

Stand-level forest management for foraging and nesting of Williamson's sapsuckers

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ABSTRACT

Williamson's Sapsuckers, like most woodpeckers, require live and dead standing trees for foraging and nesting. Forest management plans that include Williamson's Sapsucker habitat conservation guidelines currently focus on nesting trees because little is known about foraging habitat requirements, but foraging habitat in close proximity is also essential for the survival and reproduction of the species. We conducted a study on the selection of stand-level characteristics for foraging and nesting territories to improve knowledge on the habitat requirements of this endangered woodpecker in Canada during the breeding season. We tracked 27 radio-tagged Williamson's Sapsuckers in managed forest at their northern range limit in two regions of southern British Columbia. We examined the selection of forest composition and configuration characteristics at the foraging patch and stand levels by comparing use and availability, and described foraging trip distances. In the Okanagan region, sapsuckers did not show a selection pattern for foraging patch characteristics. In the Western region, Williamson's Sapsuckers selected foraging patches with higher densities of large live Douglas-fir trees. Nest patches were usually in small openings and had lower tree densities than foraging patches in the Western region, but not in the Okanagan region. Open areas (e.g., clear-cuts, seed tree cuts, pastures, roads, powerlines) were avoided during foraging trips in both regions. Regarding stand-level configuration, Williamson's Sapsuckers selected continuous stands for foraging – with $\geq 30\%$ crown closure in both regions. We used the 50th and 95th percentiles of foraging trip distances to recommend zones for nest reserve (no-harvest; 0–140 m from the nest) and nest management (Okanagan: 340 m, Western: 410 m). For the nest management zone, we recommend only partial harvesting with retained groups of trees extending from 140 to 340 m in the Okanagan region and from 140 to 410 m in the Western region. We suggest that Williamson's Sapsuckers exhibited stronger selection when foraging in the Western region, because they compensated for longer foraging distances due to higher proportions of open area in their nesting territories.

1. Introduction

Optimal foraging theory predicts that birds maximize their fitness by choosing resources that provide high food intake with low constraints such as travel distance and searching time (Schoener, 1971; Krebs et al., 1974). To optimize foraging, birds that breed in forest habitats are expected to cue on stand characteristics that are associated with high concentrations of preferred foraging substrates (feeding sites) and adequate environmental conditions for prey items (Lyons et al., 2008; Barbaro et al., 2008; Vergara et al., 2016; Dufour-Pelletier et al., 2020). For forest birds, key characteristics of stand-level foraging habitat may

include tree species composition, size class distribution of trees, density of trees, crown closure and the quantity of coarse woody debris (CWD) and stumps (Drapeau et al., 2000; Roberge et al., 2018; Wesolowski et al., 2018). Stand characteristics are considered “selected” when they are used by a species in higher proportion than their availability and represent high quality habitat (Johnson, 1980). The main driver in stand-level foraging habitat selection is the concentration of food resources or foraging trees, but other factors might be influential such as predation risk, competition, habitat conditions for prey items or proximity to nesting site (Orlans and Pearson, 1979; Lima and Dill, 1990; Tremblay et al., 2009; Geyleynse et al., 2016). The spatial arrangement of

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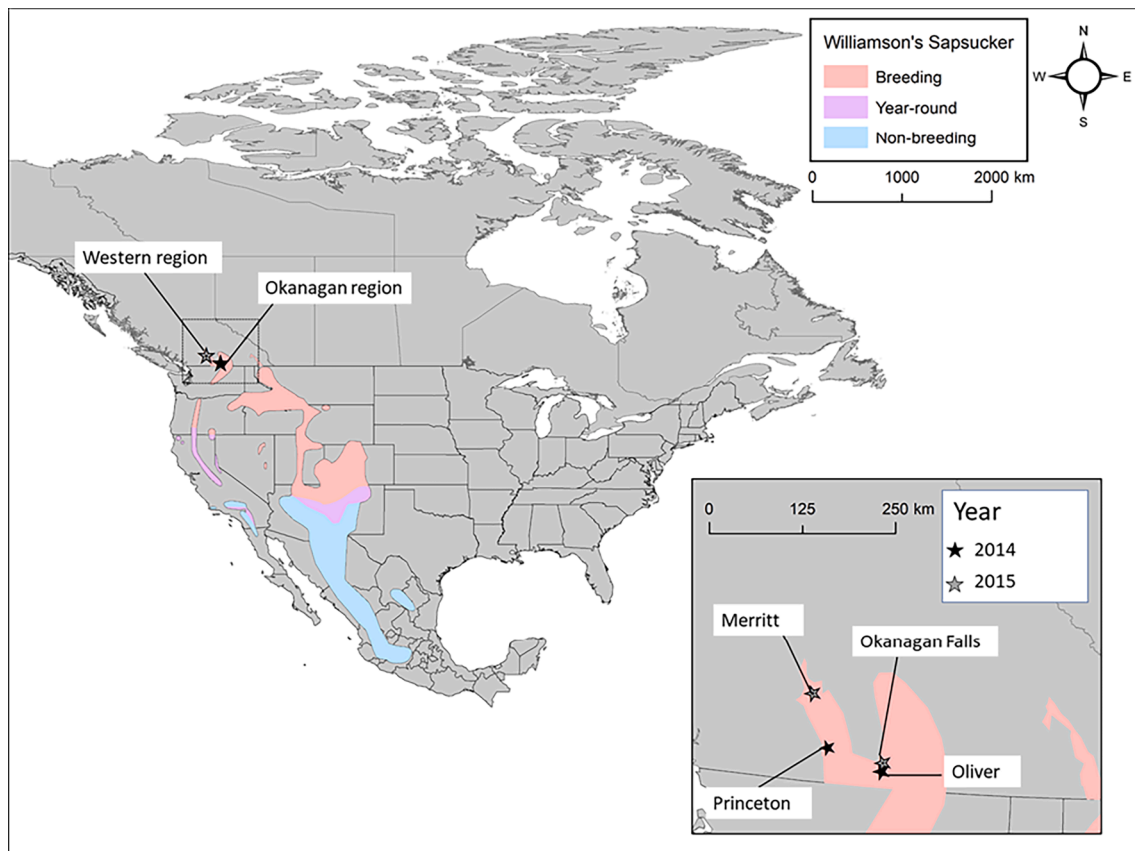


Fig. 1. Study area relative to the range of Williamson's Sapsucker for a telemetry study on foraging habitat in British Columbia, Canada, 2014–2015 (range data adapted from: Birdlife, 2021).

stands and groups of trees determines the quantity of edges and gaps (open areas) that can influence the quality of foraging habitat for birds (Turchin, 1998; Gagné et al., 2007). An edge effect occurs at the interface of two ecosystems that contrast strongly, such as where clear-cuts adjoin old forest (Matlack and Litvaitis, 1999); response to edge effects varies by species (Valente and Betts, 2019). Small gaps in the forest can benefit certain bird species; however, others avoid gaps by moving through forested areas when available (Bélisle and Desrochers, 2002). Gap avoidance may be linked to increased predation risk, limitations in perceptual range at which birds can identify suitable habitat and the absence of adequate forested habitat for foraging and perching (Lima and Zollner, 1996; Robertson and Radford, 2009).

Birds that nest in tree cavities (cavity nesters) are sensitive to forest management, because they use large trees for nesting and, in many cases, foraging (Imbeau et al., 2001; Roberge et al., 2008; Tremblay et al., 2015). The retention and recruitment of large live and dead trees that are suitable for nesting and foraging may be overlooked by forest management, and long-term declines in cavity nesters have been observed with the loss of these habitat attributes (Ibarra et al., 2017; Lamare and Tremblay, 2021). Stand-level forest management that favors woodpecker species is gaining importance since most woodpeckers are considered good indicators of avian diversity, and keystone species for their role as cavity providers (primary cavity nesters) for cavity-using vertebrates (secondary cavity nesters; Martin et al., 2004; Mikusinski et al., 2001; Drever et al., 2008; Cockle et al., 2011). In North America, the cavity nester community is comprised of approximately 85 species of birds including passerines, ducks, diurnal raptors, owls, and woodpecker species. Forest management practices that benefit woodpecker species are likely to benefit the entire community (Scott et al., 1977; Martin et al., 2021).

Williamson's Sapsuckers (*Sphyrapicus thyroideus*) are montane

woodpeckers that breed in coniferous and mixed forests in western North America from southern British Columbia to New Mexico. In Canada, Williamson's Sapsuckers have been designated as Endangered under the Species at Risk Act (2006) and are Blue-listed in British Columbia (British Columbia Conservation Data Centre, 2021), given their small population in Canada is located at the northern periphery of the species range (~960 breeding individuals; Gyug et al., 2014a; COSEWIC, 2017). In the United-States, Williamson's Sapsuckers are federally listed as a bird of conservation concern (U.S. Fish and Wildlife Service, 2008). Habitat alteration caused by human activities (primarily logging) is likely to affect the already small populations.

Drever et al. (2015) used stand-level characteristics to model Williamson's Sapsucker nesting territory occurrence, assuming that models would identify nesting and foraging habitat requirements. Overall, they found that nesting territory occurrence was best explained by stand characteristics that are directly related to the presence of suitable nest trees which are mainly western larch (*Larix occidentalis*; Gyug et al., 2009) and trembling aspen (*Populus tremuloides*; Conway and Martin, 1993). Some of these characteristics were also linked to potential foraging opportunities such as densities of very large stumps and large hybrid spruce trees (*Picea engelmannii* X *Picea glauca*), the proportion of 80–119-year-old Douglas-fir dominated stands (*Pseudotsuga menziesii* var. *glauca*) and crown closure of trees >15 m tall. The Drever et al. (2015) study was unable to make a clear distinction between nesting and foraging habitat, given a lack of data on foraging observations. In Gyug et al. (2010), the number of Williamson's Sapsucker fledglings was significantly lower in nesting territories with tree densities of <85 live trees/ha, suggesting that foraging habitat may be insufficient below this threshold. Coarse woody debris and stumps are possible key elements of Williamson's Sapsucker foraging habitat since these habitat attributes are required by colonies of the two ant groups (*Camponotus* spp. and

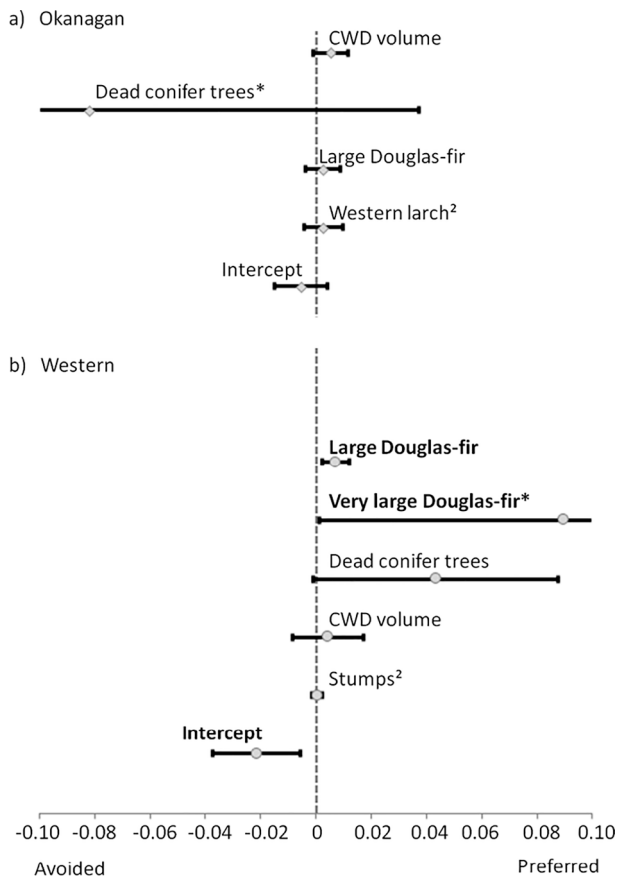


Fig. 2. Selection of stand-level characteristics (density of trees, stumps and coarse woody debris) by foraging Williamson's Sapsuckers in the a) Okanagan and b) Western regions in British Columbia, Canada. The multi-model averaged linear or quadratic coefficients of variables in the 95% confidence set of Generalized Linear Mixed Models (GLMM) are presented with their 95% confidence intervals.

Formica rufa sp. Group) that are preferred by foraging Williamson's Sapsuckers (Gyug et al., 2014b).

Only two studies on Williamson's Sapsuckers have addressed spatial use of habitat, and each of these provide an insight into the importance of foraging patch distribution. Gyug et al. (2007) used the mean distance to the nearest neighbouring nest to infer that Williamson's Sapsucker breeding home ranges probably extend to a radius of 225 m around the nest, although the birds may forage outside this area. One radio-tagged male Williamson's Sapsucker had a home range of 54.2 ha and was detected once at a maximum distance of 500 m from the nest (Manning and Cooper, 1996). Williamson's Sapsucker nesting territory occurrence

has been associated with forests disturbed by fire (Hutto et al., 2015; Hutto and Patterson, 2016) and tree harvesting (Whitcomb et al., 1981; Keller and Anderson, 1992; Drever et al., 2015), suggesting that stand configuration characteristics such as presence of forest edge might be selected for nesting or foraging.

Williamson's Sapsuckers are one of the least studied woodpecker species in North America. A study on Williamson's Sapsucker foraging habitat selection at the stand level is required to inform adaptive forestry practices, fill current knowledge gaps regarding its critical habitat and link studies on foraging selection at the tree and nesting territory levels (Environment Canada Recovery Strategy, 2014; Drever et al., 2015; St-Amand et al., 2018). No studies have been conducted on stand-level habitat characteristics that use foraging observations in relation to tree species composition, tree and stump size class distribution and CWD volumes. Knowing whether foraging and nest patches have different characteristics is relevant to forest management, because both habitats need to be present in the landscape for successful breeding of Williamson's Sapsuckers. Data on foraging trip distances using tracking devices are required to reduce spatial bias and inform more effective designs of reserve and management zones around active and recent nests. Data on the selection of stand configuration characteristics at the stand level are required to understand how forest management strategies (harvest prescriptions) might affect Williamson's Sapsucker selection of foraging and nesting habitat.

1.1. Objectives

Here, we use observations of radio-tracked adult Williamson's Sapsuckers to identify the characteristics of forest stands that should be considered by forest managers to conserve critical foraging and breeding habitat. We have three objectives related to Williamson's Sapsucker foraging patch selection and space use: 1) identify the stand-level composition and structure of foraging patches and compare with nest patches, 2) describe the space use of foraging Williamson's Sapsuckers and propose nest reserve and management zones to protect active breeding habitat and 3) evaluate the selection of within-stand configuration characteristics for foraging. We use visual foraging observations collected during three stages of the breeding season: incubation, nestling stage and up to two weeks after nesting failure or nesting success.

2. Methods

2.1. Sites, capture and telemetry

We monitored Williamson's Sapsucker foraging trips and movement during the breeding season at four sites in managed landscapes (two in each of the Okanagan and Western regions) in 2014 and 2015 (Fig. 1). The Oliver (2014) and Okanagan Falls (2015) sites were located in the Okanagan region, and the Princeton (2014) and Merritt (2015) sites were located in the Western region. All sites contained 1) a proportion of

Table 1

Summary of AICc model selection using a backward stepwise method to determine the models that best predict the selection of stand-level characteristics by foraging Williamson's Sapsuckers in the a) Okanagan ($n = 50$ plots in 9 breeding territories) and b) Western region ($n = 46$ plots in 9 territories) in British Columbia, Canada.

Region	Model variables	Rank	AICc	Δ AICc	Wi	AUC
a) Okanagan	Snags, cwd	1	72.2	0	0.31	0.67
	Cwd	2	72.4	0.2	0.28	0.63
	Null model	3	73.6	1.4	0.15	0.5
	Large Douglas-fir, snags, cwd	4	73.9	1.7	0.13	0.68
	Large Douglas-fir, snags, cwd, western larch ²	5	74.6	2.4	0.09	0.71
	Large Douglas-fir, snags, cwd, stumps ² , western larch ²	6	76.9	4.7	0.03	0.72
	Large Douglas-fir, very large Douglas-fir, snags, cwd, stumps ² , western larch ²	7	79.3	7.1	0.01	0.73
b) Western	Large Douglas-fir, very large Douglas-fir, snags	1	55.7	0	0.54	0.85
	Large Douglas-fir, very large Douglas-fir	2	57.5	1.8	0.21	0.82
	Large Douglas-fir, very large Douglas-fir, snags, cwd	3	57.9	2.2	0.18	0.85
	Large Douglas-fir, very large Douglas-fir, snags, cwd, stumps ²	4	60.2	4.6	0.05	0.85
	Large Douglas-fir, very large Douglas-fir, snags, cwd, stumps ² , ponderosa pine	5	62.8	5.2	0.01	0.85

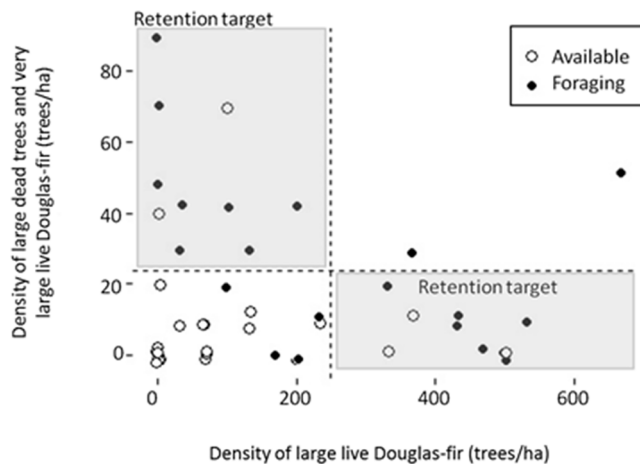


Fig. 3. Stand composition and structure of patches used and unused (available) by foraging Williamson's Sapsuckers in the Western region in southern British Columbia, Canada.

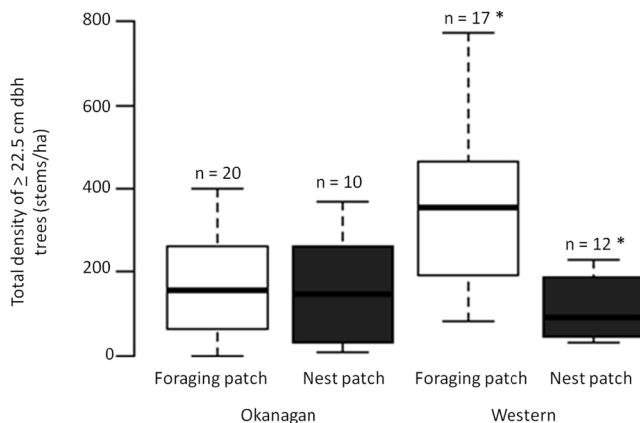


Fig. 4. Density of all trees ≥ 22.5 cm dbh in foraging patches (>60 m radius from the nest tree, white boxes) and nest patches (≤ 60 m radius, dark boxes) in both the Okanagan and Western habitats of Williamson's Sapsuckers in southern British Columbia, Canada.

protected intact mature or primary conifer or mixed forest, 2) older clear-cut (≥ 20 years old), 3) forestry and paved roads, 4) history of recent and older low to moderate intensity wildfire, and 5) insect outbreaks (mostly 10 years old mountain pine beetle; BC Vegetation Resource Inventory [VRI; [British Columbia Ministry of Forests and Range, 2016](#)], Les Gyug [Okanagan Wildlife Consulting], Brian Drobe [Weyerhaeuser Company], pers. comm.). Open areas in the Okanagan region were mostly clear-cuts and seed tree cuts (few mature trees reserved for regeneration), while in the Western region open areas were comprised of grasslands that were sometimes artificially maintained by cattle grazing and herbicides. Recent clear-cuts (< 20 years old) were only present at the sites in the Okanagan region, and partial harvesting (with retained groups) was only present at the Okanagan Falls site. Clearings for powerlines or pipelines were present in the Western region only. We located breeding adults using call-playback and a database of Williamson's Sapsucker detections from recent years ([Gyug et al., 2014a](#)). We caught adults mostly during incubation and early nestling stage from late-April to mid-June using 1) a combination of mist-nets, call-playback and a male decoy as a lure, 2) dip nets at the nesting cavity and 3) aerial mist-nets mounted on poles up to ~ 9 m. We banded Williamson's Sapsuckers with a numbered aluminium band and three coloured plastic bands and deployed a radio-transmitter (BD-2, 1.2 g, detection range 1 km; Holohil systems, Ltd., Carp, Ontario, Canada)

sutured to the two central rectrices following [Tremblay et al. \(2009\)](#). We monitored nest contents to confirm nest status using a small video camera (2–5 cm diameter) mounted on an extendable pole (maximum height 14 m).

We radio-tracked foraging adults during bouts of 0.5–4 h during morning, afternoon and evening (between 0500 and 2130 h), and alternated the order in which birds were tracked to obtain observations at different times for each bird. We tried to obtain visual observations of their behaviour, following a homing tracking protocol ([Mech, 1983](#)). We tracked radio-tagged birds on foot following the radio signal from randomly selected accessible locations within the territory to obtain more evenly spatially distributed data. We tested the detection range of the radio-transmitters on three occasions by putting two activated transmitters on stumps and walking away on a road until we lost the signal, noting the distance. Detection range varied with the terrain conditions and was on average 427 ± 182 m (range = 160–592 m, occasionally up to 1.1 km). Sapsuckers foraging in tall conifers with dense foliage can sometimes be difficult to locate visually. In 62% of cases, a relocation involved a direct observation of a behaviour of the radio-tagged bird. In the remaining 38% of cases, a spatial relocation (GPS point) was recorded if the observer could identify the tree or group of trees that the bird was using by auditory cues (pecking, calls, etc.), based on a strong and clear directional telemetry signal in that specific location, or by observations of a sapsucker in flight departing from the foraging location.

2.2. Sampling of patches used for foraging

Stands and forest patches are often used as interchangeable concepts, but we are referring to them distinctly in this study. Stands are contiguous communities of trees sufficiently uniform in compositional and structural characteristics to be distinguished from bordering communities, while assemblages of stands are referred to as forests ([Smith et al., 1997](#)). We refer to “patches” as areas within stands that are used by birds - the foraging and nest patch. Within each sapsucker territory, we sampled the characteristics of patches used for foraging and available patches in paired sets of two circular nested plots of 9.77 m radius (0.03 ha) and 17.84 m radius (0.1 ha; [Fig. A.1](#)).

We recorded the number of all standing (alive and dead) trees and stumps by species according to the following: live trees of 22.5–57.4 cm diameter at breast height (dbh) and stumps of > 22.5 cm diameter at stump height in the 0.03 ha plot, and > 57.4 cm dbh live trees and dead conifer trees > 22.5 cm dbh in the 0.1 ha plot ([Fig. 3.1](#)). We also measured CWD items > 7.5 cm diameter where they intersected either of 2 line transects (11.28 m in length), following the Vegetation Resources Inventory Ground Sampling Procedures of the [British Columbia Ministry of Forests and Range \(2007\)](#). The larger plot in the nested design allowed the sampling of very large trees and dead standing trees which were less frequent than smaller trees and stumps.

The “used for foraging” plots were centered on a used substrate (tree: $n = 47$, fallen log: $n = 1$) to overlap with the highest concentration of foraging observations. Each used plot was paired with a plot representing “available” habitat and positioned at the same distance from the nest and centered on a tree for which we had no observations of use by Williamson's Sapsuckers. The available plot was located in a random direction, but in a way that the plot did not overlap with any locations where Williamson's Sapsucker were detected (visual or foraging observations). In 2014, we sampled two paired plots per nesting territory (used and available) in the Okanagan region and four paired plots per territory in the Western region. In 2015, we measured six paired plots on nesting territories with less than 30 statistically independent relocations (see statistical analysis section for details) per pair, and ten on territories with 30 or more statistically independent relocations. In the case where three or more paired plots were measured in a territory, we positioned one paired plot in the nest patch (< 60 m from nest; used and available) and another at the furthest relocation where a visual detection occurred,

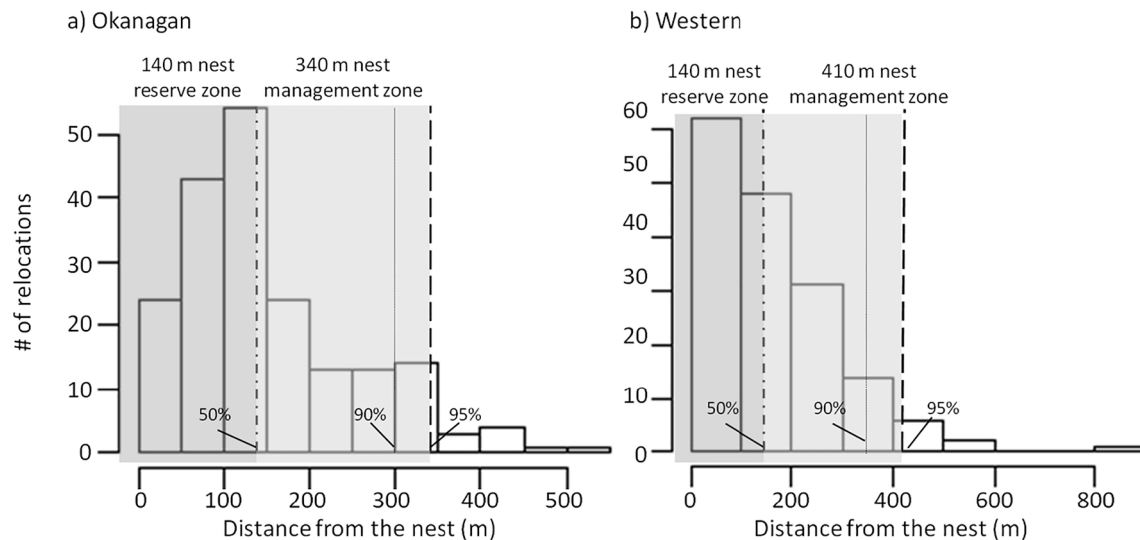


Fig. 5. Telemetry relocations of Williamson's Sapsucker adults during foraging trips to feed their nestlings in a) the Okanagan ($N = 10$ birds, 6 males, 4 females, $n = 188$ relocations) and b) Western ($N = 10$ birds, 6 males, 4 females, $n = 164$ relocations) regions, in 2014–2015. Spatio-temporal autocorrelation was tested and reduced using Time to Statistical Independence analysis (see methods).

and positioned the remaining within these two points. Also, we measured coarse woody debris (CWD) ≥ 7.5 cm diameter that lay across two 11.28 m perpendicular transect lines (north and east from the plot centre), following the Vegetation Resources Inventory Ground Sampling Procedures of the [British Columbia Ministry of Forests and Range \(2007\)](#).

We converted the sampled densities of trees and stumps to get estimates per hectare for each plot size (i.e., 0.03 or 0.1 ha). As a proxy for

potential ant nesting habitat, we calculated the volume-density of CWD (m^3/ha) in the plots from the two transect lines, using the formula $y_i \left(\frac{\text{m}^3}{\text{ha}} \right) = \frac{\pi^2}{8 \times L} \times \sum_{j=1}^{m_i} d_{ij}^2$, where L is the length of the transect ($11.28 \times 2 = 22.56$ m) and d_{ij} is the diameter of each of the CWD pieces where they crossed the transect ([Marshall et al., 2000](#)). The formula assumes that the debris pieces are relatively circular in cross-section and are lying horizontally, which was generally the case.

2.3. Characterization of stand configuration

We refer to stand configuration characteristics as the spatial arrangement of resources (trees) within stands. To estimate the availability of predefined stand configuration categories in Williamson's Sapsucker nesting territories, we created a polygon layer using ArcGIS 10.5.1 (ESRI, Redlands, California, USA) based on a combination of: 1) data from high resolution Landsat imagery (0.5 m Resolution, 10.2 m accuracy, year range 2010–2013; DigitalGlobe, Westminster, Colorado, USA), 2) a GIS database on stand characteristics maintained by the British Columbia Ministry of Forests, Lands and Natural Resource Operations (Vegetation Resource Inventory, VRI), and 3) ground validation (using our vegetation sampling data and personal observations). We used the VRI database for information on the logging history and crown closure (% cover of vertically projected crowns of trees) to support the designation of stand configuration, which was mostly based on satellite imagery and ground validation.

We delimited stands based on the distribution of trees, dividing them into six categories: 1) Open areas or areas with low densities of single trees, which included clear-cuts, seed tree cuts, forestry roads, power line clearings, fields, grasslands, pastures or clusters of ≤ 5 trees at ≥ 15 m from other tree clusters, 2) retained groups, which had $\sim 10\%$ crown closure with trees clustered in groups (natural or harvested), 3) forest edges, which was continuous forest within 15 m from an open area, 4) open stands, which were contiguous forested areas with $\leq 30\%$ crown closure with trees in a scattered configuration (usually not clustered; determined with VRI data), 5) moderate stands with 31–50% crown closure and 6) closed stand, which was contiguous forested areas with $> 50\%$ crown closure (determined with VRI data). To characterize the spacing of retained groups, we measured the smallest distance between two randomly selected distinct adjacent non-contiguous groups and calculated the mean and standard error ($n = 20$ comparisons for 8 ha). All stands were dominated by Douglas-fir, western larch or ponderosa

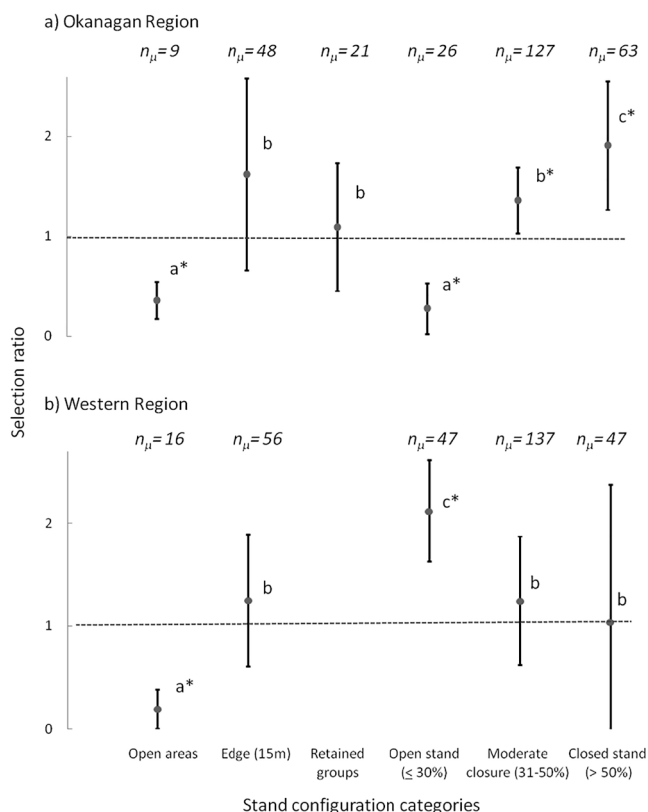


Fig. 6. Selection ratios and 95% confidence intervals of stand configuration categories used (n_μ) by foraging Williamson's Sapsuckers in the a) Okanagan and b) Western regions, in 2014–2015.

Table 2

Habitat requirements of Williamson's Sapsuckers for foraging, nesting and communication in the Okanagan and Western regions of British Columbia (combined with Gyug et al., 2009, 2010, 2014a; St-Amand et al., 2018). These habitat characteristics may be used as habitat management targets to meet recovery objectives of maintaining or increasing Williamson's Sapsucker populations.

Habitat	Okanagan	Western
Tree species composition range (%) ^a	<ul style="list-style-type: none"> Fd[†] 66–76 Lw 19–27 Other 3–9 	<ul style="list-style-type: none"> Fd 76–86 Py 13–21 Other 1–3
Tree dbh (cm)	<ul style="list-style-type: none"> 22.5 minimum overall. Average by tree species: Fd 35 Lw 50 (foraging), 70 (nesting) Deciduous 35 (At, Ew) 	<ul style="list-style-type: none"> 22.5 minimum overall. Average by tree species: Fd 40 Py 50 (foraging), 70 (nesting) Deciduous 35 (At, Ew)
Tree decay (% of trees)	<ul style="list-style-type: none"> Resin exudation (foraging): $\geq 38\%$ Fd, 23% Lw, 11% Sx[§] Nesting: Internal fungal infection (Lw, At and Ew) and broken or dead top Lw. 	<ul style="list-style-type: none"> Nesting: Recently dead Py or live At with internal fungal infection
Tree density range	<ul style="list-style-type: none"> 85–300 large live trees/ha 	<ul style="list-style-type: none"> 85–300 large live trees/ha
CWD [‡]	<ul style="list-style-type: none"> 110–180 m³/ha 	<ul style="list-style-type: none"> 20–70 m³/ha

^a Fd = Douglas-fir, Lw = western larch, Py = ponderosa pine, At = trembling aspen, Sx = hybrid spruce and Ew = water birch (*Betula occidentalis*).

[†] In higher elevations (1400 m), hybrid spruce can replace Douglas-fir.

[§] Resin exudation is synonymous to pitching, a physiological response of trees to stress.

[‡] Includes CWD ≥ 7.5 cm dbh. Recommendations are based on the mean ($\pm$ standard error) volume-densities in foraging patches, and require more studies.

Table 3

Recommended tree harvesting strategies according to Williamson's Sapsucker nest reserve and management zones. In all zones, large standing dead trees (with 2/3 of original height) should be retained with a buffer of live trees to avoid the tree being identified as hazardous, which could lead to felling. Coarse woody debris should be left after harvesting to match amounts pre-harvest.

Management zone	Clear-cut	Partial harvest
Forest where Williamson's Sapsuckers are present	<ul style="list-style-type: none"> ≤ 2 ha contiguous - Use 15-m harvest block separator if larger 	<ul style="list-style-type: none"> Retain live and dead trees >22.5 cm dbh in density of >275 trees/ha as much as possible Max opening size: 0.2 ha
Nest management [*]	Avoid	<ul style="list-style-type: none"> Retain live and dead trees >22.5 cm dbh in density of >275 trees/ha Max opening size: 0.2 ha
Nest reserve [†]	No harvest	No harvest

^{*} Extends 140–340 m from recent and active nests in the Okanagan and 140–410 m in the Western region.

[†] Extends 0–140 m from recent and active nests.

pine (*Pinus ponderosa*). We excluded from the layer, paved roads (never used by Williamson's Sapsuckers) and stands that were dominated by lodgepole pine (*Pinus contorta*; 2 uses out of 597 foraging trees), because they were different from other categories and had low use. We calculated the availability of each stand configuration category in nesting territories of radio-tracked birds using a buffer corresponding to a distance from the nest determined using the foraging trip distance data (95th percentile, more details in results section), in each region.

2.4. Statistical analysis

2.4.1. Selection of stand-level composition and structure for foraging

We identified the relevant stand-level characteristics of foraging patches by comparing our nested plot data from used patches (nested plots) and available patches (unused, no observed use) in the Okanagan and Western regions separately, since the composition of tree species in stands differed with region (St-Amand et al., 2018). We used generalized linear mixed-models (GLMM) with presence or absence as a binomial response variable (logistic) and the nesting territory (bird pair) as a random effect. We determined *a priori* the variables more likely to influence foraging patch selection by Williamson's Sapsuckers from all the stand-level variables measured, based on the tree-level selection behaviour identified in St-Amand et al. (2018). We used six explanatory variables (fixed effects) representing the density of: 1) very large Douglas-fir (≥ 57.5 cm dbh), 2) large Douglas-fir (22.5–57.4 cm dbh), 3) western larch (Okanagan region) or ponderosa pine (Western region), 4) dead standing trees (minimum height: 1.3 m), 5) stumps and 6) the volume-density of CWD. Density of live and dead trees and stumps included all trees with ≥ 22.5 cm dbh (dsh for stumps), except for live

Douglas-fir which were divided into large and very large categories. We excluded hybrid spruce from the analysis because it was present in only four of 96 plots. We divided the six explanatory variables by 100 before fitting the data to avoid convergence problems due to high eigenvalues, and divided the model outputs by the same number (100) when we present them. We fitted a linear model for each numerical variable to examine the fit of linear, quadratic and exponential terms, and included the best fitting term in a full model containing all the explanatory variables. We used a Pearson's correlation matrix to assess collinearity across variables, considering $r \geq 0.70$ as correlated.

Using backward stepwise model selection, we removed the least significant variables one by one until we obtained a model that included only significant variables. We identified the most parsimonious models using the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2004) and Akaike weights calculated with the 'AICcmodavg' package in R (Mazerolle, 2016). A model with $\leq 2 \Delta AICc$ had considerably more support, but in the case where there were several candidate models, we used multi-model averaging to calculate the averaged-weighted parameters of the variables (Burnham and Anderson, 2004). We used receiver operating curves (ROC) to assess the performance of the candidate models, calculated with the 'ROCR' package in R (Sing et al., 2005). The method consists of plotting the true positive rate against the false positive rate (Zweig and Campbell, 1993). From the plot, the area under the curve (AUC) was calculated to generate a measure of performance for the model; a value of one indicates that the model can perfectly classify Williamson's Sapsucker foraging patches, while a value of 0.5 indicates that the model performs equivalently to a random classification (Hanley and McNeil, 1982). We used plots from 18 nesting territories, including three non-breeding

males which used cavities but no eggs or nestlings were detected.

We determined tree density thresholds in foraging patches for forest management recommendations using 10 000 bootstrapped means and 90% confidence intervals of replicates of the mean tree density from the nested plots (with replacement; Efron, 1979). Bootstrapping provides a more robust estimate of the true population mean and requires no assumption of normality when computing the confidence intervals. We did not estimate thresholds using model-based techniques based on the probability of foraging occurrence, because the probability of occurrence was set to 0.5 by our used-available sampling design (see Guénette et al., 2005; Toms et al., 2015). As a post-hoc analysis, we used *t*-test to evaluate the potential differences in the availability of trees ≥ 22.5 cm dbh between the Okanagan and Western regions to compare the two habitat types.

2.4.2. Tree density in foraging and nest patches

We used multiple analysis of variance (MANOVA) tests to compare the stand characteristics between nest patches (≤ 60 m from nest) and foraging patches (> 60 m from nest) to test whether foraging patches have different tree densities than nest patches. The independent variable was whether the plot was within the nest patch (0) or used for foraging further from the nest within the nesting territory (1). Tree density of nest patches was represented by nested plots located within 60 m from the nest tree (use and available, see patch sampling section above). Foraging patches were represented by the nested plots in areas of high foraging use > 60 m from the nest tree. The *a priori* selected dependent variables were density of: large Douglas-fir, very large Douglas-fir, dead conifer trees and total tree density (trees/ha). The total tree density included all tree species, such as Douglas-fir, western larch, ponderosa pine, hybrid spruce, lodgepole pine, trembling aspen and water birch (*Betula occidentalis*). We excluded trees < 22.5 cm dbh from the analysis because they are unlikely to be used for foraging and are unlikely to influence the nesting environment, being lower than cavity height (e.g., nest cavity concealment; St-Amand et al., 2018). We used the Pillai-Bartlett trace statistic to determine significance, as it is considered the most robust for the evaluation of statistical significance with MANOVA (Olson, 1976). We could not meet the assumption of independence across observations of MANOVA tests, since we measured a mean of 2.8 pairs of used and available plots (range = 1–5) per nesting territory, potentially increasing type I error (repeated measures). The assumption of homogeneity in variance was assessed using Bray-Curtis distances, from which the dispersion was compared with an ANOVA test using the “vegan” package in the R statistical software (alpha = 0.05; Dixon, 2003). We used graphical assessments to evaluate the assumption of multivariate normality, using a Q-Q plot of the Mahalanobis distance across samples plotted against the χ^2 distributed quantiles. The homogeneity in variance assumption was achieved in both regions (Okanagan region: $F = 0.0021$ and $p = 0.96$; Western region: $F = 1.11$ and $p = 0.30$); however, there was a departure from the multivariate normal assumption. If the MANOVA test revealed a difference between nest patches and foraging patches, we tested the density of different types of trees using Bonferroni-corrected one-way ANOVA tests.

2.4.3. Foraging distances

We examined the distances from the nest at which Williamson's Sapsuckers were detected foraging to obtain an estimate of the area used for foraging during the nestling stage. We only used relocations that were statistically independent, which was determined using the time to statistical independence (TTSI) tool in the rhr package in R (Signer and Balkenhol, 2015). The TTSI were calculated for each bird ($N = 20$), but we used the mean time between observations for each region to simplify the data selection process (Okanagan region: mean $\pm$ SE = 31.7 ± 10.8 min, range = 9.3–93.1 min; Western region: mean $\pm$ SE = 37.3 ± 13.8 min, range = 3.1–111.1 min). Of the total number of Williamson's Sapsucker relocations we used, 209 (58% of 358) were based on visual observations (96% were foraging observations); the remaining 42%

were spatial relocations (undetermined behaviour). We calculated the Euclidian distances from the nest of the statistically independent Williamson's Sapsucker foraging trips using UTM's (one unit = one meter) and the formula $D = \sqrt{X^2 + Y^2}$, where X and Y are the differences between the longitudinal and latitudinal coordinates of the nest tree and the position of the relocation. We plotted the trip distances against the percentiles and used the 50th, 90th and 95th percentiles to support recommendations for habitat management zoning around nests. The data used for this analysis included only relocations for birds in the nestling stage, non-breeding individuals were excluded.

2.4.4. Selection of stand-level configuration for foraging

To evaluate the selection of stand configuration during the breeding season, we calculated selection ratios (W_i , Design III for census of available resource units; Manly et al., 2002), using the statistically independent Williamson's Sapsucker relocations combined by nesting territory (use: n_{ij}) and the GIS layer of stand configuration categories (availability: π_{ij} ; see category description in stand configuration characterization section above). We considered stand configuration categories to be selected (value > 1) or avoided (value < 1) when the 95% confidence interval of the selection ratio did not overlap one (Manly et al., 2002). We compared the values of the selection ratios with Bonferroni-corrected χ^2 tests for multiple comparisons ($\alpha = 0.05$). As a post-hoc analysis, we used a two-tailed *t*-test to test the significance of the difference in proportion of open area (habitat area with open and single trees) between the Okanagan region and Western regions to explore whether the western region had more open area. We described qualitatively the gap-crossing behaviour (crossing of open habitat) of Williamson's Sapsuckers during foraging trips. We obtained a threshold of the proportion of open area at which the selection of higher densities of trees (≥ 22.5 cm dbh) in foraging plots becomes more important, by fitting a Locally Weighted Least Squares Regression (LOESS) curve to a scatter plot of the mean tree density in foraging plots and the proportion of open area in the nesting territories. We used relocations from the incubation stage until two weeks after nesting success or failure, but we excluded relocations from non-breeding birds and birds that left their territory after nesting (birds not using and defending a specific area).

3. Results

3.1. Selection of foraging patch characteristics

We measured 48 plots that were centred on a foraging tree used by Williamson's Sapsuckers during the breeding season (foraging patch; $\bar{x} \pm$ SE = 2.9 ± 1.0 relocations, range = 1–8 relocations), and compared with 48 available plots (available patch; Table B.1). In the Okanagan region, no model explained the selection of foraging patches by Williamson's Sapsuckers significantly better than the null model, meaning that sapsuckers did not select for foraging patches at the stand level (≤ 2 Δ AICc; Fig. 2, Table 1). In the Western region, two models best predicted Williamson's Sapsucker foraging at the stand level, the three influential variables being density (trees/ha) of large live Douglas-fir (22.5–57.4 cm dbh), very large live Douglas-fir (≥ 57.5 cm dbh) and dead conifer trees (≥ 22.5 cm dbh; ≤ 2 Δ AICc; Table 1, Table B.2). The probability of a foraging patch being selected increased significantly with the density of large Douglas fir by 0.7% for each increase of one large live Douglas-fir, and by 9.4% for each additional very large live Douglas-fir (Fig. 2; Table B.2). The bootstrapped mean densities in foraging patches were 248 trees/ha (180–316 trees/ha, 90% confidence interval) for large live Douglas-fir and 24 trees/ha (16–32 trees/ha, 90% confidence interval) for very large Douglas-fir and dead conifer trees (Fig. 3). The overall densities of ≥ 22.5 cm dbh standing trees in available habitat did not differ between the Okanagan and Western regions; however, Williamson's Sapsuckers selected denser foraging patches by 116 trees/ha ($\bar{x} \pm$ SE; Okanagan: 181.7 ± 24.4 trees/ha, Western: 297.2 ± 43.8 trees/

ha; $t = 2.35$, $p = 0.02$). Nest patches (≤ 60 m from the nest) in the Okanagan region did not differ from foraging patches that were in the rest of the nesting territory (i.e., > 60 m from the nest; $F = 0.50$, $p = 0.73$; Table B.3). In the Western region, Williamson's Sapsuckers selected nest patches with a lower mean tree density than foraging patches (difference = 231.7 trees/ha of trees ≥ 22.5 cm dbh of all species; Douglas-fir = 90% of trees; Fig. 4).

All variables represent densities: trees/ha for standing trees, stumps/ha for stumps and m^3 /ha for coarse woody debris (CWD).

Positive β coefficients represent selection for a stand-level characteristic, while negative coefficients signify avoidance. Variables with confidence intervals that did not overlap zero are considered more important and are bolded. * The 95% confidence intervals of dead conifer trees in the Okanagan region (-0.20 to 0.038) and very large Douglas-fir in the Western region (0.0014 – 0.18) were too large to display.

The dashed lines represent bootstrapped (10 000 replicates) means and are presented to show retention targets. Foraging patches were selected for their high density of very large live Douglas-fir (≥ 57.5 cm dbh) and standing dead conifer (≥ 22.5 cm dbh) trees or their high density of large live Douglas-fir (22.5–57.4 cm dbh). We combined very large live Douglas-fir density with dead conifer tree density to facilitate the interpretation of foraging patches for forest management. Retention targets are any value within the two grayed areas.

Differences were tested between foraging and nest patches in each region using MANOVA and significant differences are indicated by “*”.

3.2. Foraging trip distances

Williamson's Sapsuckers feeding nestlings were detected foraging up to 556 m from the nest in the Okanagan region and 831 m in the Western region. About half of the relocations were included in the first 140 m (core area of 6.2 ha) from the nest in the Okanagan and Western regions (Okanagan: 53th percentile, Western: 50th percentile; Fig. 5). Considering that foraging trips of the last ten or five percentiles were unusual (cut-offs = 90th and 95th percentiles), the area used by Williamson's Sapsuckers extended from 300 to 340 m radius (28–36 ha) from their nest trees in the Okanagan region and 340–410 m (36–53 ha) in the Western region (Fig. A.2).

3.3. Stand configuration for foraging

In the Okanagan region, Williamson's Sapsuckers selected and used most frequently stands with closed ($> 50\%$ crown closure; $\hat{W}_i = 1.91$; 21% of relocations) and moderate crown closure (31–50% crown closure; $\hat{W}_i = 1.36$; 43% of relocations); while open stands were avoided ($\leq 30\%$ crown closure; $\hat{W}_i = 0.28$; Fig. 6, Table B.4). In the Western region, open stands with $\leq 30\%$ crown closure were the only category that was significantly selected ($\hat{W}_i = 2.12$). The mean minimal distance between clusters of trees was $16.4 \text{ m} \pm 0.9 \text{ m}$ in retained groups, which were only present in the Okanagan region (range = 2–54 m; 0.2 ha). Sapsuckers significantly avoided open areas, which was the least used category with 4% of total relocations in both regions (Okanagan: $\hat{W}_i = 0.36$, Western: $\hat{W}_i = 0.20$).

Dominant tree species in all categories were either Douglas-fir, western larch or ponderosa pine. Foraging observations from both members of a pair were pooled for the territory ($n = 15$ territories) to avoid repeated measures of available habitat. A selection ratio of 1 indicates no selection and is represented by the broken horizontal line, a value > 1 indicates selection and a value < 1 indicates avoidance. The “**” indicates that the confidence intervals of closed stand did not overlap with 1. Shared letters indicate no significant differences across stand configuration categories using Bonferroni-corrected χ^2 tests.

On average, the proportion of open area was 29% in nesting territories of the Western region compared to 9% in the Okanagan (Table B.3; $t = 6.89$, $p = 0.003$). The longest crossing of open area in the

Okanagan region was 174 m across a 5.9 ha seed tree cut; one that Williamson's Sapsuckers were seen crossing only on the way back to the nest after foraging on the other side (Fig. C.1.a). In the Western region, the longest crossing of open area was 160 m across a 12.1 ha pasture, that Williamson's Sapsuckers crossed in both directions when observed foraging on that side of the territory (Fig. C.1.g).

4. Discussion

This study offers first insights on forest stand-level characteristics selected by foraging Williamson's Sapsuckers, hence enhancing our comprehension of the critical habitat of this woodpecker, and which harvest prescriptions may maintain it. Williamson's Sapsuckers did not show selection patterns for foraging patches in our Okanagan study region; however, in the more open and fragmented Western region, sapsuckers selected foraging patches with high densities of large live Douglas-fir and large dead conifer trees, and nest patches had lower densities of large trees than foraging patches > 60 m from the nest. Williamson's Sapsuckers that were feeding nestlings were relocated 50% of the time within 140 m of their nest in both regions and 95% of relocations were within 340 m (Okanagan region) and 410 m (Western region). Open areas were avoided in both regions and stands with higher crown closure were selected for foraging in the Okanagan region ($> 30\%$), while open stands were selected in the Western region ($\leq 30\%$).

Our stand level results showed that Williamson's Sapsuckers select foraging patches with higher tree density in the Western region, but not in the Okanagan region, while there was consistent selection of individual tree characteristics detected in both the Okanagan and Western regions in our previous study looking at selection for foraging at the tree level (St-Amand et al., 2018). Birds that are feeding nestlings return to their nest frequently for every feeding bout (central place foraging); therefore, patches with higher concentration of foraging trees (benefit) are expected to be selected to compensate for large travel distances between the nest and foraging sites (cost; Orians and Pearson, 1979; Cezilly and Benhamou, 1996). Williamson's Sapsuckers may select foraging habitat in a non-hierarchical pattern in the Okanagan region, meaning that the individual foraging trees are selected regardless of foraging patch characteristics. Selection at the patch level may not have been as important for Williamson's Sapsuckers in the Okanagan region because large trees were more evenly distributed than in the Western region, which had more open areas unsuitable for foraging. These open areas consisted predominantly of managed pastures, powerlines, burnt areas and paved and non-paved roads. Williamson's Sapsuckers may be able to adapt to a certain level of landscape fragmentation in the Western region by selecting more concentrated foraging patches with higher benefit (Hutto, 1985). Similar behavioural plasticity has been observed in other woodpecker species and larger foraging distances had no negative effects on nest productivity (Tjernerberg et al., 1993; Lorenz et al., 2016).

We found that Williamson's Sapsuckers used larger nesting territories in the Western region than in the Okanagan (410 m and 340 m radius, respectively; 95% percentile), likely because of the higher proportion of open area (non-foraging). The foraging distances we observed were longer than 225 m estimated nesting territory radius in an earlier observational study of the species in this area using the nearest-neighbour distance method (Gyug et al., 2007). In a telemetry study on Red-naped Sapsuckers (*S. nuchalis*) in Interior Douglas-fir forests in north central British Columbia, nesting territory radius was 205.2 ± 58.2 m during the nestling stage using the Minimum Convex Polygon method ($n = 10$ birds, maximum distance detected from nest = 1.1 km; Walters, 1990).

Williamson's Sapsuckers selected continuous stands for foraging, but selection patterns varied by region in our study. The selection of closed stands in the Okanagan region and open stands in the Western region may be explained by the habitat requirements of preferred ant species. In a previous study, fecal sacs in the Okanagan region contained mostly

ant species that require closed stands that have more moisture (*Camponotus* spp.; Hansen and Akre, 1993); while in the Western region, fecal sacs mostly contained ant species that require openings with solar radiation as a heat source (*Formica rufa* sp.; Klotz, 2008). The abundance of both types of ants preferred for foraging by Williamson's Sapsuckers might increase close to forest openings, because of the improved solar radiation that regulates the temperature of ant colonies during cold temperatures, and higher abundance of CWD. Large openings such as clear-cuts may reduce the access to suitable foraging habitat within the nesting territory and drive local extinction of ant species (Punttila et al., 1991). Williamson's Sapsuckers likely avoided open areas because they represent unsuitable foraging habitat (tree density too low) and crossing large areas of non-foraging habitat increases the energetic cost to foraging trips (Pedley, 1977).

Gyug et al. (2014a) identified CWD and stumps as important for the ant species consumed by Williamson's Sapsuckers; however, we rarely observed Williamson's Sapsuckers foraging directly on ant colonies ($n = 2$; St-Amand, 2017). Sapsuckers forage on ants by climbing up the trunk of standing trees – as opposed to other woodpecker species that forage for insects by excavating in dead wood (*Dryocopus*: Rolstad et al., 1998; *Picoides*: Engstrom and Sanders, 1997). In our study, the density of CWD and stumps were not significant variables in the models that predicted foraging patch selection. The scale at which we sampled stand characteristics might have been insufficient to detect the importance of CWD and stumps in foraging habitat. Our 11.28 m transects may not have captured key CWD and stumps, because the ants on which Williamson's Sapsuckers forage can travel up to 200 m from the colony (Brian, 1983). A few large ant colonies within a nesting territory may provide food for a breeding pair of Williamson's Sapsuckers across the nesting territory. Similarly, as the effect of dead conifer density showed a nearly significant effect, we suggest considering large dead trees for retention because foraging patches that did not contain enough large live Douglas-fir contained high densities of dead conifer trees (Fig. 3). Dead trees were rare at our study sites, possibly because of logging operations, and the small sample size may be linked to the high variation and non-significance. In Canada and the northwestern United-States, Williamson's Sapsucker foraging habitat is mostly related to old (late-seral) forest characteristics such as large trees, late succession tree species (interior Douglas-fir), dead and decayed standing trees and decaying CWD and stumps (Thomas et al., 1979; Sanderson et al., 1980; Gyug et al., 2014a).

Our results suggest that Williamson's Sapsuckers nest near openings, but select continuous forest for foraging. Previous studies in other managed landscapes also suggested that Williamson's Sapsuckers prefer establishing their nesting territory in proximity to forest openings created by fire or logging (Whitcomb et al., 1981; Keller and Anderson, 1992; Hutto et al., 2015; Drever et al., 2015). A similar pattern of habitat selection has been reported in several other woodpecker species in North America and Europe (Rolstad et al., 2000; Drever et al., 2008; Tremblay et al., 2009; Tozer et al., 2012; Lorenz et al., 2015a; Craig et al., 2019). These woodpecker species may choose stands previously disturbed by harvesting, insects or wildfire to establish their nesting territories because of the increased number of decaying trees suitable for nesting and foraging. Internal decay is required for nest excavation, such that decay and dbh characteristics are consistently selected for nest trees by primary cavity excavators (Kilham, 1971; Martin et al., 2004; Lorenz et al., 2015b). The selection for nest trees near forest openings could also be related to the enhanced visibility for detecting and deterring smaller predators that can enter the cavity (Li and Martin, 1991; Crockett and Hansley, 1977; Paclík et al., 2009). Predation risk may also be lower in openings because areas with little cover are avoided by common nest predators such as red squirrels (*Tamiasciurus hudsonicus*; Mahon and Martin, 2006) and mustelids (*Martes* spp.) in North America and Europe (Chapin et al., 1998; Rolstad et al., 2000).

5. Management recommendations

We integrate our foraging patch selection results with earlier studies on nest patch selection to refine recommendations for breeding habitat management and conservation for this endangered woodpecker in Canada. The association that Williamson's Sapsuckers have with forest openings for foraging and nesting is likely key to their persistence in managed landscapes. Given the results in this and other studies, forest management should conserve old forest characteristics in retained tree groups, including very large and large conifers, standing dead and live decaying trees (Table 2). We recommend the minimal overall retention of >85 large live trees/ha for foraging in active and recently active nesting territories, preferably live Douglas-fir (≥ 22.5 cm dbh; Gyug et al., 2010; St-Amand et al., 2018). We recommend a no-harvest reserve zone in a 140-m radius around recent (standing) or active nest trees (nest reserve zone; Table 3). We also define a nest management zone extending from the no-harvest area (140 m from the nest) out to at least 350 m (340 m in the Okanagan and 410 m in the Western region). In the nest management zone, we recommend leaving retained tree groups with preferred foraging trees (large Douglas-fir). Retained groups should be left in densities of ~250 large live Douglas-fir trees/ha (22.5–57.5 cm dbh) and 25 very large live Douglas-fir trees/ha (≥ 57.5 cm dbh) or dead conifer trees of ≥ 45 cm dbh trees/ha (chiefly western larch and ponderosa pine; St-Amand et al., 2018).

Clear-cuts and seed tree harvest areas should be avoided in nest management zones and not exceed 2 ha in size in stands that contain Williamson's Sapsucker habitat to reduce habitat loss and constraints associated with gap-crossing. The 2 ha (150 m in diameter) threshold is based on the maximum distance we observed crossings by Williamson's Sapsuckers across open areas when forest edges were available to avoid the crossings. Multiple small retained groups of large trees with small spacing in partially harvested stands, as observed at the Okanagan Falls site, could provide quality foraging habitat and act as a "bridge" for birds to cross. Clear-cuts with an elongated shape may be easier to cross than circular clear-cuts of similar size, making resources available on the opposite side, thus reducing the effects of habitat loss on a single nesting territory.

Our recommendations will be most effective if applied to forests dominated by Douglas-fir, lodgepole pine, hybrid spruce and western larch – which is the main habitat in the northern and central range of Williamson's Sapsuckers in the United-States (Crockett and Adow, 1975; Winternitz, 1976; Conway and Martin, 1993). In dissimilar stands dominated by other tree species such as subalpine fir, our relevant recommendations are likely regarding nest reserve zones and open area management (retention of tree groups and clear-cut guidelines). Although our results present first insights on gap-crossing by Williamson's Sapsuckers, more information is needed to better understand how different openings and different partial harvesting designs affect space use and foraging strategies of Williamson's Sapsuckers. Such research may be conducted using GPS trackers attached to the birds during the breeding season to collect more data with reduced spatial bias (e.g., Evens et al., 2018).

CRediT authorship contribution statement

Julien St-Amand: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Junior A. Tremblay:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing - review & editing, Supervision. **Kathy Martin:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

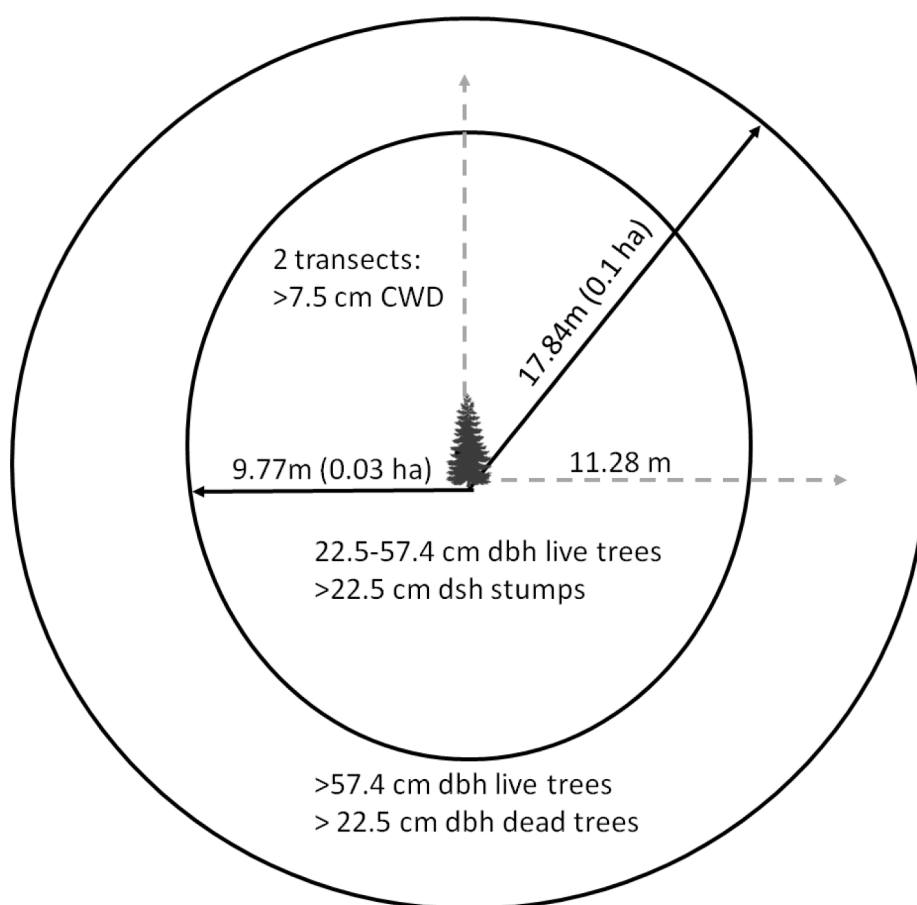


Fig. A1. Design of nested plots used to measure forest stand characteristics relevant to foraging for Williamson's Sapsuckers. Nested plots were centered on a foraging substrate (used habitat; $n = 47$ trees, 1 log) or a randomly selected similar substrate on which foraging or signs of foraging were not observed (available habitat; total = 96 used and available nested plot sets).

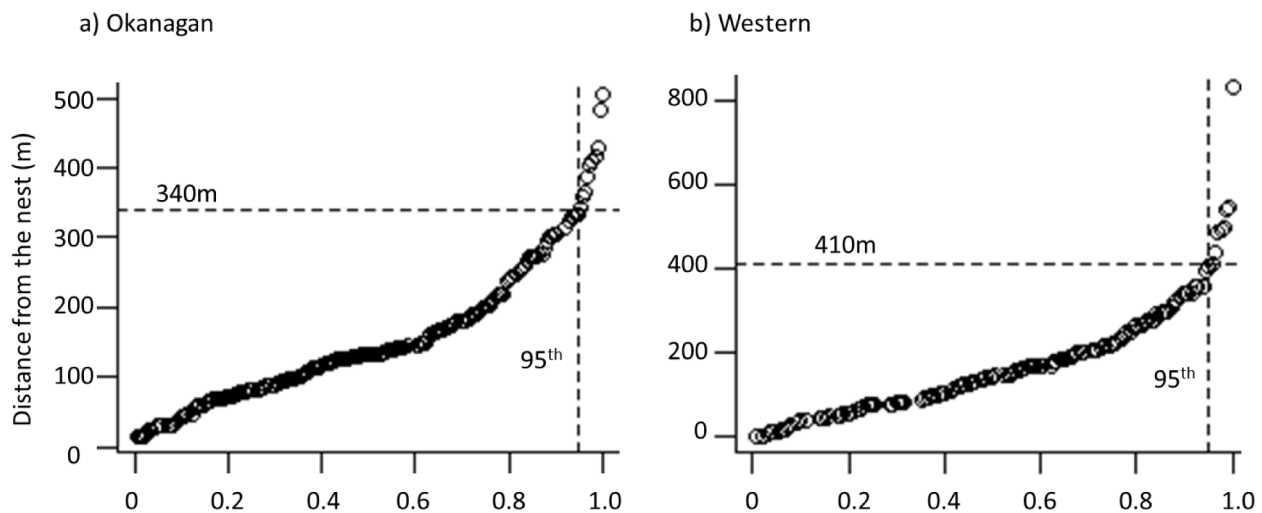


Fig. A2. Distance from the nest against percentile distribution, used to identify gaps in relocation distances of Williamson's Sapsuckers and determine distance thresholds for reserve and management zones in the a) Okanagan and b) Western regions of Williamson's Sapsuckers in southern British Columbia, Canada (Okanagan: $n = 188$ relocations, 10 birds; Western: $n = 164$ relocations, 10 birds). Horizontal line indicates the distance for the 95th percentile for all relocation distances measured for each region.

Appendix B

Table B1

Number of nested plots (0.03 and 0.1 ha) measured to contrast stand-level differences between patches used (foraging) and available (not observed to be used) by Williamson's Sapsuckers in a telemetry study in the Okanagan and Western regions in British Columbia, Canada. The used plots were centered on a foraging substrate and paired with a randomly selected plot (with no sign of use) centered on a similar substrate (i.e., tree or log); while controlling for the distance from the nest, for an even sample of data for used and available plots.

Year	Region	Vegetation plots to measure foraging habitat		Nesting territories*
		Used	Available	
2014	Okanagan	5	5	5
	Western	9	9	5
2015	Okanagan	20	20	4
	Western	14	14	4
	Total	48	48	
		96	18	

* Includes three territories of non-breeding birds and one territory of a pair for which data was collected only before the nestling stage.

Table B2

Relative influence (W+) and model-averaged parameter estimates of variables in AICc-selected models to identify stand-level characteristics that influence selection for foraging by Williamson's Sapsuckers in British Columbia, Canada (Okanagan region: $n = 50$ plots, 9 nesting territories; Western region: $n = 46$ plots, 9 nesting territories). Variables are significant (bolded) if the 95% confidence intervals on their parameter estimates do not overlap zero. Western larch and stump density were included as quadratic variables in the models.

	Variable	Densities $\bar{x} \pm SE$ (range)		W+	β (95% Conf. Int.)	SE	Odds-ratio (95% Conf. Int.)
		Foraging	Available				
a) Okanagan	Intercept	–	–	0	–0.0051 (–0.015–0.0046)	0.0049	1.005 (0.985–1.005)
	CWD (m^3/ha)	144.6 $\pm$ 30.7 (0–583.5)	79.1 $\pm$ 18.6 (0–405.6)	0.69	0.0056 (–0.0005–0.012)	0.0031	1.006 (1.000–1.012)
	Dead conifers	0.8 $\pm$ 0.6 (0–10.0)	2.4 $\pm$ 1.7 (0–40.0)	0.49	–0.082 (–0.20–0.038)	0.061	0.921 (0.817–1.038)
	Large Doug.-fir	114.7 $\pm$ 22.3 (0–366.7)	76.0 $\pm$ 18.0 (0–266.7)	0.25	0.0028 (–0.0033–0.0089)	0.0089	1.003 (0.997–1.009)
	Western larch ²	35.3 $\pm$ 14.5 (0–360.0)	25.6 $\pm$ 6.6 (0–110)	0.07	0.0029 (–0.0040–0.0099)	0.0029	1.003 (0.996–1.010)
	Stumps ²	90.7 $\pm$ 17.5 (0–266.7)	110.7 $\pm$ 21.1 (0–333.3)	0.07	–0.0008 (–0.0034–0.0017)	0.0013	0.999 (0.997–1.002)
	Very l. Doug.-fir	8.4 $\pm$ 3.4 (0–80)	4.8 $\pm$ 2.1 (0–30.0)	0.01	0.016 (–0.030–0.063)	0.024	1.016 (0.969–1.064)
b) Western	Intercept	–	–	0	–0.021 (–0.037 – –0.0052)	0.0081	0.979 (0.963–0.994)
	Large Doug.-fir	247.8 $\pm$ 42.2 (0–666.7)	94 $\pm$ 28.6 (0–500.0)	1	0.0073 (0.0024–0.012)	0.0025	1.007 (1.002–1.012)
	Very l. Doug.-fir	10.0 $\pm$ 3.4 (0–50.0)	2.6 $\pm$ 1.1 (0–20.0)	1	0.090 (0.0014–0.18)	4.50	1.094 (1.001–1.194)
	Dead conifers	13.9 $\pm$ 3.8 (0–70.0)	6.1 $\pm$ 3.2 (0–70.0)	0.76	0.044 (–0.0009–0.088)	0.023	1.044 (0.999–1.091)
	CWD (m^3/ha)	54.9 $\pm$ 12.7 (0–283.7)	41.8 $\pm$ 9.8 (0–191.7)	0.25	0.0047 (–0.0081–0.018)	0.0065	1.005 (0.991–1.017)
	Stumps ²	69.6 $\pm$ 17.4 (0–333.3)	76.8 $\pm$ 24.2 (0–466.7)	0.09	0.0007 (–0.0013–0.0027)	0.0010	1.001 (0.998–1.002)
	Ponderosa pine	25.5 $\pm$ 10.7 (0–230.0)	24.3 $\pm$ 9.3 (0–166.7)	0.03	0.0055 (–0.014–0.025)	0.0098	1.006 (0.986–1.025)

Table B3

Difference in stand composition and structure between nesting and foraging patches of Williamson's Sapsuckers in southern British Columbia, Canada.

	Test	$\bar{x} \pm \text{SE}$ (trees/ha)		t (F)	p
		Nest patch	Foraging		
a) Okanagan (8 pairs)	MANOVA			(0.50)	0.73
	Large live Douglas-fir density	73.3 $\pm$ 27.6	120.0 $\pm$ 26.2	-1.11	0.28
	Very large Douglas-fir density	8.0 $\pm$ 3.3	8.5 $\pm$ 4.2	-0.08	0.94
	Dead conifer density	1.0 $\pm$ 1.0	1.0 $\pm$ 0.7	0	1
	Total density	161.0 $\pm$ 39.0	169.5 $\pm$ 28.3	-0.18	0.86
	Sample size (# of plots)	10	20		
b) Western (7 pairs)	MANOVA			(3.65)	0.02
	Large live Douglas-fir density	72.2 $\pm$ 20.0	303.9 $\pm$ 49.3	-3.78	0.008
	Very large Douglas-fir density	8.3 $\pm$ 4.41	9.4 $\pm$ 3.69	-0.19	0.85
	Dead conifer density	15.8 $\pm$ 7.6	13.5 $\pm$ 3.4	0.3	0.76
	Total density	94.2 $\pm$ 20.8	342.2 $\pm$ 53.4	-3.75	<0.001
	Sample size (# of plots)	12	17		

Bolded text indicates significant differences. Bonferroni-corrected t-tests were used to identify differences among the nesting and foraging patches for each variable ($\alpha = 0.0125$).

Table B4

Use and availability of stand configuration categories in Williamson's Sapsucker nesting territories (buffers around nests) in southern British Columbia, in 2014–2015. The mean proportion represents the available stand configuration within the nesting territory, and $\bar{W}_i$ is the selection ratio for each category. A $\bar{W}_i$ value above one indicates selection for a category relative to its availability, and a value below one indicates avoidance. Bolded categories with asterisks were significantly selected (95% confidence intervals do not overlap with one) and bolded only represent categories that were significantly avoided. The data were collected through incubation, nestling stage and up to 10 days after nestlings fledged. All stands were dominated by Douglas-fir, ponderosa pine or western larch (see Table 2). Crown closure from trees was classified as open stands ($\leq 30\%$), moderate (31–50%) and closed ($> 50\%$ closure). The analyses were performed by nesting territory, because breeding pairs share the same available habitat.

	Configuration	# of uses	Mean availability $\pm$ SE (range)	$\bar{W}_i$ (95% Conf. Int.)
a) Okanagan (8 territories, 11 birds)	Open areas	9	0.09 $\pm$ 0.02 (0.05–0.18)	0.36 (0.17–0.55)
	Edge (15 m)	48	0.10 $\pm$ 0.01 (0.07–0.14)	1.62 (0.66–2.58)
	Retained groups	21	0.06 $\pm$ 0.04 (0–0.27)	1.09 (0.45–1.73)
	Open stand ($\leq 30\%$)	26	0.30 $\pm$ 0.05 (0.04–0.44)	0.28 (0.02–0.53)
	* Moderate closure (31–50%)	127	0.32 $\pm$ 0.08 (0.06–0.70)	1.36 (1.03–1.69)
	* Closed stand ($> 50\%$)	63	0.12 $\pm$ 0.04 (0–0.33)	1.91 (1.27–2.56)
	Total	294		
b) Western (7 territories, 12 birds)	Open areas	16	0.29 $\pm$ 0.05 (0.12–0.48)	0.20 (0–0.39)
	Edge (15 m)	56	0.15 $\pm$ 0.02 (0.09–0.22)	1.25 (0.61–1.89)
	* Open stand ($\leq 30\%$)	47	0.15 $\pm$ 0.07 (0–0.43)	2.12 (1.63–2.61)
	Moderate closure (31–50%)	137	0.30 $\pm$ 0.10 (0–0.64)	1.25 (0.63–1.87)
	Closed stand ($> 50\%$)	47	0.11 $\pm$ 0.05 (0–0.34)	1.04 (–0.30 to 2.38)
	Total	303		

Appendix C

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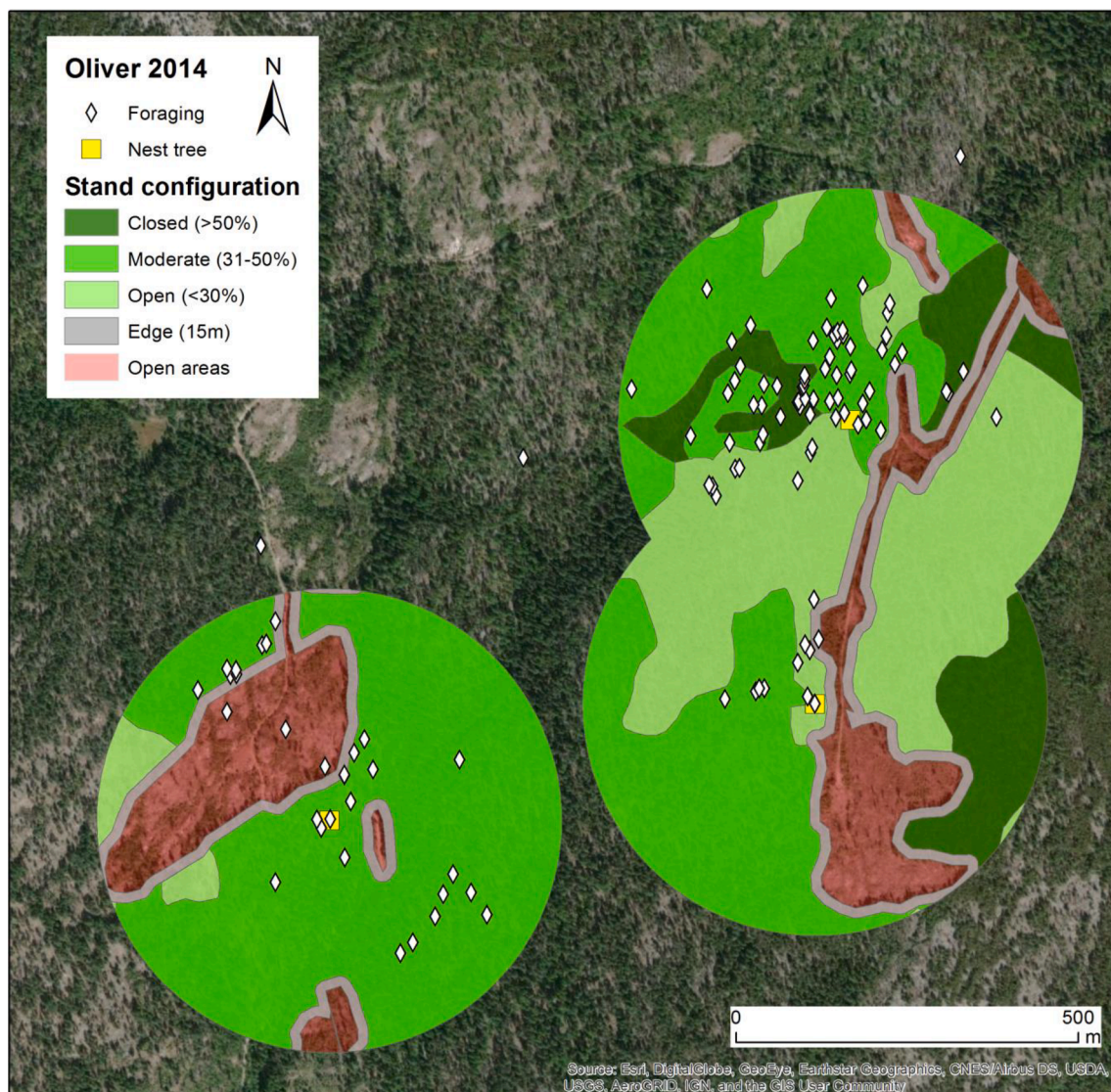


Fig. C1. Available stand configuration categories, nest location and foraging trip relocations in 15 Williamson's Sapsucker nesting territories at the a-b) Oliver, c-d) Okanagan Falls, e) Princeton and f-g) Merritt sites, in 2014–2015. The availability of stand configuration categories is defined in buffers of 340 m in the Okanagan (a-d) and 410 m in the Western regions (e-g). Crown closure from trees was classified as closed (>50% closure), moderate (31–50%) and open stands ($\leq 30\%$). Edges represent the ecotone between open areas and stands in a 15-m buffer. Open areas include clear-cuts, seed tree cuts, forestry roads, paved roads, power line and pipeline clearings, fields, grasslands and pastures. At the Okanagan Falls site d), two breeding pairs nested within 150 m and shared foraging patches (the only example of this behaviour observed during the study). Also, at the Merritt site f) one female nested in two nest cavities simultaneously with two different males (polyandry; two nests 430 m apart on left side of map). The longest observed crossings of open area were a) 174 m in the Okanagan and g) 160 m in the Western regions.

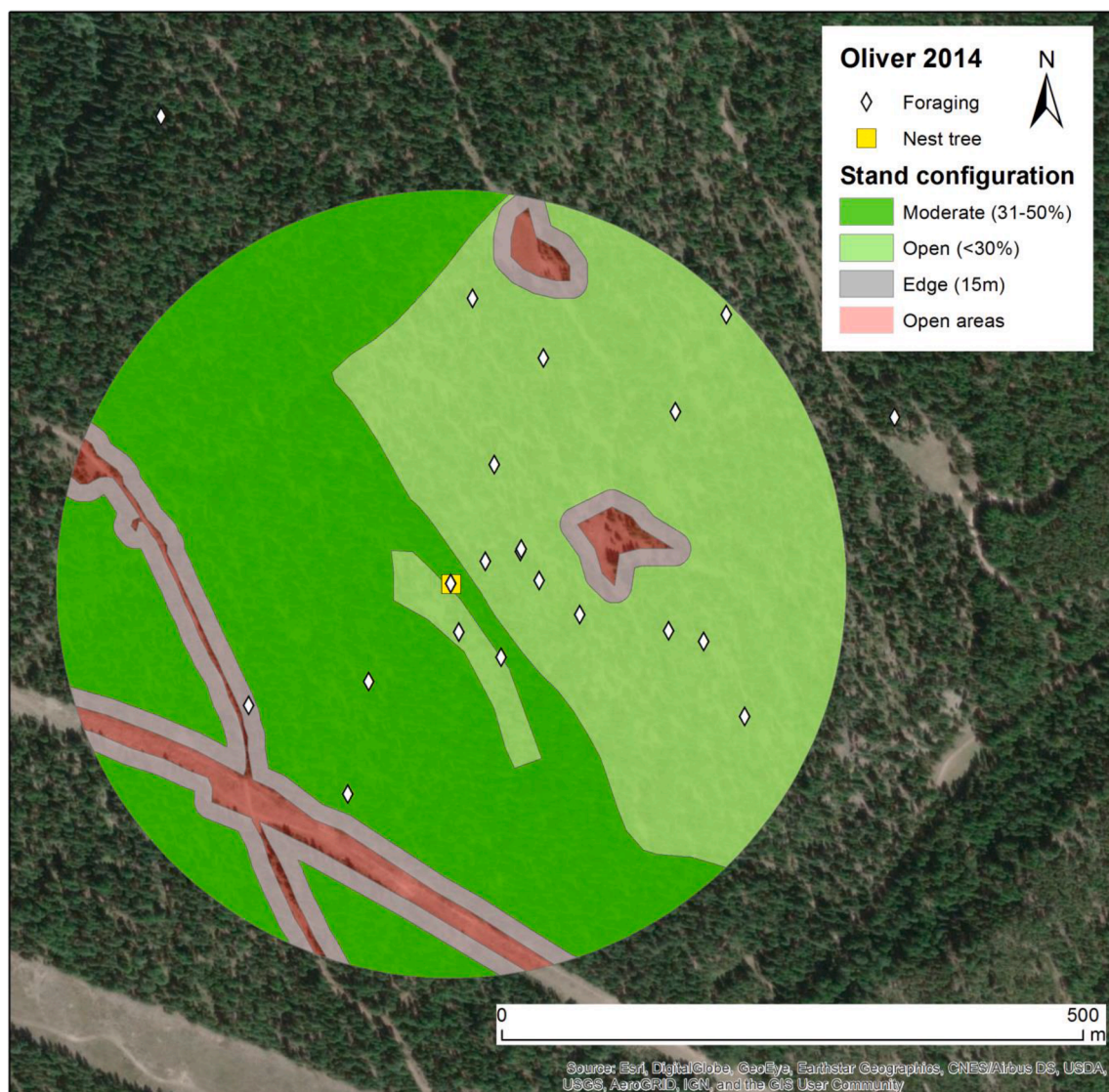


Fig. C1. (continued).

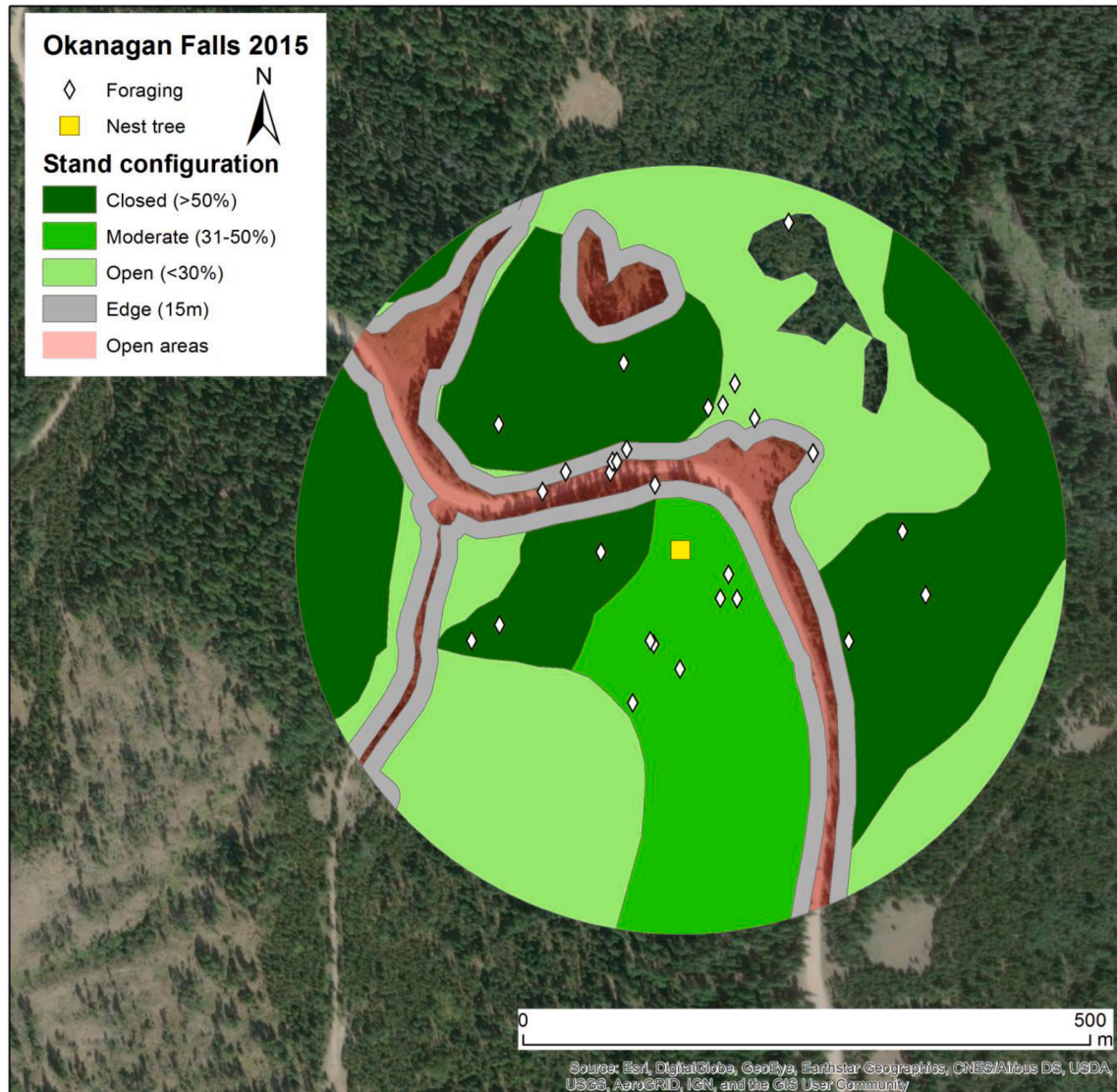


Fig. C1. (continued).

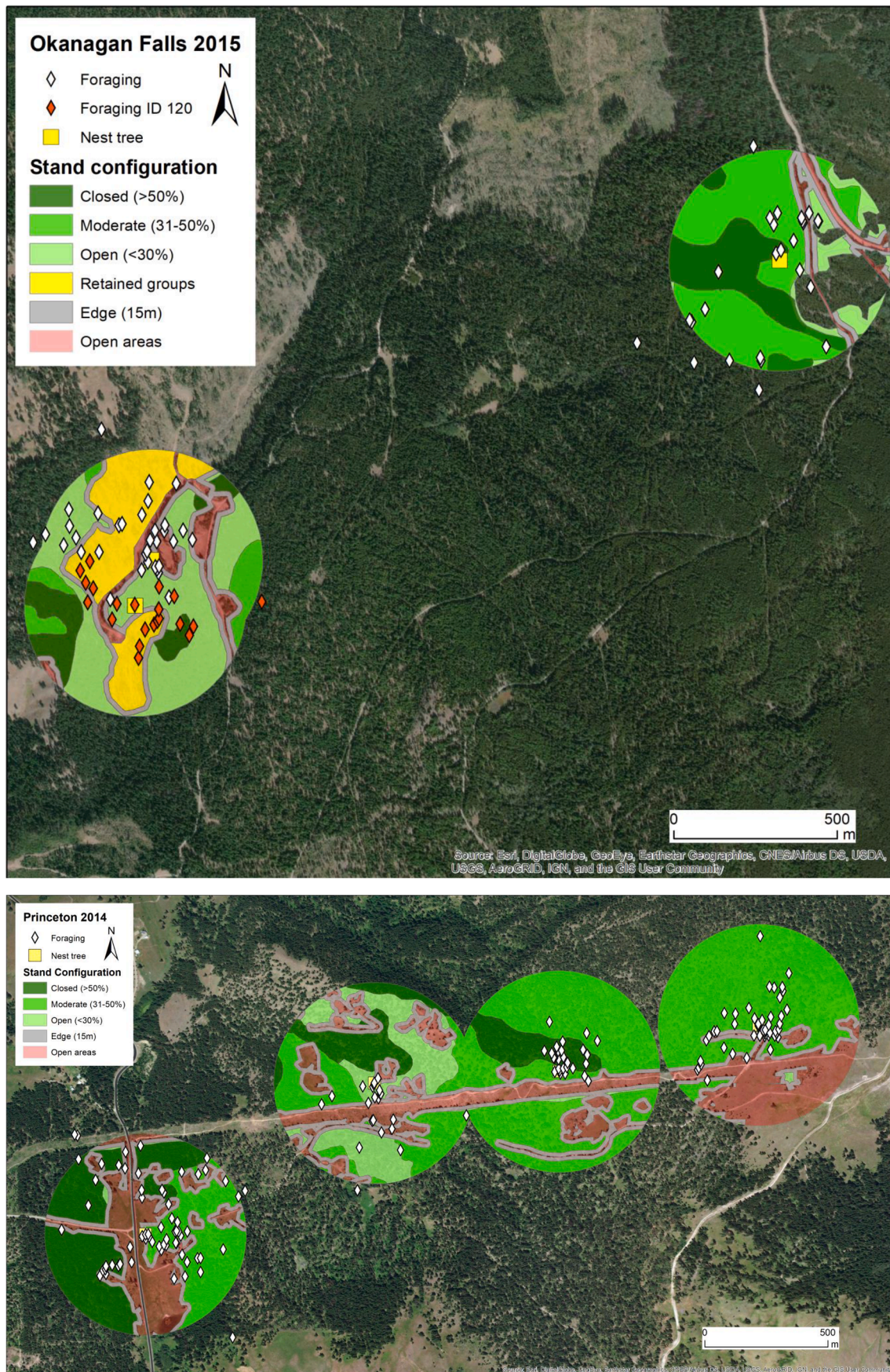


Fig. C1. (continued).

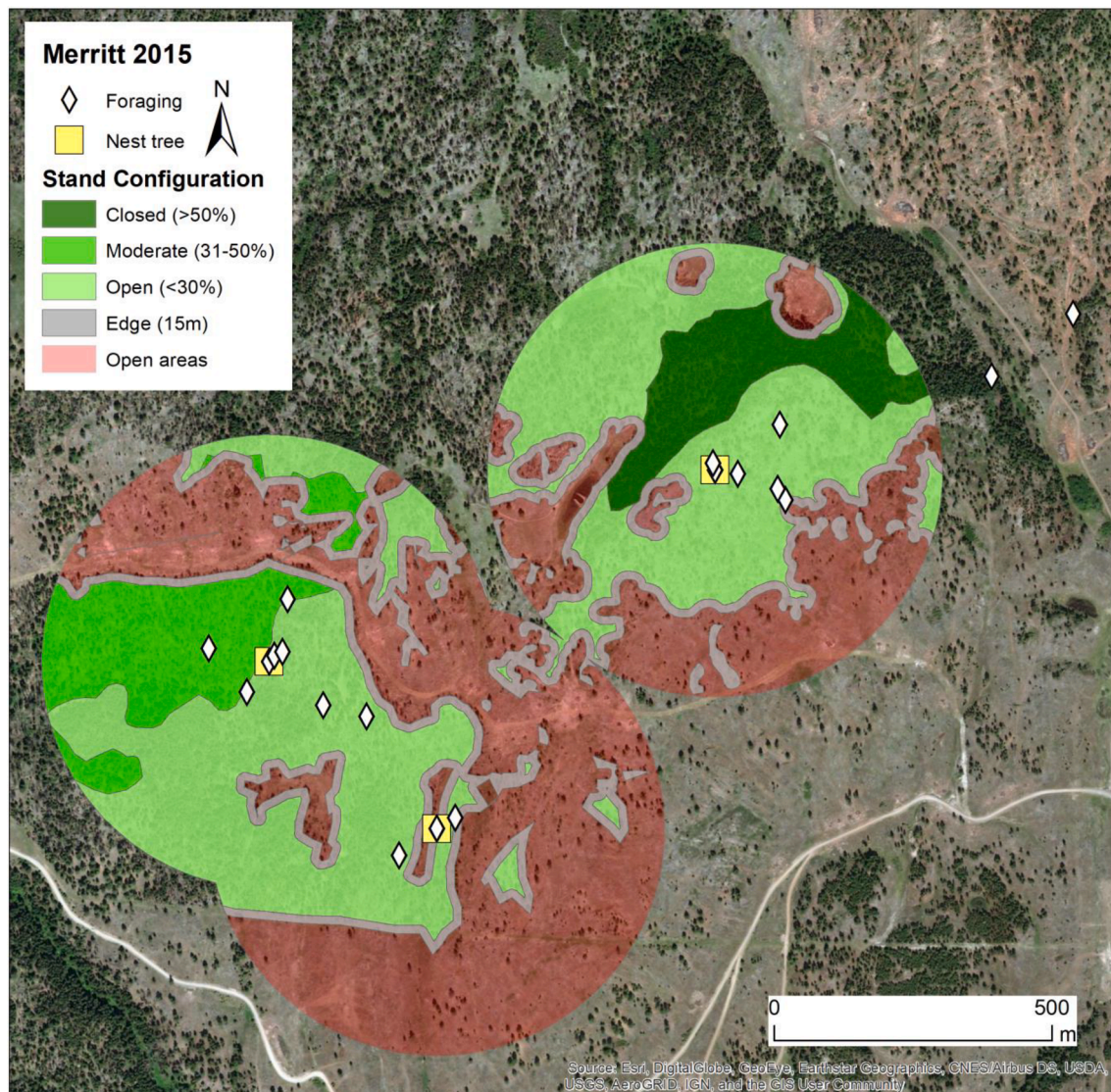


Fig. C1. (continued).

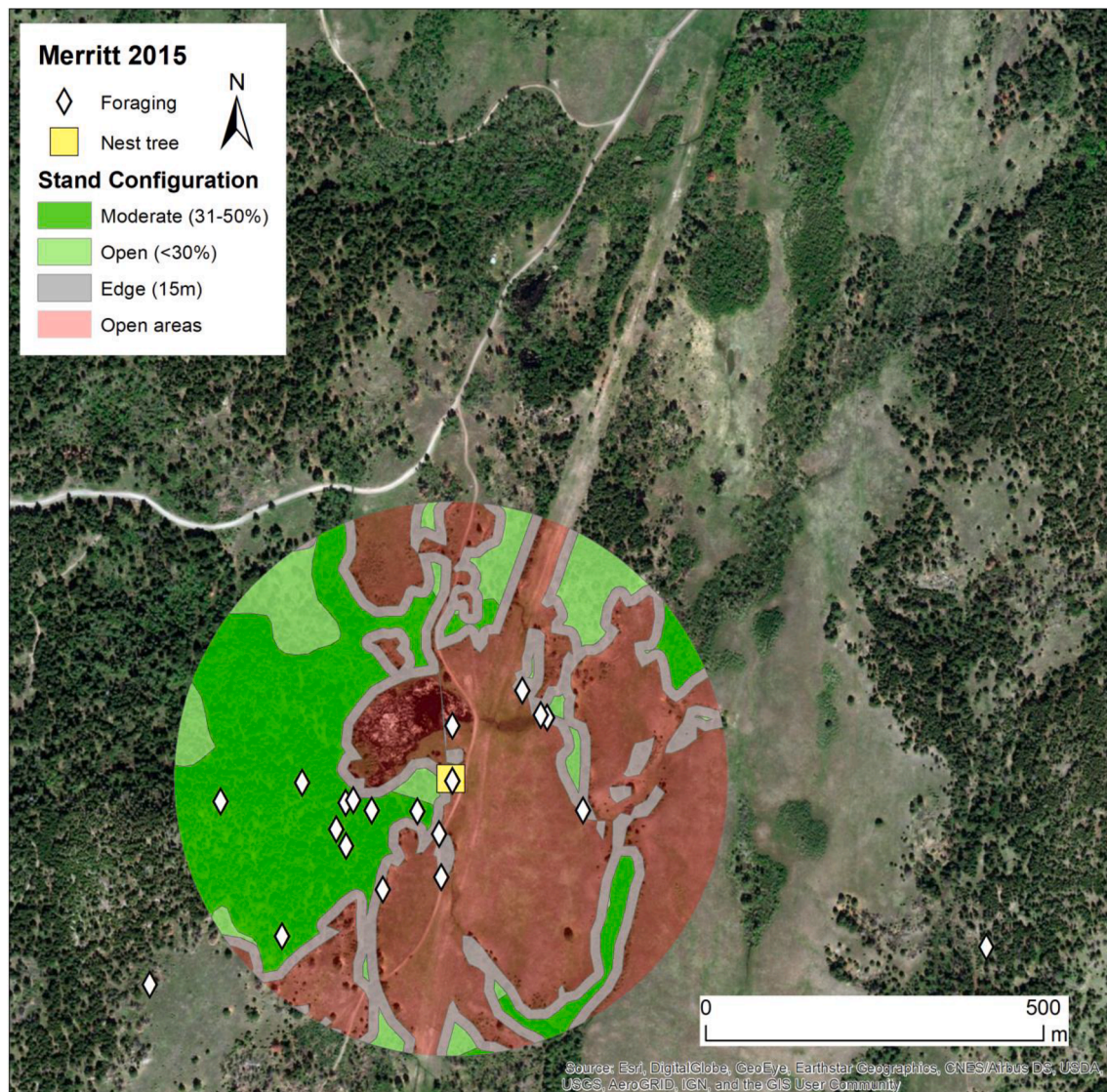


Fig. C1. (continued).

Appendix D. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119223>.

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