/hts/vri/). Harvest operations include clear-cutting and harvesting with tree cluster retention. Unforested areas include roads, utility lines, grasslands, and pastures.

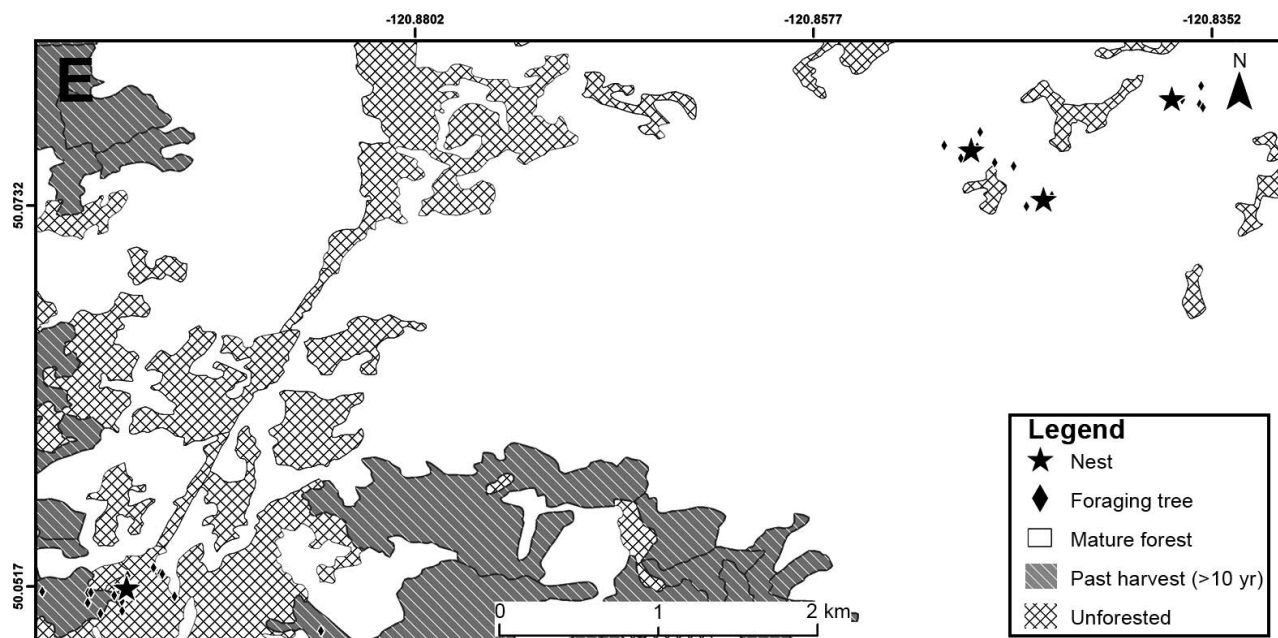


FIGURE 2. Continued. Locations of foraging and nesting trees used by Williamson's Sapsuckers at 4 sites in southern British Columbia, Canada, in 2014 and 2015: (E) Merritt (see Figure 1 for study site location). Forest polygons include mature forest (forest undisturbed by logging) and areas that have been harvested in the past (>10 yr ago = 'past harvest'; British Columbia Vegetation Resource Inventory, www.for.gov.bc.ca/hts/vri/). Harvest operations include clear-cutting and harvesting with tree cluster retention. Unforested areas include roads, utility lines, grasslands, and pastures.

bird was first observed or landed on a tree, and we recorded the occurrence of any of the above behaviors. For the analysis of tree characteristics by foraging mode, we included individual trees that were used for multiple foraging modes in each of the corresponding data subsets (gleaning, sap feeding, etc.).

Measurements of Used and Available Substrates

We flagged and georeferenced foraging trees with a handheld GPS unit (Garmin 62S; Garmin, Olathe, Kansas, USA). We returned at the end of the breeding season (July–August) to measure the foraging tree and habitat characteristics that could potentially influence resource selection at the substrate level, including tree species, diameter at breast height (dbh), tree height, decay class, signs of decay, and canopy cover (terms defined in Appendix Table 1). We took the same measurements for an equal number of "available" trees that were never observed being used during the study and bore no signs of feeding by Williamson's Sapsuckers. We selected available trees alternately at a point 15 m east or west of each of the used trees. If no unused trees were present at the selected point, we selected the closest tree from that point in a direction opposite or perpendicular to the used tree (to remain >15 m from the used tree). The 15-m buffer around used trees was a tradeoff between reducing the chances of selecting a tree genetically related to the used

tree (i.e. a clone or sibling) and remaining within the general area of the foraging tree. The available tree had to be rooted in the ground and at least 8.1 cm dbh in 2014 and 3.5 cm dbh in 2015. We determined the minimum dbh threshold for available trees according to the smallest tree that Williamson's Sapsuckers used each year at both sites for that year, assuming that trees below the minimum size were not suitable for foraging. The available tree also had to be in the same state (live or dead) as the used tree, to allow the comparison of live and dead tree characteristics separately. We used the decay classification adopted by the British Columbia wildlife tree classification system for coniferous trees, except that we divided decay classes 2 ("Live/unhealthy") into 2 categories (2A: stressed, and 2B: senescent; Appendix Table 1) to better characterize the decay of live trees that were sometimes partially dead (senescent), especially western larches (Thomas et al. 1979). The decay class of trees was evaluated by the same person (J. St-Amand) for all foraging and available trees. In the Western region, we pooled decay classes 2A and 2B for analysis because there were only a few trees in the latter class. Canopy cover was measured with a concave densiometer using measurements taken 1.0 m from the substrate at the north and south cardinal points only, instead of at all 4 cardinal points (Forestry Suppliers 2005). We did not sample the east and west cardinal points because they would have

TABLE 1. Candidate model sets in model selection of live tree characteristic selection for foraging by 27 radio-tracked Williamson's Sapsuckers in the (A) Okanagan and (B) Western study regions of southern British Columbia, Canada (see Figure 1 for locations), and (C) overall. Models are ranked by the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). Only the 95% confidence AIC_c model sets are presented. Best-supported models ($\Delta AIC_c \leq 2$) are highlighted with bold font. The Area Under the Curve (AUC) is a measure of performance of the model; $AUC = 1$ indicates that the model perfectly classified foraging trees and available trees (unused). Also shown are the model Akaike weight (w_i), cumulative model weights (W), and maximized log-likelihood ($-2\ln L$). See Appendix Table 1 for descriptions of variables considered in models.

Region	Model variables	Rank	K	$-2\ln L$	ΔAIC_c	w_i	W	AUC
(A) Okanagan	Tree sp., dbh, blistering^a	1	7	-263.54	0.00^b	0.43	0.43	0.78
	Tree sp., dbh, blistering, boring insects	2	8	-262.60	0.30	0.37	0.80	0.78
	Tree sp., dbh, blistering, boring insects, tree top condition	3	9	-262.24	1.60	0.19	0.99	0.78
(B) Western	Tree sp., dbh	1	4	-252.53	0.00^c	0.38	0.38	0.79
	Tree sp., dbh, canopy cover	2	5	-252.12	1.17	0.21	0.60	0.79
	Tree sp., dbh, ant nest	3	5	-252.15	1.30	0.20	0.80	0.79
	Tree sp., dbh, decay class, canopy cover	4	6	-251.95	2.96	0.09	0.89	0.79
	Tree sp., dbh, ant nest, blistering	5	6	-252.13	3.33	0.07	0.96	0.79
(C) Overall	Tree sp., dbh, blistering, boring insects	1	9	-524.66	0.00^d	0.39	0.39	0.77
	Tree sp., dbh, blistering	2	8	-526.13	0.90	0.25	0.64	0.77
	Tree sp., dbh, ant nest, blistering, boring insects	3	10	-524.25	1.23	0.21	0.85	0.77
	Tree sp., dbh, ant nest, blistering, boring insects, burn	4	11	-524.03	2.84	0.09	0.95	0.77

^a Blistering includes resin exudation.

^b Minimum AIC_c value = 499.9.

^c Minimum AIC_c value = 514.7.

^d Minimum AIC_c value = 1067.5.

been close to the available tree located in one of those directions.

Statistical Analyses

Foraging tree selection model construction. We used generalized linear mixed-effects models (GLMM; binomial) to assess the selection of tree characteristics by foraging Williamson's Sapsuckers using the lme4 package (Bates et al. 2015) in R (R Core Team 2016). We used bird ID as a random effect to account for correlations among observations of the same individual, and tree characteristics as predictor variables (tree species, dbh, height, decay class, signs of decay, and canopy cover). We compared the fit of linear, quadratic, and exponential terms in linear models for each continuous predictor variable (dbh, height, and canopy cover). We examined the significance of all possible 2-way interaction terms between significant variables by including them in post hoc models (for all models of the 95% confidence set), but none improved model fit per χ^2 likelihood ratio tests (Moya-Laraño and Wise 2007).

Foraging tree model selection and weighted multi-model averaging. We used backward stepwise model selection based on P -values to obtain a set of candidate GLMMs for each region separately and pooled (overall). The overall models representing both regions pooled did not perform as well as the models for each region separately (based on Area Under the Curve values; AUC); therefore, we present results separately for each region. We compared the relative fit of models using

Akaike's information criterion corrected for small sample sizes (AIC_c) and model weights (w_i); if several models were plausible ($\Delta AIC_c < 2$), we averaged coefficients across the 95% confidence set of models weighted by their respective w_i (Burnham and Anderson 2004).

Model validation. To assess the goodness of fit of all models, we used receiver operating curves (ROC) and AUC values calculated with the ROCR package (Sing et al. 2005) in R (R Core Team 2016). We assessed the sensitivity of β coefficients to individual sapsuckers using Cook's distance, DFBETA statistics, and by refitting the models with each bird removed one at a time to compare the significance of variables (using the influence package; Nieuwenhuis et al. 2015). One bird was considered to have high leverage with a Cook's distance of 0.44 (cutoff = 0.37) in the Okanagan region, but there was no bird with high leverage in the Western region (cutoff = 0.44). The DFBETA values indicated variability across birds in the selection of foraging tree characteristics in the Okanagan region only, with 6 of 11 birds having at least 1 value above the cutoff (0.60 in the Okanagan region and 0.67 in the Western region). None of the birds changed the significance of the tree characteristic variables when excluded from the top model of any of the candidate sets in the Okanagan and Western regions, or from the combined (overall) models.

Data manipulation and screening. We modeled data from the Okanagan and Western regions separately because the tree species differed, with only Douglas-fir



FIGURE 3. Examples of Williamson's Sapsucker nesting territories during a study on foraging habitat selection in southern British Columbia, Canada, in 2014 and 2015: **(A)** Clear-cut from 1999 with regenerating lodgepole pine within a matrix of mature western larch and Douglas-fir trees that were retained as seed trees, during a revisit of the Oliver site in 2016; **(B)** Williamson's Sapsucker nesting territory in the Okanagan Falls site in 2015, within a stand that was partially harvested in 2007 (western larch nesting tree indicated by arrow); **(C)** Recent clear-cut with small tree retention within a nesting territory during a revisit of the Princeton site in 2015 (the nest failed during the nestling stage following the initiation of harvest); and **(D)** Mature stand of Douglas-fir trees used for foraging in the Merritt site in 2015. See Figure 1 for study site locations.

and aspen present in both regions (>5 trees measured). Ponderosa pine trees were excluded from the Okanagan region analysis because only 3 trees were measured (1 used and 2 available). We disallowed 1 pair of variables (dbh and tree height) with a Pearson's correlation coefficient >0.70; we excluded tree height from the models because dbh was easier to measure accurately and was directly relevant to forest management. The decay class variable included signs of decay that may not have been relevant to sapsucker foraging; therefore, we built a separate model set using signs of decay that were present on >5% of the trees that were used for foraging (decay class and signs of decay were not included in the same models). We included individual trees only once in the foraging tree selection models (reutilized trees were included in a subsequent analysis; see below).

For all analyses, we pooled the data by bird sex and age classes because these factors were unrelated to the selection of tree characteristics (per nonparametric tests;

St-Amand 2017). We restricted the dataset to trees identified during the nestling stage (largest sample size), since Williamson's Sapsuckers used smaller trees for foraging during the nestling stage compared with other nesting stages (St-Amand 2017). We pooled individual trees that were used by Williamson's Sapsuckers for gleaning, pecking, or sap feeding to allow for a sufficient sample size and to cover all foraging requirements; however, we used Bonferroni-corrected χ^2 tests and Bonferroni-corrected Mann-Whitney-Wilcoxon tests to investigate differences in the characteristics of used trees by foraging mode.

Selection ratio for dbh. To provide precise recommendations for more effective forest management, we performed a selection ratio analysis to further explore the size (dbh) of live Douglas-fir trees selected for foraging by breeding Williamson's Sapsuckers (Design III for sample of available resource units; Manly et al. 2002). To represent used habitat (n_u), we included Douglas-fir trees that were

TABLE 2. Differences in characteristics of trees that were used once or reutilized (≥ 2 times) for foraging by Williamson's Sapsuckers in the Okanagan and Western study regions of southern British Columbia, Canada, in 2014–2015, per Mann-Whitney-Wilcoxon tests (W ; nonparametric) and χ^2 tests. Significant differences are indicated with bold font. Lw = western larch, Py = ponderosa pine.

Region	Tree characteristic	$\bar{x} \pm SE$		χ^2 (W)	df	P
		Used 1×	Reused $\geq 2\times$			
Okanagan ($n = 294$ used 1×, 74 reused)	dbh	35.7 $\pm$ 1.0	40.2 $\pm$ 2.1	(8,246)	1	0.001
	% dead tree	4.1 $\pm$ 2.1	9.5 $\pm$ 11.1	NA ^a	NA	NA
	% Lw	21.1 $\pm$ 2.3	29.7 $\pm$ 4.8	2.04	1	0.15
Western ($n = 301$ used 1×, 103 reused)	dbh	41.1 $\pm$ 0.9	43.5 $\pm$ 1.9	(14,696)	1	0.43
	% dead tree	11.3 $\pm$ 2.7	15.5 $\pm$ 7.9	0.91	1	0.34
	% Py	16.6 $\pm$ 2.8	20.4 $\pm$ 6.5	0.52	1	0.47
Overall ($n = 772$ used 1×, 177 reused)	dbh	37.8 $\pm$ 0.7	42.2 $\pm$ 1.4	(44,364)	1	0.001
	% dead tree	7.7 $\pm$ 1.6	13.0 $\pm$ 5.7	4.02	1	0.04
	% Lw + Py	19.2 $\pm$ 1.7	24.3 $\pm$ 3.6	1.91	1	0.17

^a The proportions of dead trees in the Okanagan region could not be tested because of low sample sizes of dead trees.

used by either member of a pair (combined male or female) to avoid repeated measures, given that the availability of habitat (π_{ij} ; available Douglas-fir) was the same for both birds in the area surrounding the nest (nesting territory). Dbh categories were selected (selection ratio >1) or avoided (<1) when the 95% confidence interval of the selection ratio did not overlap 1 (Manly et al. 2002). We compared the values of the selection ratios with Bonferroni-corrected χ^2 tests for multiple comparisons ($\alpha = 0.05$).

We found differences in the dbh of used live Douglas-firs between the Okanagan and Western regions and across foraging modes in the Okanagan region; therefore, we analyzed the data for both regions and for sap feeding (Okanagan only) separately (St-Amand 2017). We defined dbh categories following the tree size categories used by Drever et al. (2015): small trees (≤ 22.4 cm dbh), large trees (22.5–57.4 cm dbh), and very large trees (≥ 57.5 cm dbh). We further separated the large and very large trees into 3 size categories (22.5–33.9, 34.0–45.4, and ≥ 45.5 cm dbh) to get more precision for the large tree category as it contained most of the foraging observations.

Reutilization of trees. Quantifying the reutilization of trees (used multiple times for foraging) and their characteristics constitutes valuable information about foraging habitat selection, as trees used more than once are likely to be of higher importance for foraging. We pooled the observations of both members of a pair to obtain the number of utilizations of each tree. We tested the effect of year on the reutilization rate ($\frac{\text{\# uses of tree}}{\text{\# observations of bird}}$) with a Mann-Whitney-Wilcoxon test to determine whether pooling the 2014 and 2015 data was acceptable. We compared some of the characteristics (dbh, tree species, and live or dead) of reutilized foraging trees with those of trees that were used only once for foraging in the Okanagan and Western regions and overall, using χ^2 and Mann-Whitney-Wilcoxon tests. For tree species, to reduce

the degrees of freedom used in the χ^2 tests, we only compared the proportions of western larch and ponderosa pine as they were the most reused tree species overall. To obtain an accurate measure of the dbh of dead trees (highly reused trees), we used 10,000 bootstrapped means and 95% confidence intervals of replicates of the mean sampled dbh of dead and partially dead western larch and ponderosa pine trees that were used for foraging during all 4 nesting stages (with replacement; Efron 1979). We present means $\pm$ SE throughout the Results, unless specified otherwise.

RESULTS

We collected 1,224 foraging mode observations from 27 radio-tagged adult Williamson's Sapsuckers (16 birds in 2014 and 11 in 2015; Appendix Table 2); 1,075 foraging observations were on live trees (88%, $n = 660$ trees), 136 on dead trees (11%, $n = 112$ trees), 6 on the ground, 5 on fallen logs, 1 on a stump, and 1 on a wooden utility pole. The observations on the ground, fallen logs, and stump were all associated with gleaning, and the utility pole and one of the fallen logs were used for pecking.

Tree Selection for Foraging

The characteristics of live trees ($n = 660$) that were important for foraging by Williamson's Sapsuckers in both the Okanagan and Western regions during the nestling stage were tree species and dbh. Blistering and resin exudation was also important, but only in the Okanagan region (Table 1). The odds of a live tree being selected for foraging were higher for Douglas-fir (Okanagan: odds ratio [O.R.] = 2.41; Western: O.R. = 6.23), larger dbh (Okanagan: O.R. = 1.05 per 1 cm increase in dbh; Western: 1.07 per 1 cm), and blistering and resin exudation (Okanagan: O.R. = 2.27; Figures 4A and 4B, Appendix Table 3). The tree species that were included in the model were compared with the reference group (avoided tree species), and thus

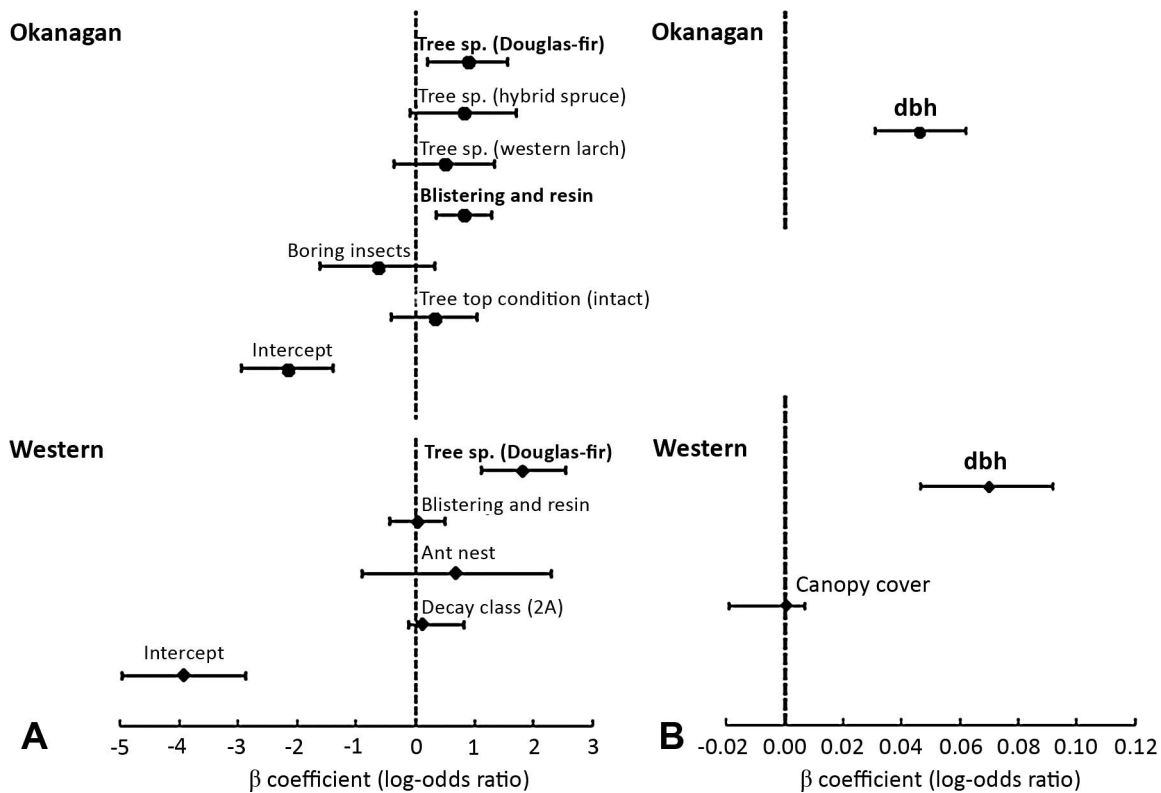


FIGURE 4. Generalized linear mixed models of the selection of live tree characteristics (species, size, and decay class) for foraging by 20 radio-tagged Williamson's Sapsuckers during the nestling stage in 2 study regions (See Figure 1 for locations) in southern British Columbia, Canada. Multimodel averaged β coefficients and 95% confidence intervals for the (A) categorical and (B) continuous variables of the 95% confidence set are presented. Variables with confidence intervals that do not overlap 0 are considered more important and are highlighted in bold font. Reference levels (intercepts) for the tree species factor were the avoided tree species groups (Okanagan region: lodgepole pine and deciduous trees; Western region: ponderosa pine and deciduous trees).

Douglas-fir trees were only selected over lodgepole pine and deciduous trees in the Okanagan region, and over ponderosa pine and deciduous trees in the Western region (Figure 4A).

Characteristics of Foraging Trees by Foraging Mode

In the Okanagan region, Williamson's Sapsuckers used a higher proportion of Douglas-fir for sap feeding (84%) than for gleaning (52%), while pecking was chiefly observed on western larch (49%; Figure 5A, Appendix Table 4A). The mean dbh of trees used for sap feeding (28.9 ± 1.6 cm) was significantly smaller than that of trees used for gleaning (35.9 ± 1.3 cm) and pecking (40.1 ± 2.0 cm; Appendix Table 4A). The decay class for live trees also differed for sap feeding (median decay class = 1) compared with gleaning and pecking (median decay class = 2A for each; $\chi^2_1 = 3.90\text{--}14.01$, $P < 0.001$, $\alpha = 0.02$). The proportion of dead trees used for pecking (17%) was higher than the proportion used for gleaning (3%) and sap feeding (0%; $\chi^2_1 = 63.15\text{--}173.32$, $P < 0.001$, $\alpha = 0.02$).

In the Western region, the proportion of tree species used did not differ for gleaning (88% Douglas-fir) and sap

feeding (99% Douglas-fir), while trees used for pecking were mostly ponderosa pine (54%; Figure 5B, Appendix Table 4B). Mean dbh did not differ among trees used for gleaning (44.6 ± 1.0 cm), pecking (43.8 ± 1.8 cm), and sap feeding (38.0 ± 1.5 cm). The decay classes used did not differ for live trees among foraging modes; however, 43% of trees used for pecking were dead, significantly more than those used for gleaning (4%) and sap feeding (0%; $\chi^2_1 = 226.93\text{--}277.76$, $P < 0.001$, $\alpha = 0.02$).

Selection Ratios for Size Categories of Live Douglas-fir

We used selection ratios to identify forest management targets by examining the selection of size categories of live Douglas-fir for foraging in the Okanagan (sap feeding separately; see Methods) and Western regions. In both regions, Williamson's Sapsuckers avoided small Douglas-fir trees (<22.5 cm dbh) and selected trees in the larger size categories (Figure 6). For sap feeding in the Okanagan region, as well as avoiding small Douglas-firs, sapsuckers avoided live Douglas-fir trees of ≥ 45.5 cm dbh (although the sample size was small for this largest dbh class) and selected live Douglas-fir trees of 22.5–45.4 cm dbh.

TABLE 3. Conflicts between nesting and foraging resources and harvest priorities in Williamson's Sapsucker habitat in Canada for the most common tree species encountered. Results are from this study and previous publications for nesting trees. 'Very high' importance indicates that Douglas-fir trees were selected for foraging in every nesting territory; 'high' importance indicates that the tree species were selected when present. Softwood tree species are considered harvest priorities in Williamson's Sapsucker habitat, creating a conflict as these tree species are also selected for foraging and nesting.

Tree species	Importance	Use	Conflict	Available for harvest	Suggested management strategy
Douglas-fir	Very high	Gleaning, sap feeding, pecking	✓		Partial harvest. Leave oversized and decayed trees as legacy trees. Promote abundance and growth.
Hybrid spruce	High [§]	Gleaning	✓		Partial harvest. Leave oversized and decayed trees as legacy trees. Promote abundance and growth.
Western larch + ponderosa pine	High	Gleaning, pecking, nesting [†]	✓		Partial harvest. Leave oversized and decayed trees as legacy trees. Promote growth.
Quaking aspen	Medium	Nesting			Leave intact where present. Partially harvest groups of >10 trees if needed.
Water birch	Low	Nesting			Leave intact where present. Partially harvest groups of >10 trees if needed.
Black cottonwood	Low	Nesting			Leave intact where it grows.
Grand fir + subalpine fir	None [‡]	None		✓	Harvest.
Lodgepole pine	Negative	None		✓	Harvest.

[§] Hybrid spruce might only be of high importance at high elevations ($\geq 1,400$ m).

[†] Nesting trees are described by Gyug et al. (2009a) and Drever et al. (2015).

[‡] Grand fir and subalpine fir trees were present in the Okanagan sites, but were not selected for either nesting or foraging by Williamson's Sapsuckers.

Reutilization of Foraging Trees

Of the 772 individual trees (660 live and 112 dead) recorded being used for foraging, 177 (23%) were observed being utilized for foraging more than once (both regions combined). The reutilization rate of individual trees did not differ between years ($W = 9967.5$, $P = 0.18$), so we pooled the data from 2014 and 2015. Overall, reutilized trees were 4.4 cm larger in dbh than trees used only once and were more often dead (used once: 8% dead; reused: 13% dead; Table 2, Appendix Table 3). Western larches and ponderosa pines were not reutilized more often for foraging than other tree species, but represented most (81%) of the 112 dead trees used twice or more for foraging. The bootstrapped mean dbh of dead western larches and ponderosa pines used for foraging was 46.0 cm (95% bootstrapped CI: 42.0–50.2 cm dbh, $n = 70$ trees).

DISCUSSION

Our study of Williamson's Sapsuckers identifies foraging habitat requirements that can be incorporated into effective forest management plans to ensure available resources for all foraging modes during the breeding

season. In both Canadian regions that we studied, large, live Douglas-fir trees were used most often for sap feeding and gleaning arthropods (mostly ants). In the Okanagan region, the trees used for sap feeding were smaller (dbh) than the trees used for gleaning or pecking. Large senescent or dead trees (mainly western larches in the Okanagan region and ponderosa pines in the Western region) were used chiefly for pecking. Considering foraging patterns in both regions overall, Williamson's Sapsuckers used a range of tree types, but selected large, live Douglas-fir trees most strongly (≥ 22.5 cm dbh). Large trees and standing dead trees were most likely to be used multiple times for foraging.

Tree size was the most important predictor of foraging tree selection; Williamson's Sapsuckers selected and reused larger trees for foraging more often than smaller trees, in agreement with studies of other woodpecker species in North America (e.g., Raley and Aubry 2006, Tremblay et al. 2010). Larger trees may provide more food resources for foraging sapsuckers because they provide a larger surface with more bark furrows and fungi that favor arthropod abundance (subcortical larvae; Grove 2002, Miller et al. 2007). Also, larger trees are likely to provide shelter for

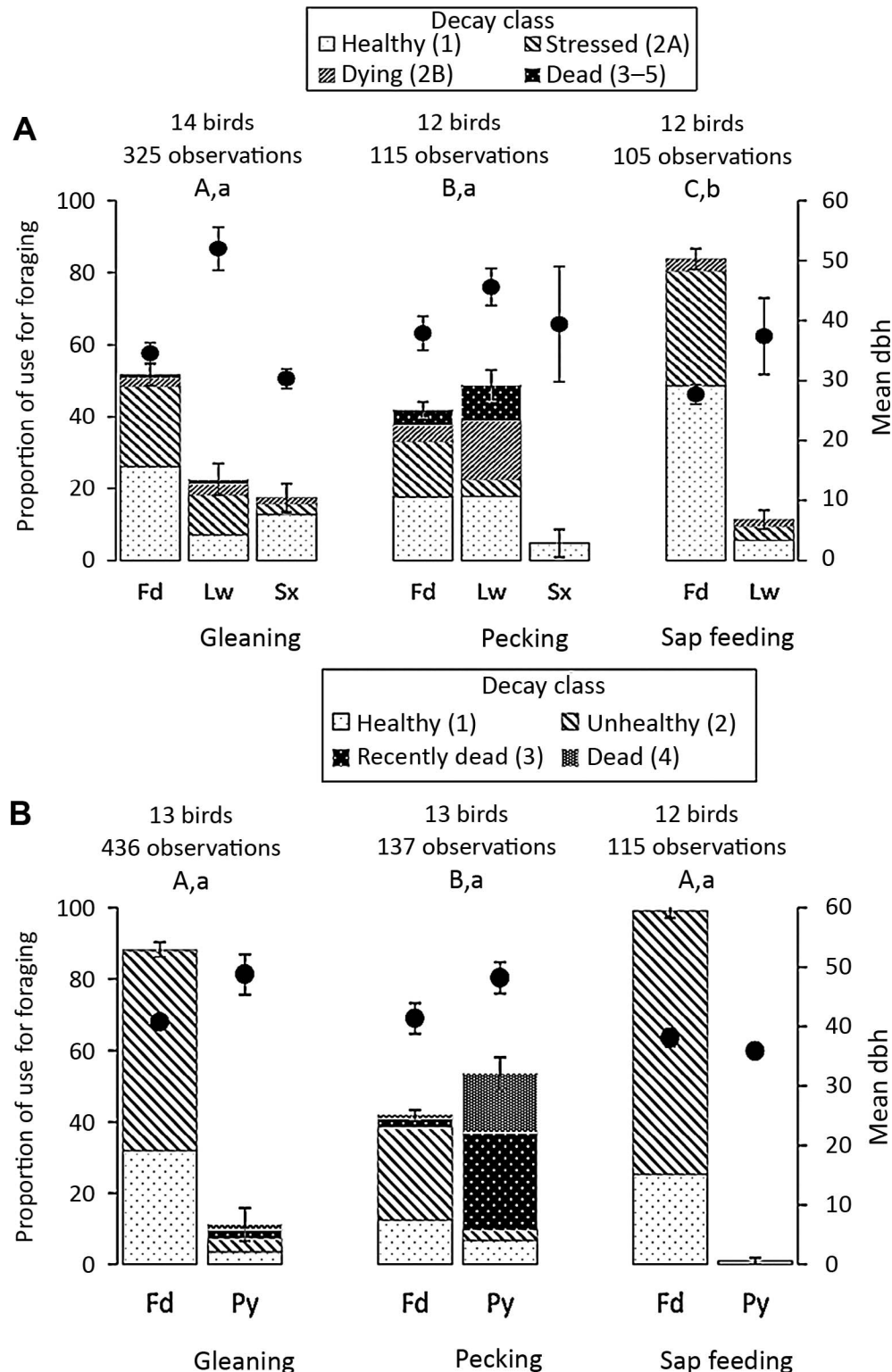


FIGURE 5. Proportion of tree species (full bars), mean dbh (filled circles), and decay categories (stacked bars) of live and dead trees used for gleaning, pecking, and sap feeding by 27 radio-tracked Williamson's Sapsuckers in the (A) Okanagan and (B) Western study regions in southern British Columbia, Canada (see Figure 1 for study region locations). Shared letters indicate no difference in the proportion of tree species (capitalized; Bonferroni-corrected χ^2 tests) and mean dbh (lowercase; Bonferroni-corrected Mann-Whitney-Wilcoxon tests) of trees used for each foraging mode ($\alpha=0.017$). The error bars represent the standard error of tree species proportion and mean dbh. The proportions of tree species do not total 100% because tree species that were used for <10% in total are not presented. Fd = Douglas-fir, Lw = western larch, Sx = hybrid spruce, and Py = ponderosa pine.

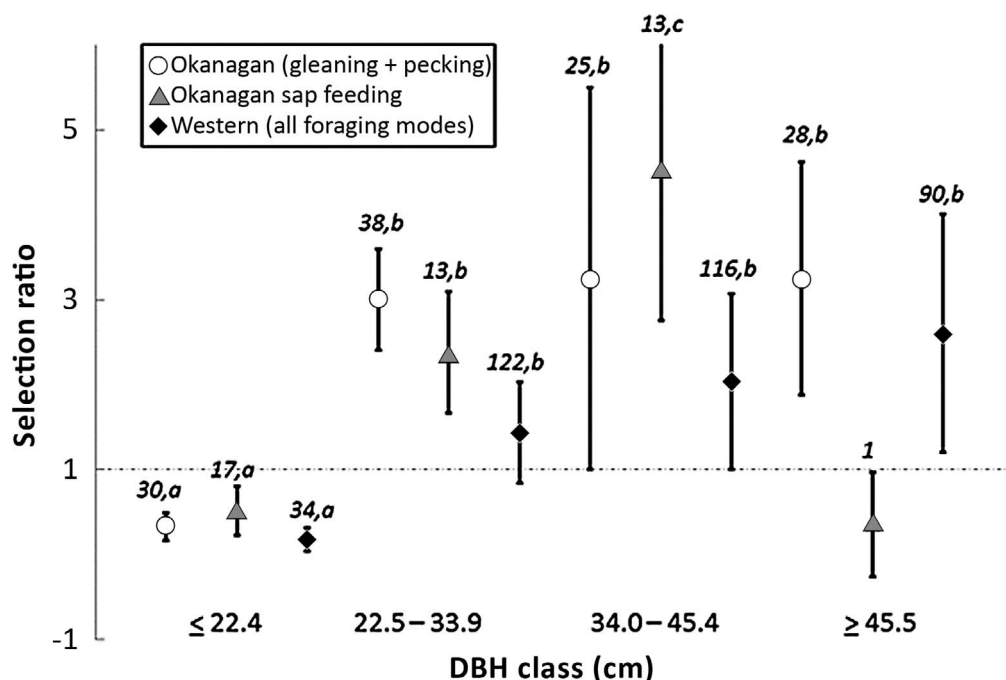


FIGURE 6. Selection ratios and 95% confidence intervals of dbh categories of live Douglas-fir used for foraging by Williamson's Sapsuckers in 2 study regions (see Figure 1 for locations) in southern British Columbia, Canada ($n = 7$ nesting territories in each region). Foraging observations from both members of each pair were pooled to avoid repeated measures of available habitat. A selection ratio of 1 indicates no selection and is represented by the broken line. Selection is indicated by a value above 1 and avoidance by a value below 1. The number of uses is indicated above the bars. Shared letters indicate no significant differences across dbh categories within a region, using Bonferroni-corrected χ^2 tests.

foraging sapsuckers from adverse weather (rain and wind), as well as concealment from aerial predators such as Cooper's Hawks (*Accipiter cooperii*) and Northern Goshawks (*A. gentilis*; Crockett 1975, Tozer et al. 2011). Williamson's Sapsuckers forage more often on the top part of trunks compared with the bottom (Crockett 1975, St-Amand 2017); therefore, tree height, which was positively correlated with tree size, could also affect the quality of foraging trees.

Combining data from the Okanagan and Western regions, trees that were used for the 3 main foraging modes (gleaning, pecking, and sap feeding) had similar dbh, excluding sap feeding in the Okanagan region, which involved trees with sizes similar to available trees. In a previous study that included our study sites in the Okanagan region, sap trees had a larger mean dbh ($\bar{x} = 37.7$ cm dbh, range = 8–75 cm, $n = 71$ trees; Gyug et al. 2009b) compared with those in our study (28.1 ± 1.7 cm dbh, range = 12.4–76.5 cm, $n = 44$ trees). Our results suggest that tree size is not as important for sap feeding as it is for gleaning and pecking. Other characteristics such as local injuries on the trunk of the tree might be more influential for sap tree selection (Dority et al. 2016).

We found that Williamson's Sapsuckers specialized in foraging on coniferous trees, in contrast with sympatric

Red-naped Sapsuckers (*Sphyrapicus nuchalis*) and Red-breasted Sapsuckers (*S. ruber*), which forage on a range of deciduous and coniferous trees, and allopatric Yellow-bellied Sapsuckers (*S. varius*), which forage mostly on deciduous trees (Rushmore 1969, Raphael and White 1984, Walters 1996). Williamson's Sapsuckers may select Douglas-fir trees because they support foraging ants, the main food item in their diet during the breeding season. In western Oregon, USA, ants such as *Camponotus* spp. and *Formica* spp. climb Douglas-fir trunks up to the canopy to tend aphids and forage on insects and spiders (Halaj et al. 1997). Also, some characteristics of the trunk of younger, growing sections of Douglas-fir could facilitate foraging, such as thinner bark for sap well excavation and smoothness that reduces hiding places for ants. Ant nest presence had a positive, but nonsignificant, effect on the odds of foraging by Williamson's Sapsuckers in our models. However, we likely underestimated the number of ant nests, as we sometimes suspected the presence of an ant nest, but were only able to confirm presence after seeing several ants entering the trunk of a tree, which was not always possible. Live Douglas-fir was also used for pecking, probably for feeding on the larvae of bark beetles (Scolytinae), especially the Douglas-fir beetle (*Dendroctonus pseudotsugae*). While they occurred in low frequency,

hybrid spruce trees were selected by Williamson's Sapsuckers in the Okanagan region for foraging in nesting territories close to their elevational range limit, 1,400–1,560 m. At these elevations, hybrid spruce replaces Douglas-fir in forest stands where Williamson's Sapsuckers breed.

Dead trees, especially recently dead western larches and ponderosa pines, were used in high proportions for pecking, were used more often before and after the nestling stage (St-Amand 2017), and were also reused more than live trees. Williamson's Sapsuckers selected recently dead and senescent trees for pecking probably because they generally hold the highest densities and diversity of arthropods, mostly bark beetle subcortical larvae that forage on the inner bark (Stokland et al. 2012). Large dead trees offer optimal habitat for subcortical larvae because they have large volumes of heartwood and thick bark, which regulate temperature and protect larvae against several types of predator (Paine et al. 1997, Wilhelmsson et al. 2002).

Blistering and resin in the Okanagan region was the only tree decay variable that influenced tree selection for foraging. Blistering and resin exudations are a defense mechanism of the tree that can be caused by events such as fire, drought, insect attack, and mechanical damage (Bois and Lieutier 1997). Bark beetles can trigger the exudation of resin, which can provide a source of food for other insects (potential sapsucker prey) such as ants (Formicidae), fruit flies (Drosophilidae), sap beetles (Nitidulidae), and rove beetles (Staphylinidae; Yoshimoto et al. 2005, Yoshimoto and Nishida 2007). Also, blistering and resin can be associated with a wounded section of a tree, making it suitable for sap well production (Eberhardt 2000). Sap wells are drilled above previous wounds on the trunk because sap accumulation occurs above injured woody stems, increasing the sap flow (Salisbury and Ross 1992). Previous studies have reported that sapsuckers select trees with mechanical damage for sap feeding; therefore, damage inflicted to trees during forest operations could be beneficial to sapsuckers by creating foraging habitat (Gyug et al. 2009b). However, widespread damage could limit tree growth and thus negatively affect trees used for gleaning and pecking.

Management Recommendations

Drever et al. (2015) recommended the maintenance and recruitment of large western larch and ponderosa pine trees (>57.5 cm dbh) and quaking aspen trees (17.5–57.5 cm dbh), since these trees were predictors of Williamson's Sapsucker nest site occurrence. Here, we have identified characteristics of trees selected by Williamson's Sapsuckers for foraging to provide additional forest management guidelines for more effective and more comprehensive habitat conservation for the species. Overall, the tree

species selected by Williamson's Sapsuckers for foraging and nesting are also priorities for harvest (Table 3; Drever et al. 2015). We recommend including Douglas-fir, hybrid spruce, ponderosa pine, and western larch as elements of critical foraging habitat for Williamson's Sapsuckers. Retention and recruitment in forests managed for foraging should prioritize large live Douglas-fir trees (≥ 22.5 cm dbh), or hybrid spruce when Douglas-fir is not available, and large western larch and ponderosa pine trees (≥ 45 cm dbh) to provide a supply of senescent and dead trees for nesting and pecking for subcortical larvae and insects (Gyug et al. 2009a, Drever et al. 2015). We recommend preserving heterogeneity in the size of live Douglas-fir trees ≥ 22.5 cm dbh as live Douglas-firs of 22.5–45.4 cm dbh were selected over smaller trees for sap feeding in the Okanagan region. Dead trees can be considered hazardous during forest management operations; therefore, we recommend buffers of live trees around dead and senescent trees to support their retention. Trees >80 cm dbh represent good foraging habitat for Williamson's Sapsuckers and other woodpeckers that breed in montane forests, and their large size makes them unsuitable for forestry equipment to handle (Lemaître and Villard 2005, Tremblay et al. 2010, B. Drobe personal communication).

Our forest management recommendations should be applicable throughout the breeding range of Williamson's Sapsuckers as they breed in forest stands that provide similar nesting trees (larch, pine, or aspen) and foraging trees (Douglas-fir or spruce). In accordance with our results, habitat variables that predicted the distribution of Williamson's Sapsuckers at the landscape scale in the United States were the range of Jeffrey pine (*Pinus jeffreyi*), Douglas-fir, and ponderosa pine (van Riper et al. 2014). The structure of Williamson's Sapsucker habitat in field studies in Arizona, Colorado, Oregon, and Washington, USA, was similar to that in our study in Canada, with Douglas-fir trees always present, mixed with western larch, ponderosa pine, or aspen (Crockett 1975, Winternitz 1976, Bull et al. 1986, Li and Martin 1991, Conway and Martin 1993, Altman 2000). In contrast, Williamson's Sapsucker habitat in Wyoming, USA, lacked Douglas-fir trees and the birds foraged mostly in old lodgepole pine stands and aspen-dominated stands mixed with subalpine fir and spruce trees (selection for foraging not quantified; Loose and Anderson 1995). It is possible that spruce trees were selected for foraging in Wyoming, given the high elevation of the study site (2,499–3,139 m above sea level [asl]), in agreement with our findings in British Columbia (spruce was selected at $>1,400$ m asl).

Tree removal threatens habitat integrity for many woodpecker species in North America and Europe (Angelstam and Mikusiński 1994, Savignac and Machtans 2006, Nappi et al. 2015, Tremblay et al. 2015a). Late-successional tree species such as Douglas-fir, large trees,

and dead trees are characteristics of mature forests, which typically decline in availability in managed landscapes. Fire suppression is also a management strategy that threatens Williamson's Sapsucker habitat since low-intensity fires are beneficial to maintaining stands dominated by large Douglas-fir, western larch, or ponderosa pine trees (Barrett et al. 1991, Spies et al. 2006). Fire suppression could potentially lead to habitat loss because forest fuels accumulate and increase the frequency of stand-replacing fires that are likely to be recolonized by lodgepole pine (Brown 1975).

Mature forest characteristics can be maintained or restored with passive management strategies (Tremblay et al. 2015b), including the protection of portions of mature forest from anthropogenic disturbance. Active restoration strategies can accelerate the recovery of mature forest characteristics, and include creating small gaps to obtain vertical and horizontal heterogeneity, killing large live trees to create standing dead trees and coarse woody debris, conducting prescribed burns, and cutting smaller trees that compete for nutrients with larger ones (thinning; Franklin et al. 2002, Keeton 2005). We stress that the continuous recruitment of nesting and foraging trees within the current and predicted future range of the Williamson's Sapsucker is necessary to maintain healthy populations in the long term, as well as providing provisions for monitoring to investigate whether management actions are achieving the required resource supply to maintain breeding populations. Selective and partial tree cutting can be compatible with maintaining suitable Williamson's Sapsucker nesting and foraging habitat, but more research is necessary to predict the response of the species to stand-level habitat disturbances, including the creation of edges, gaps, and open areas.

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Author contributions: All authors conceived the study design and designed the methods. J.S-A. collected the data, performed the analysis, and wrote the article. J.A.T. and K.M. substantially edited the article.

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APPENDIX TABLE 1. Description of measurements taken for the used and available substrates, and their use in statistical analyses of substrate selection for foraging by Williamson's Sapsuckers in southern British Columbia, Canada.

Variable name	Description	Variable type
Substrate use	Williamson's Sapsucker occurrence (response variable): 1. No use observed (0; available) 2. Used for foraging (1)	Binomial
Tree species	1. Douglas-fir 2. Ponderosa pine 3. Deciduous 4. Western larch 5. Lodgepole pine 6. Hybrid spruce (Engelmann spruce × white spruce)	Categorical
dbh	Diameter at breast height (dbh, in cm) of the tree	Continuous
Tree height	Height of the tree (m), measured with a clinometer	Continuous
Decay class	Decay class of the tree: 1. Healthy tree, no visible signs of decay 2A. Healthy tree with minor signs of decay 2B. Live tree with 1 major or ≥3 minor signs of decay (Okanagan region only) 3. Recently dead tree with needles or twigs still on and tight bark 4. Dead tree with no needles or fine twigs and with ~50% of major branches lost 5. Dead tree with ≤2/3 of original height and sapwood or heartwood sloughing from the top	Categorical
Signs of decay (contribution to determining decay class)	A combination of: 1. Blistering or resin exudation on the bark (minor) 2. Signs of boring insects (minor) 3. Mechanical damage (not considered decay) 4. Burned (not considered decay) 5. Brown needles (minor or major) 6. Trunk gall (minor) 7. Fungus (major) 8. Heart rot (major) 9. Signs of ants nesting (major) 10. Dead branches (minor or major) 11. Damaged or forked tree top (major) 12. No signs of injury or decay	Categorical (11 levels, although some levels were combined). Presence-absence (binomial) in models

APPENDIX TABLE 2. Number of foraging modes observed, substrate use observations, and standing trees used by radio-tracked Williamson's Sapsuckers during the 2014–2015 breeding season in southern British Columbia, Canada. One substrate use observation can represent several foraging modes (e.g., gleaning, pecking), and trees can contain several substrate use observations (reutilization).

Study region and bird group	Number of birds	Foraging modes	Substrate use observations	Trees
Okanagan				
Males	8	308	285	202
Females	6	232	215	166
Total	14	540	500	368
Western				
Males	8	453	408	247
Females	5	231	224	157
Total	13	684	632	404
Overall				
Males	16	761	693	449
Females	11	463	439	323
Total	27	1,224	1,132	772

APPENDIX TABLE 3. Characteristics of trees that were available (unused), used for foraging at least once, and reused for foraging (≥ 2 times) by 27 radio-tracked Williamson's Sapsuckers in 2 regions of southern British Columbia, Canada. Two sites (Oliver and Okanagan Falls) are grouped in the **(A)** Okanagan region, while the **(B)** Princeton and **(C)** Merritt sites (Western region) are presented separately because of differences in tree characteristics. The mean and median values are presented for diameter at breast height (dbh) and decay class, respectively. The sample sizes represent the number of unique trees that were measured as available, used for foraging once or multiple times, or reused. The percentage of tree species is calculated using the number of trees for each category as the denominator. Quaking aspen, lodgepole pine, and water birch were included in the statistics, but their characteristics are not presented in the table ($<10\%$ use); therefore, overall percentages of tree species do not sum to 100%. Blistering includes resin exudation. See Appendix Table 1 for descriptions of characteristics.

		Value $\pm$ SE (range)	Value $\pm$ SE (range)	Value $\pm$ SE (range)
Characteristic		Available	Foraging $\geq 1\times$	Foraging $\geq 2\times$
(A) Okanagan region ($n = 14$ birds)		$n = 368$ trees	$n = 368$ trees	$n = 74$ trees
Douglas-fir	% tree sp.	50.3 $\pm$ 2.6	58.7 $\pm$ 2.5	54.1 $\pm$ 2.6
	dbh (cm)	19.5 $\pm$ 1.2 (4.0–99.3)	33.6 $\pm$ 1.2 (4.5–91.8)	36.6 $\pm$ 2.6 (12.2–76.5)
	Decay class	1 (1–3)	1 (1–4)	1 (1–4)
	% alive	96.7 $\pm$ 2.7	97.2 $\pm$ 2.6	97.5 $\pm$ 6.0
	% blistering	23.9 $\pm$ 3.0	51.0 $\pm$ 3.4	55.0 $\pm$ 7.4
Western larch	% tree sp.	18.9 $\pm$ 2.0	22.6 $\pm$ 2.2	28.4 $\pm$ 4.8
	dbh (cm)	26.8 $\pm$ 2.5 (3.6–86.0)	48.6 $\pm$ 2.4 (6.2–108.0)	53.3 $\pm$ 3.4 (29.8–85.2)
	Decay class	1 (1–5)	2A (1–5)	2A (1–5)
	% alive	95.7 $\pm$ 2.1	89.2 $\pm$ 2.2	71.4 $\pm$ 5.1
	% blistering	18.8 $\pm$ 2.3	26.5 $\pm$ 2.9	14.3 $\pm$ 5.5
Hybrid spruce	% tree sp.	12.6 $\pm$ 1.7	12.2 $\pm$ 1.7	12.2 $\pm$ 6.0
	dbh (cm)	22.8 $\pm$ 1.6 (4.7–51.0)	30.9 $\pm$ 1.6 (13.4–58.5)	35.9 $\pm$ 3.7 (19.8–58.5)
	Decay class	1 (1–5)	1 (1–2B)	1 (1–2B)
	% alive	95.7 $\pm$ 1.8	100	100
	% blistering	6.5 $\pm$ 2.1	15.6 $\pm$ 1.7	44.4 $\pm$ 4.8
Overall	% tree sp.	81.8	93.5	94.7
	dbh (cm)	20.6 $\pm$ 0.8 (3.6–99.3)	35.7 $\pm$ 1.0 (4.5–108.0)	40.2 $\pm$ 2.1 (12.2–85.2)
	Decay class	1 (1–5)	2A (1–5)	2A (1–5)
	% alive [‡]	94.9	94.9	90.5 $\pm$ 4.9
	% blistering	21.6 $\pm$ 1.9	41.0 $\pm$ 2.0	40.5 $\pm$ 5.1
(B) Princeton site ($n = 8$ birds)		$n = 286$ trees	$n = 286$ trees	$n = 71$ trees
Douglas-fir	% tree sp.	70.3 $\pm$ 2.7	85.0 $\pm$ 2.1	85.9 $\pm$ 2.5
	dbh (cm)	26.2 $\pm$ 1.0 (8.1–75.0)	38.5 $\pm$ 0.8 (10.0–103.0)	37.8 $\pm$ 1.4 (11.0–58.9)
	Decay class	2A (1–4)	2A (1–4)	2A (1–2B)
	% alive	97.0 $\pm$ 2.6	98.8 $\pm$ 1.3	100
	% blistering	41.3 $\pm$ 2.2	62.6 $\pm$ 1.1	65.6 $\pm$ 2.4
Ponderosa pine	% tree sp.	29.0 $\pm$ 2.7	15.0 $\pm$ 2.1	14.1 $\pm$ 4.1
	dbh (cm)	27.4 $\pm$ 1.6 (8.4–66.9)	44.5 $\pm$ 2.6 (19.2–104.4)	50.0 $\pm$ 7.7 (27.1–104.1)
	Decay class	1 (1–5)	3 (1–4)	3 (3–4)
	% alive	65.1 $\pm$ 2.6	27.9 $\pm$ 4.9	0
	% blistering	4.8 $\pm$ 3.5	7.0 $\pm$ 1.1	10.0 $\pm$ 8.4
Overall	% tree sp.	99.3	100	100
	dbh (cm)	26.6 $\pm$ 0.8 (8.1–75.0)	39.4 $\pm$ 0.8 (10.0–104.4)	39.5 $\pm$ 1.7 (11.0–104.1)
	Decay class	2A (1–5)	2A (1–4)	2A (1–4)
	% alive [‡]	87.8	87.8	85.9 $\pm$ 2.5
	% blistering	30.4 $\pm$ 2.0	54.2 $\pm$ 1.0	57.7 $\pm$ 2.2
(C) Merritt site ($n = 5$ birds)		$n = 118$ trees	$n = 118$ trees	$n = 30$ trees
Douglas-fir	% tree sp.	58.8 $\pm$ 4.5	72.0 $\pm$ 4.1	59.4 $\pm$ 4.5
	dbh (cm)	23.2 $\pm$ 2.4 (4.5–107.2)	46.4 $\pm$ 2.3 (16.3–141.8)	52.0 $\pm$ 6.3 (26.0–141.8)
	Decay class	2A (1–5)	2A (1–3)	2A (1–2A)
	% alive	91.4 $\pm$ 4.8	97.6 $\pm$ 3.9	100
	% blistering	31.4 $\pm$ 5.2	56.5 $\pm$ 2.0	57.9 $\pm$ 8.0
Ponderosa pine	% tree sp.	24.4 $\pm$ 3.9	23.7 $\pm$ 3.9	34.4 $\pm$ 8.4
	dbh (cm)	31.4 $\pm$ 3.8 (4.5–85.5)	54.1 $\pm$ 3.2 (27.4–90.8)	57.2 $\pm$ 5.8 (30.8–90.8)
	Decay class	2A (1–5)	2A (1–4)	2A (1–4)
	% alive	69.0 $\pm$ 3.9	57.1 $\pm$ 3.6	54.5 $\pm$ 8.3
	% blistering	13.8 $\pm$ 4.6	3.6 $\pm$ 2.0	9.1 $\pm$ 8.0

APPENDIX TABLE 3. Continued.

		Value $\pm$ SE (range)	Value $\pm$ SE (range)	Value $\pm$ SE (range)
Characteristic		Available	Foraging $\geq 1\times$	Foraging $\geq 2\times$
Overall	% tree sp.	83.2	95.7	93.8
	dbh (cm)	23.7 $\pm$ 1.8 (4.5–107.2)	47.2 $\pm$ 1.9 (16.3–141.8)	52.3 $\pm$ 4.4 (26.0–141.8)
	Decay class	2A (1–5)	2A (1–4)	2A (1–4)
	% alive [‡]	85.9	85.9	81.3 $\pm$ 7.0
	% blistering	21.8 $\pm$ 4.3	40.5 $\pm$ 1.8	42.2 $\pm$ 7.6

[‡]The overall percentages of live used and available trees are the same because of the sampling design.

APPENDIX TABLE 4. Proportion of use and measurements of tree species characteristics using substrate use observations of 27 radio-tracked Williamson's Sapsuckers for the 3 main foraging modes (gleaning, pecking, and sap feeding) in the (A) Okanagan and (B) Western study regions of British Columbia, Canada, in 2014–2015. The mean and median statistics are presented for diameter at breast height (dbh) and decay class, respectively. Standard error of the mean and standard error of the proportion are presented accordingly. Values in bold font represent the characteristics of the tree species that were used in higher proportions for each foraging mode (using substrate use observations). Quaking aspen, lodgepole pine, and water birch were included in the statistics, but their characteristics are not presented in the table (because their use was <10%); thus, overall percentages of tree species do not sum to 100%. Blistering includes resin exudation. See Appendix Table 1 for descriptions of tree species characteristics.

Characteristic		Value $\pm$ SE (range)	Value $\pm$ SE (range)	Value $\pm$ SE (range)	Value $\pm$ SE (total)
(A) Okanagan		Douglas-fir	Western larch	Hybrid spruce	Overall
Gleaning ($n = 325$ obs., 236 trees)	% tree sp.	51.6 $\pm$ 3.0	22.6 $\pm$ 4.4	17.4 $\pm$ 3.9	(91.6)
	dbh (cm)	34.6 $\pm$ 1.7 (4.5–91.8)	52.0 $\pm$ 3.6 (6.2–108.0)	30.3 $\pm$ 1.6 (13.4–56.0)	35.9 $\pm$ 1.3
	Decay class	1 (1–4)	2A (1–5)	1 (1–2B)	2A
	% alive	98.4 $\pm$ 3.4	93.6 $\pm$ 5.7	100	97.5 $\pm$ 2.5
Pecking ($n = 115$ obs., 75 trees)	% blistering	51.6 $\pm$ 4.7	25.5 $\pm$ 6.3	16.7 $\pm$ 4.4	40.3 $\pm$ 1.7
	% tree sp.	41.9 $\pm$ 2.2	48.6 $\pm$ 4.3	4.8 $\pm$ 3.9	(95.3)
	dbh (cm)	37.9 $\pm$ 2.8 (12.2–80.9)	45.6 $\pm$ 3.1 (15.4–85.2)	39.4 $\pm$ 9.6 (29.4–58.5)	40.1 $\pm$ 2.0
	Decay class	1 (1–4)	2B (1–5)	1	2A
Sap feeding ($n = 105$ obs., 57 trees)	% alive	89.5 $\pm$ 2.5	80 $\pm$ 5.4	100	82.7 $\pm$ 2.0
	% blistering	50.0 $\pm$ 3.6	23.3 $\pm$ 6.2	0	36.0 $\pm$ 2.7
	% tree sp.	83.8 $\pm$ 2.8	11.4 $\pm$ 2.6	0	(95.2)
	dbh (cm)	27.7 $\pm$ 1.6 (12.4–76.5)	37.4 $\pm$ 6.4 (20.9–62.5)	NA	28.9 $\pm$ 1.6
(B) Western	Decay class	1 (1–2B)	1 (1–2B)	NA	1
	% alive	100	100	NA	100
	% blistering	50.0 $\pm$ 4.0	50.0 $\pm$ 2.8	NA	50.6 $\pm$ 2.0
		Douglas-fir	Ponderosa pine		Overall
Gleaning ($n = 436$ obs., 271 trees)	% tree sp.	88.3 $\pm$ 2.1	11.2 $\pm$ 4.6		(99.5)
	dbh (cm)	40.8 $\pm$ 1.0 (10.0–141.8)	48.8 $\pm$ 3.4 (19.2–90.8)		44.6 $\pm$ 1.0
	Decay class	2A (1–4)	2A (1–4)		2A
	% alive	99.6 $\pm$ 2.5	64.5 $\pm$ 6.7		95.6 $\pm$ 3.0
Pecking ($n = 137$ obs., 89 trees)	% blistering	63.4 $\pm$ 3.0	6.5 $\pm$ 6.0		56.5 $\pm$ 1.4
	% tree sp.	41.9 $\pm$ 1.4	53.5 $\pm$ 4.6		(97.4)
	dbh (cm)	41.4 $\pm$ 2.6 (16.3–109.5)	48.2 $\pm$ 2.6 (27.1–104.4)		43.8 $\pm$ 1.8
	Decay class	2A (1–4)	3 (1–4)		3
Sap feeding ($n = 115$ obs., 44 trees)	% alive	91.5 $\pm$ 1.8	17.9 $\pm$ 6.7		57.3 $\pm$ 2.5
	% blistering	41.8 $\pm$ 2.2	5.1 $\pm$ 6.1		27.0 $\pm$ 2.9
	% tree sp.	99.1 $\pm$ 1.9	0.9 $\pm$ 0.9		(100)
	dbh (cm)	38.1 $\pm$ 1.5 (18.7–59.0)	35.9		38.0 $\pm$ 1.5
	Decay class	2A (1–2B)	1		2A
	% alive	100	100		100
	% blistering	62.8 $\pm$ 2.4	0		61.4 $\pm$ 1.4