FORAGING ECOLOGY OF ENDANGERED WILLIAMSON'S SAPSUCKERS IN CANADA: MULTI-SCALE HABITAT SELECTION IN TWO BIOGEOCLIMATIC ZONES

by

JULIEN ST-AMAND

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Abstract

Williamson's Sapsuckers are Endangered woodpeckers in Canada that breed in montane forests only in British Columbia and require protection of their critical habitat. While there is reasonable knowledge of their distribution and nesting habitat requirements, there are knowledge gaps regarding foraging habitat of Williamson's Sapsuckers. I investigated the selection of foraging habitat in managed forest at the foraging substrate and patch scales using visual observations of foraging behaviour of 27 radio-tagged Williamson's Sapsuckers in the two biogeoclimatic zones where they are found in Canada, the Montane Spruce and Interior Douglas-fir. The characteristics of foraging trees differed with foraging mode and nesting status, but not with bird gender or age. Williamson's Sapsuckers preferred large live Douglas-fir ($\geq$ 22.5 cm dbh) for gleaning and sap feeding in both biogeoclimatic zones, while trees used for pecking were mostly large dying western larch in the Montane Spruce zone and large dead ponderosa pine in the Interior Douglas-fir zone. At the foraging patch scale, Williamson's Sapsuckers did not prefer any stand-level characteristics in the Montane Spruce zone, while in the Interior Douglas-fir zone, they selected foraging patches with higher densities of their preferred foraging substrate (*i.e.*, large live Douglas-fir). Areas of open habitat and single trees were avoided during foraging trips in both biogeoclimatic zones and this habitat type was found in significantly lower proportions in the Montane Spruce than in the Interior Douglas-fir zone. Williamson's Sapsuckers showed no significant preferences for within-stand configuration characteristics (retained groups, forest edges, open stands and closed stands) in the Montane Spruce zone, but they preferred foraging along forest edges and in closed stands in the Interior Douglas-fir zone. I used foraging trip distances to recommend nest reserve (no-logging; 0-140 m from the nest) and nest management zones. For the nest management zone, I recommend only partial harvesting with retained groups of trees extending from 140-340 m in the Montane Spruce zone and from 140-410 m in the Interior Douglas-fir zone. My study on Williamson's Sapsuckers is the first to provide a comprehensive representation of foraging habitat requirements for the species.

Preface

This project was aimed at addressing some of the knowledge gaps regarding the critical foraging habitat of Williamson's Sapsuckers, this research need was highlighted in the 2014 Species at Risk Recovery Strategy. I assumed the main responsibility for study design, collection and analyses of data, and the preparation of manuscripts for submission. I received support and feedback from members of the Williamson's Sapsucker Recovery Team, and guidance from my supervisor Dr. Kathy Martin and members of my thesis committee. Collaborators who were involved on individual projects in development, fieldwork, data analyses or manuscript preparation are listed as coauthors on articles that will be submitted for publication. All study procedures were conducted following the guidelines of the Canadian Council of Animal Care administered by the University of British Columbia (A14-0061).

Chapter 2: Substrate selection for foraging and drumming by Williamson's Sapsuckers in the Montane Spruce and Interior Douglas-fir habitats.

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Chapter 3: Selection of forest stand-level composition, structure and configuration for foraging and nesting of Williamson's Sapsuckers.

Authors: Julien St-Amand and Kathy Martin.

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Honourable mention to Sarah Hudson who helped me in the field in 2016 and reviewed early versions of Chapter 2. Infinite thank you to Mark Drever and Valerie Lemay for enlightenment on the data analyses, which guided through the sometimes-dark world of statistics. My greatest gratitude to Daryl Cockle for assembling and fixing the tree-top-peepers. Enormous bunch of flowers to my friends and colleagues at UBC who provided advices and moral support, but more than anything, went for lunch with me! These fantastic people include Devin de Zwaan, Tomás Ibarra, Jennifer Greenwood, Andrew Huang, Merle Crombie, Cora Skaien, Nina Morrell, Hannah Visty, Sean Naman, Roseanna Gamlen-Greene and Katie McMahen. Also, thanks to Marc-Antoine Leclerc, Merle, Cora, Dr. Peter Arcese, Nina, Dr. John Richardson, Roseanna, David Tavernini and others for the music jams!

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Chapter 1 - General introduction and methods

1.1 Introduction

The success of management actions aimed at conserving imperilled species depends on our understanding of their habitat requirements (Hoekstra *et al.* 2002). Habitat is defined as the distinct set of resources and (biophysical) conditions required to promote occupancy and persistence by a species, assuming that animals will select habitat in order to maximize their fitness (Hall *et al.* 1997). Selection is defined as the act of using a resource unit if it is encountered (Lele *et al*. 2013). Habitat selection describes the behavioural mechanisms that may result in disproportionate use of a resource type relative to its availability (preference or avoidance), which may influence individual survival and fitness (Hall *et al.* 1997, Jones 2001). Habitat selection studies need to consider key life history requirements (*e.g.*, nesting, foraging, communication and concealment), scale-dependence (*e.g.* substrate vs. patch) and temporal factors, as requirements and resource availability change through time (Hall *et al.* 1997). Therefore, a key element of habitat selection studies involves understanding the factors that might alter habitat requirements at different stages of the life cycle of the target species, and at different spatial scales. Habitat selection incorporates all life history requirements, which interact with each other. For example, in birds, the nesting site provides a focal point that spatially centres foraging activity in the nesting territory, although the abundance and quality of foraging resources is known to be a driver of nest site selection (Norris and Martin 2008). Habitat selection for foraging is generally less studied than habitat for nesting, even though foraging habitat might be as limiting as nesting habitat for bird populations (Imbeau *et al.* 2001).

A basic element of foraging habitat is the foraging substrate, being the physical surface from which animals collect their food. Foraging substrates are important because they regulate the microhabitat conditions that prey items require (Siitonen, 2001; Stokland *et al.*, 2012). Foraging substrate selection is often species-specific, and animals will choose foraging substrates based on their rate of food intake and protection against adverse weather and predation risk (Partridge 1978, Huey 1991, Brown and Kotler 2004). Food intake is influenced by the abundance and accessibility of prey items. For example, Dunlin (*Calidris alpina*) prefer muddy flats over sandy and rocky shores as foraging substrates because of the smaller size of the particles that allows easier penetration of the bill to search for and capture invertebrates (Kelsey and Hassall 1989). Species that specialize on specific foraging substrates may be more sensitive to habitat loss if the characteristics of alternative foraging substrates do not enable adequate foraging conditions (Sargeant 2007).

Habitat selection for foraging can also be influenced by variables at the patch scale. I refer to foraging patches as biotic and abiotic resources that can be grouped because they share similar characteristics and proximity (*e.g.,* group of trees). The patch scale could be particularly important for central place foragers, such as birds that must return to their nest frequently to feed nestlings (Orians and Pearson 1979). Central place foragers can minimize the energy spent traveling by targeting patches of higher quality rather than more dispersed substrates located in separate patches (Schoener 1969, Cezilly and Benhamou 1996). To understand habitat selection of foraging patches, three components can be considered: the type of resources available (composition), the configuration of resources within the patch and the distribution of foraging patches. The configuration of resources within foraging patches can affect their environmental conditions (*e.g.,* solar radiation, temperature on the ground) and modify habitat characteristics such as concealment properties, microclimate and food availability (Matlack and Litvaitis 1999). The effect of edges is an example of how within-patch configuration can affect the quality of foraging habitat for birds. Edge avoidance and edge-associated variation in foraging success have been reported for bird species, because of higher predation risk or lower prey availability (Lima and Dill 1990, Murphy and Lehnausen 1998, Bélisle and Desrochers 2002, Schlaepfler *et al.* 2002, Hinam and St. Clair 2008). The distribution of foraging patches in the nesting territory is important for birds since a provisioning trip to a distant patch is only energetically efficient when the benefits are higher than the traveling cost (Naef-Daenzer 1999).

1.1.1 Study species – Williamson's Sapsucker

Williamson's Sapsuckers (*Sphyrapicus thyroideus* [WISA]) are medium-sized sexually dimorphic migratory woodpeckers that are restricted to North America, breeding in montane forests from southern British Columbia to northern New Mexico (Gyug *et al.* 2012). WISA are listed as a species of Least Concern globally (IUCN Red list 2015). However, the species obtained a concern score of 12 in the 2016 State of the Birds of North America Report, almost placing WISA on the Watch List (score of 14 required; NACBI 2016). WISA are listed as Endangered in Canada under the Species at Risk Act (SARA; 2006) and are Blue-listed in British Columbia (BC Conservation Data Centre 2015). WISA are the least studied among the sapsucker species (*Sphyrapicus sp.*) with few studies on population monitoring, landscape scale habitat selection and only one field study that followed individuals during breeding in Colorado (Crockett 1975). The species is not well covered by the national and continental landbird monitoring programs such as the Breeding Bird Survey or eBird (Sullivan *et al.* 2009) given that their montane habitat have restricted road access. Habitat loss, possibly caused by tree harvesting, is considered the main threat for the species in Canada, and WISA populations in Canada cope with a very limited distribution of suitable habitat that is naturally fragmented, since they occur at the northernmost periphery of the species distribution (Environment Canada Recovery Strategy 2014). In Canada, WISA are found in montane interior Douglas-fir- (*Pseudotsuga menziesii* var. *Glauca*) dominated forests, in three discrete geographically-separated populations classified as Areas of Occupancy (AO), which are a designation of the area within the species range boundaries (Quinn *et al.* 1996). The present study focussed on two Areas of Occupancy of WISA; the Okanagan-Boundary AO (henceforth referred to as the Okanagan) and the Western AO, with (calculated) population estimates of 424 and 374 breeding adults respectively (Figure 1.1; Gyug 2012). One of the current objectives of the SARA Recovery Strategy is to incorporate foraging requirements into the definition of critical habitat of the species, to mitigate the effects of habitat loss on the already low WISA numbers in Canada (Environment Canada Recovery Strategy 2014).

Adults feed on sap mostly before the nestling stage by excavating and maintaining sap wells on coniferous trees, with Douglas-fir being the preferred sap tree species in Colorado and British Columbia with 54% and 85% use, respectively (Crockett 1975, Gyug *et al.* 2009a). During the nestling stage, adult foraging behaviour changes dramatically to increase the frequency of gleaning for ants, mostly *Formica rufa group* and *Camponotus sp*p., which compose 98% of the arthropods found in the fecal sacs of nestlings (Gyug *et al.* 2014b). This abrupt transition from sap feeding to ant gleaning during the breeding season is likely tied to dietary requirements of nestlings and is unique among woodpeckers (Crockett 1975). Another foraging mode for WISA is pecking into a woody substrate for subcortical larvae, a typical foraging mode for other temperate woodpeckers (mostly *Picoides;* Raphael and White 1984). Less frequent foraging behaviours are opportunistic aerial foraging (fly catching) and gleaning from the foliage of coniferous trees, which are performed intensively for short periods of time when these alternative prey are abundant (Crockett 1975). So far, attempts to better understand WISA foraging behaviours have been limited to utilizing opportunistic foraging behaviour observations around nest trees and describing trees used for sap feeding (Crockett 1975, Gyug *et al.* 2009a). Some positive associations have been made between live tree densities of > 85 trees/ha and WISA productivity (# of fledglings), as well as coarse woody debris (CWD) abundance and densities of the ant species that are part of WISA diet (Gyug *et al.* 2010, Gyug *et al.* 2014b). A more direct and more extensive approach such as a radio-telemetry study of individual males and females is required to advance the limited knowledge of foraging behaviour and foraging habitat selection.

WISA defend their nesting and foraging habitat from conspecifics early in the breeding season, and drumming is used for territory defense and mating (Type A territoriality; Brown 1969, Crockett 1975, Renken and Wiggers 1989, Reed and Dobson 1993). WISA are primary cavity nesters, meaning that they excavate cavities in trees that they use for nesting and roosting (Crockett 1975; Martin *et al.* 2004). In Canada, WISA typically nest in large to very large (29-163 cm diameter at breast height [dbh]) western larch (*Larix occidentalis*) and ponderosa pine (*Pinus ponderosa*), as well as large (22-54 cm dbh) trembling aspen (*Populus tremuloides*; Gyug *et al.* 2009b). Drever *et al.* (2015) described the characteristics of 138 nesting territories in southern British Columbia; using the logic of the central place foraging theory that predicts that animals choose their nesting habitat according to the availability of surrounding habitat for foraging (Orians and Pearson 1979). WISA territorial occupancy was most strongly correlated with the presence of potential nest trees (Drever *et al.* 2015). However, some of the other characteristics identified by Drever *et al.* (2015) might have been linked to foraging opportunities such as the abundance of very large stumps, density of large hybrid spruce (*Picea engelmannii* X *Picea glauca*), area of 80-119 years old Douglas-fir stands and crown closure of > 15m tall trees. An examination of WISA habitat selection within the nesting territory is necessary to confirm the importance for foraging of the habitat characteristics that were identified at the nesting territory scale by Drever *et al.* (2015), and to obtain precise information to include in WISA critical habitat and forest management plans.

1.2 Objectives

The main objective of my study is to refine the knowledge of habitat selection and requirements for foraging and other life history traits of Williamson's Sapsuckers throughout the different stages of the breeding season in southern British Columbia, using radio-telemetry to monitor the habitat use and foraging behaviours of individual birds. The broader objective is to incorporate foraging requirements into the critical habitat knowledge of WISA, as defined by the Canadian Species at Risk Act (2002). My study addresses two general questions related to foraging habitat selection during the breeding season:

1. Which foraging modes are used by breeding WISA in Canada and what associated characteristics of foraging substrates represent critical habitat? To answer this question, I considered variation in foraging substrate selection related to individual ecological traits (gender, nesting status and age).
2. What are the composition, structure and within-stand configuration characteristics preferred by WISA at the foraging patch scale (stand-level) and territory scale (*i.e.* connectivity and distance from the nest)? Answering this question is critical to inform retention patch designs in forest management and conservation plans.

1.3 General methods

1.3.1 Study system

During the summers of 2014 and 2015, I studied Williamson's Sapsuckers at four sites, two in each of the Okanagan and Western Areas of Occupancy (AO, details above; Figure 1.1). After identifying clusters of breeding territories using a database of known WISA nest locations, 1994 to 2013 (Gyug *et al.* 2014a, Drever *et al.* 2015), I selected sites based on road access, WISA density and proximity of nesting territories. In each of the four sites, 4 to 28 WISA pairs had been detected in previous years. Each year I studied one site in the Okanagan and one site in the Western AO and I tried to obtain balanced sample sizes (sites and year) to reduce potential year effects when comparing between the AOs. The distances between sites in two geographic regions each year were 80 km and 140 km in 2014 and 2015, respectively. All sites were located in managed landscapes and contained proportions of clear-cutting, partial harvesting and protected intact forest (Les Gyug [Okanagan Wildlife Consulting], and Brian Drobe [Weyerhaeuser Company], pers. comm.).

In the Okanagan Area of Occupancy, I studied a site west of Oliver (Oliver site; 49°10'N, 119°21'W) in 2014, and a site southwest of Okanagan Falls (Okanagan Falls site; 49°19'N, 119°25'W) in 2015. Both Okanagan sites were located in the Montane Spruce biogeoclimatic zone (MS zone), dominated by Douglas-fir, lodgepole pine (*Pinus contorta*), hybrid spruce and trembling aspen (Meidinger and Pojar 1991). Atypical for the Montane Spruce zone, the Okanagan sites contained stands dominated by western larch and some water birch (*Betula occidentalis*). Elevation was 1020-1450m above sea level (A.S.L.) at the Oliver site and 1150-1370m A.S.L. at the Okanagan Falls site. The two sites in the Okanagan AO were separated by a steep canyon (not connected by a road), but were geographically close (~10 km). Some of the WISA nesting territories at the Oliver site had high amounts of standing and downed trees (mostly lodgepole pine) due to a mountain pine beetle (*Dendroctonus ponderosae*) outbreak between 1990-2003 (Aukema *et al.* 2006; Brian Drobe [Weyerhaeuser Company], pers. comm.).

In the Western Area of Occupancy, I studied WISA on one site southeast of Princeton (Princeton site; 49°25'N, 120°28'W) in 2014, and a site south of Merritt (Merritt site; 49°58'N, 120°42'W) in 2015. Both sites were located in the Interior Douglas-Fir biogeoclimatic zone (IDF zone), dominated by Douglas-fir and ponderosa pine, with some trembling aspen in wet areas (Meidinger and Pojar 1991). Elevation was 800m-950m A.S.L. at the Princeton site, and 880m-1180m A.S.L. at the Merritt site. The Merritt site is one of the northernmost clusters of WISA breeding territories in BC, located ~ 75km north of the Princeton site.

1.3.2 Location and capture of Williamson's Sapsuckers

I used call-playbacks of territorial WISA calls to find and confirm breeding territories. I attempted to catch both members of a pair using three different methods: 1) I lured adult males into mist nets by using call-playbacks and a male WISA decoy before the nestling stage when males were showing territorial behaviour (Figure 1.2a), 2) I 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 14m) in order to block the entrance of the nest cavity when the bird was inside, 3) I caught females by positioning aerial mist nets supported by poles (up to ~9m high) to intercept them in flight, when the nest cavity was not accessible with the dip net. On capturing a bird, I measured its body mass, wing length, bill length, bill width, age and gender (Pyle 1997). Each individual was fitted with a numbered U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminum band, three coloured plastic bands (max. of 2 bands/leg) and a radio-transmitter (BD-2 or BD-2G, 1.2g; Holohil systems, Ltd., Carp, Ontario, Canada). The radio-transmitters, with an expected battery life of 56 days, were tail-mounted by suturing the radio-tag onto the two central rectrices following Tremblay *et al.* (2009; Figure 1.2b). The tail-mount was designed for the bird to lose the radio-transmitter during the moult of their rectrices, before migration (Pyle 1997). Birds were banded under the Environment and Climate Change Canada Federal banding sub-permit number 10365BO. All handling procedures were approved by the University of British Columbia Animal Care Committee (application A14-0061).

1.3.3 Telemetry

I used radio-telemetry to locate WISA across their home range during their foraging trips and other activities, as it is difficult to follow birds once they leave the nest patch (*i.e.* > 60 m from the nest). I tracked radio-tagged WISA using an RA-2AK H-type antenna (Telonics inc., Mesa, Arizona, United States) and an R-1000 receiver (Communications Specialist Inc., Orange, California, United States). I tried to locate each individual a minimum of 30 times using a homing method tracking protocol (*i.e.* trying to see the animal; Mech 1983). I tracked radio-tagged individuals from the day after they were captured until they left the site or the radio-transmitter battery was depleted. In 2014, I tracked WISA for periods of 0.5-3 hours at least once every three days throughout their breeding cycle. The increased distance between the two study sites in 2015 made it difficult to visit the two sites with the same frequency as in 2014. Thus, in 2015, I tracked radio-marked birds daily for 10 days, followed by a 10-day break as the team moved to monitor birds in the other Area of Occupancy. I tried to approach slowly and quietly when close to a bird (strong telemetry signal), to avoid influencing its foraging behaviour.

1.3.4 Behavioural observations

I recorded WISA activity from the initial visual observation and, when possible, I followed the bird to the next substrate until it moved out of sight or until the observer made a stop to record the data (generally three consecutive observations, range = 1-6). During an observation, I recorded the WISA behaviours (more details in Chapter 2), the beginning and end times of the observation, the tree section used (basal, middle or top) and the location used on the tree (trunk or branch). Once the sapsucker was lost from sight, I returned to the used trees to take a GPS location and mark the tree with flagging tape. I measured the characteristics of foraging trees, foraging patches and available habitat at the end of the season after all nesting activity was completed (more details in chapter 2).

1.3.5 Nest searching and monitoring

Some nests were found opportunistically while looking for breeding pairs to capture, but most nests were found while tracking radio-tagged birds. I monitored nests to obtain data on reproductive success and nesting status, as it might explain some variation in the use of different foraging modes by the adults. Nest status and nest contents were monitored every 3-4 days in 2014 and every 3-4 days during each 10-day cycle in 2015 (see above) using a video camera attached to an extendible fiberglass pole (Tree-top peeper [modified]; Sandpiper Technologies Inc., Manteca, California, U.S.A.). If nests were too high to access using the camera (> 14 m), I assessed nesting status using behavioural observations of the adults (switching every 30 minutes during incubation or carrying food, *etc*.), or of the young (hear begging calls, see young at the nest entrance, *etc.*).

1.4 Supplementary data on reproductive traits

1.4.1 Nesting phenology and productivity

In this section, I report supplementary data on WISA nesting phenology and productivity that I did not analyze in the thesis (Tables 1.1, 1.2). When I discovered a new nest with young nestlings, I aged them comparing pictures of nestlings of known age to estimate the date of first hatch. I found an average clutch size of 6.3 ± 0.9 SD eggs (range = 5-8, n = 16), which is almost two eggs more than reported for a population in Colorado (4.38 eggs, n = 8) and 4.91 ± 0.15 SE (n = 23) in Arizona (Crockett and Hansley 1977, Gyug *et al*. 2012). My results indicated an average incubation time was 13 days with a large range (9-16 days) due to uncertainty when estimating the date of first hatch. This result is comparable with incubation times of 13 days (12-14 days) reported in Colorado and Arizona (Crockett and Hansley 1977, Gyug *et al*. 2012). I estimated an average nestling period of 28 days (range = 25-32 days) from hatching until nest departure, comparable with 31-32 days in Arizona (range 26-33 days; Martin and Li 1992). The average proportion of nests that were successful (*i.e.*, produced $\geq$ 1 fledgling) in my study (64%, n = 25 nests) seemed lower than in Arizona ($\bar{x}$ = 96.1%, range = 89.4-100%, n = 204 nests) and previous studies in British Columbia (89%, n = 175 nests Gyug *et al*. 2010). The mean nest productivity for all nests (including depredated nests) in my study was 2.2-2.8 fledglings/nest (n = 25), while Gyug *et al*. (2010) reported 3.24 fledglings/nest ± 0.11 SE in all nests and 3.63 fledglings/nest ± 0.08 SE in successful nests. In the United-States, successful nests produced an average of 3.67 fledglings/nest ± 0.21 SE (n = 18 nests) in Arizona (Gyug *et al*. 2012), 3.17 fledgling/nest (n = 12 nests) in a study in Colorado (Crockett and Hansley 1977), and 3.58 fledgling/nest in another (n = 12, McGrath 2004). Overall, the incubation and nestling periods are comparable with other studies, while the average clutch size and predation rate I reported seemed higher.

I found the largest clutch (8 eggs) ever reported for the species when revisiting the Princeton site in 2015 (Gyug *et al*. 2012) - the eggs were laid by a pair that I radio-tracked in 2014, which reused the same nest tree. I recorded the first case of polyandry for the species at the Merritt site in 2015. The banded female was paired with two different males and laid six and five eggs in two nests consecutively. The female incubated and fed nestlings in both nests, which produced four and three fledglings – holding the record for highest individual annual reproductive success (7 fledglings) for the species (Gyug *et al*. 2012).

1.4.2 Site fidelity and adult survival

I returned to previous study sites between May 12-15 in 2015 (Oliver and Princeton) and April 29 – May 1st in 2016 (Oliver, Princeton, Okanagan Falls and Merritt), in early May, to survey for WISA that I banded in previous years. I used call-playbacks to locate WISA at the location of the nest tree of previously radio-tracked WISA and where each bird was last detected during radio-tracking and previous call-playback surveys. In late April-early May, breeding pairs are formed and WISA home ranges usually do not overlap because of territoriality, therefore only one male and one female occupied each survey location. When a WISA replied to the call-playbacks, I located both the male and female to determine whether they were banded and their identity if banded. Females required an intensive search effort because they rarely reply to call-playbacks and are more cryptic. I found and identified females using color bands in all cases where a male was detected in 2016, but search effort was sufficient only for three females out of six in 2015, because of time constraints.

Neighbouring males sometimes replied to the playbacks without defending the location of the survey, therefore I moved to the adjacent nesting territory or new nest tree location and identified both the male and female. I recorded whether the same nesting territory was used (same nest tree location), or a new nest tree or new defended location was used with overlap in resource availability (new nest tree location within ~ 400 m; territory shifting). I recorded that the location was unoccupied when no WISA replied after two bouts of 10-minutes call-playback in all directions, separated by 30 minutes. I tried to locate nest trees and verify nest contents, however, eggs are not usually expected at this time of the breeding season.

After one year, I obtained a mean annual return rate of 33.3% (8 of 24 banded adults), compared to 48.5% (n = 33 banded adults) in Colorado (Crockett 1975) and 22% in Arizona (n = 65 banded adults; Gyug *et al*. 2012). After two years, my results indicated a return rate of 12.5% (2 of 16 banded adults), while 44% of banded adults returned in Colorado (n = 9). The search effort for banded birds in Colorado covered more nesting territories than my study, because I conducted surveys only in location that were occupied by banded adults in previous years. This could explain differences in banded adult detection and survival.

1.5 Thesis overview

In this thesis, I use observations of behaviours, resource use and spatial movement of radio-tracked Williamson's Sapsuckers to study habitat characteristic selection at different scales, while considering all relevant life history requirements (individual traits) during the breeding season. In Chapter 2, I report the foraging and communication behaviour of Williamson's Sapsuckers and fine-scale (foraging substrate) habitat selection, considering different foraging modes and individual ecological traits (gender, nesting status and age). In Chapter 3, I study the selection of stand-level composition and configuration characteristics for foraging and nesting within the nesting territory. This chapter also contains information on space use and foraging trip distances of Williamson's Sapsuckers during the nestling stage, during which adults are spatially constrained around a central location, their nest. In Chapter 4, I synthesize my findings and merge them with previous knowledge of WISA critical habitat, and recommend overall management strategies in British Columbia to maintain the integrity of breeding habitat for this endangered woodpecker.

1.6 Chapter 1 figures

Fig. 1-1

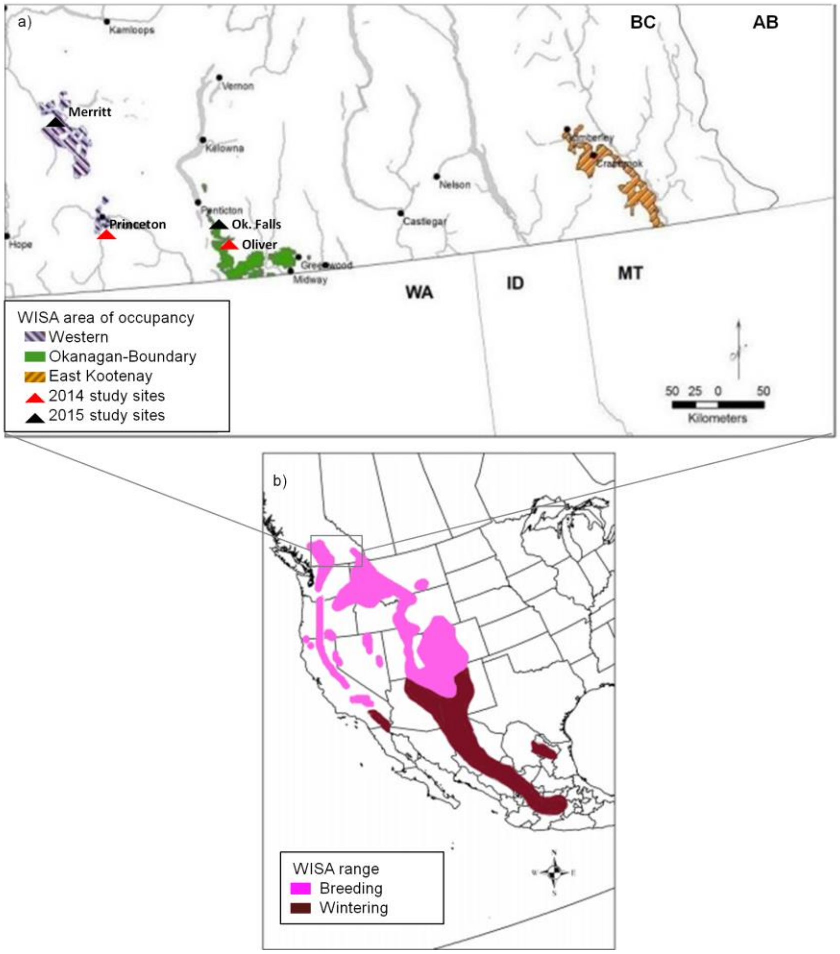


Figure 1.1. Areas of Occupancy of Williamson’s Sapsuckers in a) British Columbia and b) distribution of the species in North America (adapted from BC Ministry of Environment 2012). Both the Oliver and Okanagan Falls sites were representative of the Montane Spruce biogeoclimatic zone, while the Princeton and Merritt sites were representative of the Interior Douglas-fir biogeoclimatic zone.

Fig. 1.2

Figure 1.2. Photos of a) male decoy and b) radio-transmitter attachment. I used the decoy, in combination with call-playbacks of male territorial calls, to attract male WISA into mist-nets. I sewed the radio-transmitter onto the central rectrices of WISA to track their foraging behaviour and other movements with radio-telemetry. Notice the three-points of contact designed to reduce the movement constrains on the rectrices by the radio-transmitter (compared to a four-points design).

1.7 Chapter 1 tables

Table 1.1. Reproductive phenology of 19 Williamson's Sapsucker nests in British Columbia. Incubation begins when the clutch is complete until the first egg hatching, and the nestling period is measured from the first egg hatching until the day the first chick leaves the nest. Variation is reported using standard deviation of the mean.

			Duration (days)			
Year	Site	B. zone*	Incubation†	Nestlings†	DFE‡	n (nests)
2014	Oliver	MS	12 ± 2	28 ± 2	May 20 ± 3 (16-25)	7
	Princeton	IDF	14 ± 1	28 ± 2	May 9 ± 2 (8-12)	3
2015	O. Falls	MS	13 ± 1	27 ± 1	May 9 ± 6 (2-13)	3
	Merritt	IDF	14 ± 2	28 ± 2	May 19 ± 13 (May 7 - June 7)	6
Overall (mean ± SD)			13 ± 2	28 ± 2	May 16 ± 9 (May 2 - June7)	
n (nests)			5	9	19	19

* Biogeoclimatic zones: MS = Montane Spruce, IDF = Interior Douglas-fir.

† The standard deviation describes the uncertainty in estimating incubation, hatching and fledgling dates, not to individual variation.

‡ Date of first egg (DFE) was determined directly for six nests, while DFE for 13 nests were extrapolated subtracting the average incubation (13 days) and egg-laying periods from the hatch date.

Table 1.2. Reproductive (nesting) parameters of 26 breeding pairs of Williamson's Sapsuckers during the breeding season in Canada. Clutch size is defined by the number of eggs/nest, egg viability by the proportion of eggs that hatched (excluding predation), % fledgling by the proportion of nestlings that survived to fledgling and mean productivity by fledglings/nest. A successful nest produced at least one fledgling. Variation is reported using standard deviation of the mean.

Year	Site	B. zone*	Mean clutch size ± SD (range)	% egg viability	% fledged	Mean productivity†	% nest success	Cause of nest failure	n (nests)
2014	Oliver	MS	6.8 ± 0.5 (6-7)	85.2	43.5	1.4	28.6	Mustelid (3X), cavity collapse, male WISA disappeared	7
	Princeton	IDF	6.6 ± 0.9 (6-8)	80.0	65.0	3.0-3.8	83.3	Bear	7
2015	O. Falls	MS	6.5 ± 0.7 (6-7)	84.6	36.4	2.8-3.8	80.0	Squirrel	5
	Merritt	IDF	5.4 ± 0.5 (5-6)	77.8‡	80.0	1.9-2.4	71.4	Unknown - rodent suspected (2X)	7
Overall (mean ± SD)			6.3 ± 0.9 (5-8)	81.9	56.5	2.2-2.8	64.0		
n (nests)			16	92¤	69§	25	25		26¥

* Biogeoclimatic zones: MS = Montane Spruce, IDF = Interior Douglas-fir.

† The reported range represents the possible number of fledglings for nests that could not be monitored with a camera attached to an extensible pole (> 14 m). For these nests, I used the number of observed fledglings as the lower limit (up to three) and five fledglings as the upper limit.

‡ Excludes one predation event of a 6-egg clutch, the total hatch percentage is 55.6%.

¤ Number of eggs.

¥ Number of nestlings.

§ For one nest, only the clutch size was known.

Table 1.3. Detections of 29 banded Williamson's Sapsuckers on the former breeding territory or location of last detection, to estimate adult survival and site fidelity in British Columbia. The surveys were conducted one or two years after the season of their initial banding in late April – early May in 2015 and 2016.

Year of banding (# banded)	Year of survey	Site	Biogeoclimatic zone*	# redetections	# birds surveyed†	% returns
2014 (n = 8)	2015	Oliver	MS	1	5	20
2014 (n = 8)		Princeton	IDF	3	6	50
2014	2016	Oliver (2nd year)	MS	0	8	0
2014		Princeton (2nd year)	IDF	2	8	25
2015 (n = 7)		O.Falls	MS	1	7	14
2015 (n = 6)		Merritt	IDF	3	6	50
Overall				10	40	25

* Biogeoclimatic zones: MS = Montane Spruce, IDF = Interior Douglas-fir.

† Number of birds that were sampled according to the protocol – the bird was considered absent if another territorial Williamson's Sapsucker of the same sex was defending the former territory or no response from call-playbacks was recorded. In 2015, evidence of absence was insufficient for four females and one male.

Chapter 2 - Substrate selection for foraging and drumming by Williamson's Sapsuckers in the Montane Spruce and Interior Douglas-fir habitats

2.1 Introduction

Birds regularly make decisions about foraging substrates, as substrates vary in the type, quantity and quality of food resources. Foraging substrate characteristics are measurable physical attributes (*e.g.,* tree species, size, decay stage, branches and concealment properties), that 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 substrates are important for conservation, being a fine-scale habitat component and contributing to the occupancy, fitness and persistence of bird species (Hall *et al.* 1997). Foraging substrates can be identified using habitat selection studies, which describe the use of habitat characteristics in relation to their availability (Hutto 1985). Habitat characteristics are considered preferred when used in higher proportion than their availability, and conversely, avoided when used in lower proportion to their availability (Johnson 1980). Some foraging substrates might be suitable to fulfill the requirements of several foraging modes, offering cumulative individual fitness benefits, while others are more specific to a certain activity (Klopfer and Ganzhorn 1985). For example, White-headed Woodpeckers (*Picoides albolarvatus*) used larger ponderosa pine trees (*Pinus ponderosa*) for most of their activities (*e.g.,* nesting, gleaning, cone-feeding, pecking and drumming), but they used small ponderosa pine trees for sap feeding because smaller trees have thinner bark that may facilitate excavation of sap wells (Dixon 1995a, Kozma 2010). Thus, we expect that large ponderosa pine trees provide most of the characteristics that increase the general fitness of White-headed Woodpeckers, but which select small pines specifically for sap feeding.

Foraging substrate selection can vary according to individual ecological traits (nesting status, gender and age). Birds that are feeding nestlings usually have more specialized foraging behaviours than birds foraging for self-maintenance, due to specific diet requirements of the nestlings (Partridge and Green 1985). Also, food availability changes with time and temperature during the breeding season (*e.g.,* exposed insect resources available for gleaning), likely influencing foraging behaviour of birds across their nesting stages. Selection of foraging substrates and prey items may differ between genders, especially in dimorphic bird species. For example, male arboreal woodpeckers may forage on larger substrates than females, because of their larger bills (Austin 1976, Jenkins 1979, Aulen and Lundberg 1991) and social dominance (Peters and Grubb 1983). The age of individual birds can influence foraging habitat selection as older birds are often dominant over first time breeders and may exclude younger birds from the best foraging habitats (Reese and Kadlec 1985, Marchetti and Price 1989). Individual ecological traits add complexity to habitat selection studies and all cohorts, in a bird population, including non-breeders, need to be included when identifying foraging habitat.

In forest ecosystems, live or dead tree trunks are important nesting and foraging substrates used by cavity nesters and bark-foraging birds that feed on insects by gleaning or pecking (excavating). Woodpeckers (*Picidae*) are the most diverse group of bark-foraging birds in North America. Woodpecker groups such as *Picoides* and *Dryocopus* generally forage by pecking for saproxylic insects in dead wood (Raphael and White 1984). However, the sapsucker group (*Sphyrapicus spp*.), represent an exception by foraging mostly on live trees. Morphological adaptations (short tongue and weaker pecking force) of sapsuckers would make them less efficient than other arboreal woodpecker species (*e.g., Picoides*) at extracting food from crevices of (mostly) dead trees (Spring 1965). Instead, sapsuckers spend more time gleaning insects or sap feeding, but can also consume bast (cambium), fruit and seeds, depending on the species and the time of the year (Raphael and White 1984, Walters 1996, Williams 1975). Insects are gleaned from the surface of tree trunks or by removing bark pieces (Raphael and White 1984). 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). Sapsuckers can forage and nest in a variety of deciduous and coniferous trees, the latter being used more often for sap feeding in the spring (Kilham 1964).

Drumming is an important communication behaviour for territory defense and conspecific attraction and mating in woodpeckers (Renken and Wiggers 1989, Reed and Dobson 1993), playing a similar role to singing for songbirds (Lawrence 1967). However, drumming is a particular way of communication as it relies on environmental features (drumming substrates). Woodpecker drumming substrates are usually dead trees with specific characteristics such as decay class (partially dead or recently dead), large dbh, little bark cover and broken tops and limbs (Imbeau and Desrochers 2002). Drumming substrates are believed to be selected by sapsuckers for their acoustic properties that are associated with long distance propagation (Eberhart 1997). The relative contribution of drumming substrates to reproduction and survival of sapsuckers is unknown, however it is likely less significant than foraging and nesting substrates.

Williamson's Sapsuckers (*Sphyrapicus thyroideus* [WISA]) are listed as Endangered in Canada under the Species at Risk Act (SARA; 2006) and are Blue-listed in British Columbia (BC Conservation Data Centre 2015). The populations in Canada are restricted to a very limited distribution and with significant fragmentation of their habitat, since they occur at the northernmost periphery of the species distribution (only in British Columbia).

The present study focuses on two Areas of Occupancy (AO) of WISA; the Okanagan AO and the Western AO (see Chapter 1 Methods for more details; Figure 1.1). The Okanagan and Western AO are located in the Montane Spruce (MS) and Interior Douglas-fir (IDF) biogeoclimatic zones, respectively, where forestry operations represent a considerable disturbance. One of the current objectives of the SARA Recovery Strategy is to incorporate foraging requirements into its definition of critical habitat, to mitigate the effects of habitat loss on the already low WISA numbers in Canada (Environment Canada Recovery Strategy 2014).

Foraging substrates are key elements for the survival and recovery of WISA populations in Canada, and few data are available on selection mechanisms and preference. WISA foraging substrate selection has been described in previous studies using opportunistic observations of sap trees and foraging trees near the nest. Because of the importance of ants in the diet of adults and nestlings, gleaning substrates are probably the most important and limiting foraging substrates (Bolles 1892, Crockett 1975). Even though ants will re-colonize substrates, they will be scarce for a prolonged period after a WISA foraging event due to the emission of alarm pheromones that induce escaping (Wilson and Regnier 1971). The only available description of substrates used for gleaning by WISA lacks detail, being limited to: “the trunks and limbs of live coniferous trees (mostly ponderosa pine), on fallen logs or on the ground” (Crockett 1975). In Northeastern California, Colorado and British Columbia, WISA sap trees were mostly medium- (8-22 cm diameter at breast height [dbh]) to large- (23-57 cm dbh) sized conifers, chiefly Douglas-fir (54% of trees used in Colorado, 85% in BC; Oliver 1970, Crockett 1975, Gyug *et al.* 2009a). Preference for sap feeding on Douglas-fir could be related to characteristics of the phloem such as sugar and amino acid content, secondary chemicals and volume of sap flow, although studies on conifer phloem are limited (Snyder 1992, Dixon 1995a, Woodruff 2013). Gyug *et al.* (2009a) suggested that sap trees are not a limiting resource in Canada because of the high availability of medium-sized Douglas-fir, especially in managed landscapes. Pecking for subcortical insects was described as a frequent foraging behaviour outside the nestling stage in Colorado (Crockett 1975). Data on WISA pecking substrates are lacking, but for other North American woodpecker species, pecking substrates are typically large dead standing trees and fallen logs (Nappi *et al.* 2015). Two to four favourite drumming sites were found per WISA territory, mostly using dead limbs or dead trunks (Hadow 1977, Short 1982). Data are lacking on substrate characteristic selection for drumming such as tree species, size or decay class. Specific recommendations might be necessary if drumming substrates differ from foraging or nesting substrates.

There is little information available on how foraging substrate selection varies with individual ecological traits (nesting status, gender and age) of WISA in Canada. Adults that are feeding nestlings may have to increase the frequency of ant gleaning to meet the nutritional requirements of their nestlings (Crockett 1975); therefore, the selection of substrates by breeders may be influenced by the availability of ants, while non-breeders should be more generalist foragers. WISA may adapt their diet according to the changing availability of food resources during different stages of the breeding season, as ant activity and abundance increase during the summer (Crockett 1975). Male and female WISA could exhibit different preferences for foraging substrates due to their exceptional sexual dimorphism in plumage color, which could have effects on predation risk or dominance, and this could lead to management implications by gender. In Colorado, female WISA were found foraging more often on the top part of tree trunks and less often on the ground compared to males (Crockett 1975). The age of individual birds can influence foraging habitat selection as older birds are often dominant over first time breeders and may exclude younger birds from the best foraging habitats (Reese and Kadlec 1985, Marchetti and Price 1989).

WISA critical habitat requirements at the substrate scale must be described to meet the standards outlined by the Species at Risk Act (SARA; Species at Risk Act 2002) and implement conservation plans based on the WISA Recovery Strategy (Environment Canada Recovery Strategy 2014). Data are lacking to support recommendations to forest managers and to ensure a sufficient quantity of foraging and drumming substrates on WISA territories during the breeding season, especially for ant gleaning during the nestling stage. Substrates used by WISA for pecking and drumming must also be characterized and incorporated into habitat management plans. Critical habitat and forest management plans need to include habitat for foraging and drumming that include relevant variation caused by individual ecological traits and behaviour-specific preferences. An improved understanding of WISA foraging and drumming substrate selection would make it easier to identify the habitat characteristics that may be declining in abundance or quality because of human activities (chiefly logging) in WISA Areas of Occupancy, or that could be promoted by forest management practices.

2.2 Objectives

In this chapter, I describe the foraging ecology of Williamson's Sapsuckers using observations of radio-marked individuals to identify foraging and drumming habitat characteristics at the substrate scale to characterize the critical habitat in Canada. I have three specific objectives related to foraging and drumming at the substrate level: to 1) describe WISA foraging behaviour during the breeding season, 2) determine how foraging substrate use varies according to gender, nesting status, age or foraging mode and 3) characterize the tree species, size, decay and surrounding canopy cover of foraging trees compared to the available substrates (selection).

2.3 Methods

2.3.1 Capture and tracking

During the 2014 and 2015 summers (April to July), I monitored Williamson's Sapsucker foraging behaviour at four study sites: two at each of the WISA Areas of Occupancy (Okanagan and Western). I caught WISA using call-playbacks and a male decoy surrounded by mist nets, aerial mist nets (raised up to 8m high) or a dip net affixed on an extensible pole. I aged, determined gender and banded individuals with one numbered aluminum and three coloured plastic bands for identification and later monitoring of individuals (Pyle 1997). I also affixed a radio-transmitter as a tail-mount to radio-track them for 12 to 60 days. I used a homing tracking protocol to monitor the foraging behaviour of individual WISA and identify their foraging substrates, by following them during telemetry sessions from early-May to mid-July, until 5-6 days after the last fledgling left the last nest (Mech 1983). To increase the sample size of foraging observations in the nest patch in 2015, I collected foraging observations within a 60-m radius of nests, without using telemetry (91 foraging observations [8% of total], 10 observation sessions of 30-60 minutes each, in 5 nesting territories).

2.3.2 Behavioural observations

When I located a radio-tagged bird, I recorded its foraging and other behaviours, the beginning and end time of the observation, tree species, tree section used (basal, middle or top) and location used on the tree (branch vs. trunk). The observed foraging modes were sap feeding (excavating to create sap wells and sipping sap), gleaning on wood (picking insects on the surface of a trunk or branch), gleaning on vegetation (feeding on coniferous needles while hanging on the branches), bark scaling (removing segments of the bark from the trunk to uncover insects), pecking (hitting a woody surface to excavate for insects or subcortical larvae) and aerial foraging (catching an insect in flight). Gleaning on wood and vegetation and bark scaling were combined for the statistical analyses due to their similarity and the low frequency of vegetation gleaning and bark scaling. A behavioural observation started when the bird was observed or landed on the substrate, I then recorded the occurrence of any of the above behaviours, thus multiple behaviours could be recorded within an observation (on one tree). I recorded one duration per substrate use observation, instead of one duration per behaviour, because I needed to focus on watching the bird and could not record the time during the observation. I limited the maximum number of consecutive observation to six (generally 1-3) and I fitted models using trees for which observations were separated by five minutes to assess the potential effect of temporal autocorrelation (see section 2.3.5). I also recorded communication behaviours including drumming and territorial call (chyah sound; Gyug 2009, Gyug *et al.* 2012).

2.3.3 Measurements of used and available substrates

I flagged and geo-referenced used substrates with a handheld GPS Garmin 62S unit (Garmin, Lenexa, Kansas, U.S.A.), and 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 scale, including tree species, diameter at breast height (dbh), tree height, decay class, signs of decay, tree top condition and canopy cover (terms defined in Table 2.1 and Table A1.1). I took the same measurements for an equal number of trees that WISA were not observed using ("available" trees), selecting alternately at a point 15m east or west from each of the used trees. If no unused trees were present at the location, I selected the closest tree from that 15m point in a direction opposite or perpendicular to the used tree (to remain > 15 m from the used tree). The 15m buffer around the used trees was a trade-off between reducing the chances of selecting trees that are genetically related to the used tree (*i.e.* a clone or sibling) and minimizing the time spent locating "available" trees 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 and 3.5 cm dbh, in 2014 and 2015 respectively. I determined the minimum dbh threshold of available trees according to the absolute smallest tree that WISA used each year at both sites for that year, assuming that trees below the minimal size are probably not considered suitable by WISA. The "available" tree also had to be in the same state (live or dead) as the used tree, allowing the comparison of live and dead tree characteristics separately. I used the decay classification adopted by the BC wildlife tree classification for coniferous trees, except that I divided decay class 2 (alive unhealthy) in two categories (2A: stressed and 2B: dying) to better characterize the decay of live trees that were sometimes partially dead (dying), especially western larch (Thomas *et al.* 1979; Table 2.1 for details). The decay class of trees was evaluated by the same person for all foraging and available trees. In the IDF zone, I pooled decay class 2A and 2B for the analysis because there were only a few trees in the latter class. The canopy cover was measured with a densiometer using a standard protocol (Forest Suppliers Inc. 2005), with the exception that measurements were taken one meter from the substrate at the north and south cardinal points instead of the four cardinal points. I did not sample the east and west cardinal points because those measurements would have overlapped between the foraging tree and the "available" tree located in one of those directions.

2.3.4 Nest monitoring and nesting status

Where possible (nest cavities $\leq$ 14 m high), I monitored nest contents to confirm the nesting status of the radio-tagged WISA using a video camera attached to an extensible fiberglass pole (see Chapter 1 General Methods section for details). Nesting stages were divided in four categories: 1) the pre-nestling stage is from the arrival of the adults on breeding sites until nestlings reach 2 days of age (after which no incubation behaviour is observed), 2) the nestling stage occurs from when the nestlings reach 3 days of age until 4 days after fledging of the last nestling (~30 days), 3) the post-breeding stage is > 4 days after fledging (the majority of the adults were not seen feeding their fledglings after that time) or immediately after nest failure and 4) non-breeders are birds that were not observed to produce any eggs or nestlings during the breeding season. I categorized the nesting stages in this manner to better represent the behavioural shifts of the adults during the breeding season.

2.3.5 Statistical analyses

I used χ^2 tests, Mann-Whitney-Wilcoxon tests and Kruskal-Wallis rank sum tests to investigate differences in the use of foraging modes, foraging height, foraging location on the tree and the selection of tree characteristics, according to gender, nesting status, age and site. I analysed the data separately for the Montane Spruce and Interior Douglas-fir zones because the tree species differed and could not be pooled, with only Douglas-fir and aspen being present in sufficient numbers in both biogeoclimatic zones. I first performed univariate tests to decide whether to pool data from birds with different gender, nesting status, age and from different sites, when modeling selection of live foraging tree characteristics. These interaction factors could not be included in the models because they required more degrees of freedom than the data would support. There were not enough observations to test for differences in dead tree characteristics, however I included them in foraging tree data summaries. To simplify age categories when testing for differences, because the sample size was limited, I classified birds as second year (SY; first year as an adult) and after second year (ASY). In the MS zone, hybrid spruce (*Picea engelmannii* X *Picea glauca*) was available in only four of 14 territories and 66% of the use was by one male, in the highest elevation nesting territory (~ 1400m above sea level [A.S.L.]). Three WISA used hybrid spruce in similar proportions as other birds used Douglas-fir, therefore I pooled Douglas-fir and hybrid spruce for the univariate tests to avoid spurious results associated with a low sample size for hybrid spruce. I also pooled lodgepole pine and the deciduous trees because they were avoided by WISA in similar proportion and had low overall use, making testing for species-level significance difficult. Ponderosa pine was excluded from the MS zone analysis because only three trees were measured (one used and two available). In the IDF zone, live ponderosa pine was pooled with live deciduous trees because of their low use (avoided trees), unless specified otherwise.

Foraging substrate selection model construction

I used generalized linear mixed-effects models (GLMM) to calculate the odds ratio of selection of foraging substrates (used vs. unused, binomial) according to *a priori* defined covariates representing tree characteristics (tree species, dbh, height, decay class, signs of decay and canopy cover). Mixed-effects models incorporate both fixed effects, which explain variation in the response variable, and random effects (I used bird ID), which serve as additional error terms to account for correlations among observations from the same individual (lme4 package in R; Gillies *et al.* 2006, Bates *et al.* 2015). GLMMs are appropriate to analyse resource selection, however their use should be limited to assessing the relative importance of variables, since the probabilities are not representative of the true probability of selection during the breeding season (Lele and Keim 2006). I only considered foraging occurrence (used vs. unused) as the response variable and not duration for the statistical analyses, as there were sources of noise in the duration of use data in the observations. The observer would occasionally leave or involuntarily scare the bird away during some long observations (typically during sap feeding, which could last over one hour in the pre-nestling stage). I fitted a model for each continuous predictor variable (dbh, height and canopy cover) to examine the fit of linear, quadratic and exponential terms, the best fit being linear in all cases.

I examined collinearity across the predictor variables using a Pearson's correlation matrix and conserved the most relevant variable when the correlation (r) was $\geq$ 0.7. The Pearson's correlation matrix revealed that only dbh and tree height were correlated (r = 0.82), the next highest correlation was 0.09. Tree height was discarded from the analysis since dbh is a measure that is easier to obtain accurately and is directly relevant to forest management. Because the decay class variable includes signs of decay that may not be relevant to WISA foraging, I built a separate model set using signs of decay that were present on more than 5% of the trees that were used for foraging (decay class and signs of decay were not included in the same models). I analysed Douglas-fir and hybrid spruce tree species separately in the GLMM with bird ID as a random effect controlling for the high availability of hybrid spruce for birds in higher elevation. Tree top condition was considered a sign of decay, and dead, forked and broken tree tops were grouped into a "damaged top" category, because their frequency was relatively low. I examined the significance of all possible two-way interaction terms between significant variables by including them in post-hoc models (for all models of the 95% confidence set) and assessed if they significantly improved the fit of the model using χ^2 likelihood ratio tests (Moya-Larano and Wise 2007). I only included individual trees once in the dataset, even though 22% of the trees were used several times (trees that were used multiple times are described in section 2.4.5). I used individual trees that were used for gleaning, pecking or sap feeding to allow a sufficient sample size and cover all WISA foraging requirements. I did not include gender, nesting status, age or site as interaction factors in the models, as their effect was assessed with univariate tests (see above).

Foraging substrate model selection and weighted multi-model averaging

I used backward stepwise model selection to obtain a set of candidate models (GLMM) for each biogeoclimatic zone separately and pooled (overall). I compared the fit of the models using the bias-corrected Akaike Information Criterion (AICc), which represents a measure of quality (goodness of fit) of a model within a set of candidate models, and AICc weights (Wi), which represent the probability of the model to be the best within the model set (Burnham and Anderson 2004). If several models were considered parsimonious (≤ 2 ΔAICc), I used a weighted multi-model averaging of the coefficients in the 95% confidence set of models (cumulative Wi [W] = 0.95; 'AICcmodavg' package in R (Mazerolle 2016); Burnham & Anderson 2004).

I also tested a conditional logistic regression model approach with bird ID as the strata, but the outcomes were qualitatively the same as using GLMM with bird ID as a random effect. Temporal autocorrelation was probable with 47% of the foraging observations recorded within five minutes from another consecutive foraging observation ($\bar{x} \pm SD = 18 \pm 38$ minutes). Temporal autocorrelation is known to cause correlation in the residuals of models and thus potentially underestimate the confidence intervals of the coefficients (Koper and Manseau 2012). Therefore, for comparison, I refitted the GLMMs with a reduced dataset (n = 610 foraging and available tree pairs) in which observations were separated by at least five minutes. This approach resulted in the same qualitative outcome (same significant variables). Similarly, spatial autocorrelation was possible as the location of used trees was spatially aggregated. I used quasi-likelihood GLMM with a correlation structure that accounts for spatial dependence in a separate analysis (MASS package in R; Venables and Ripley 2002). These model outputs were similar to the original GLMMs, therefore spatial autocorrelation was unlikely significantly influencing my results. Consecutive observations were rarely within 15 m from each other, therefore the sampling design for available trees chosen in proximity of used trees likely attenuated the effect of the spatial aggregation of used trees. I did not model the selection of drumming trees because reutilization rates were high and the sample size of individual trees was low.

Model performance assessment

To assess model performance, I used receiver operating curves (ROC) calculated with the 'ROCR' package in R (Sing *et al.* 2005). The method consists of plotting the true positive rate (correct classification) against the false positive rate (incorrect classification; 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 WISA foraging trees and unused trees, while a value of 0.5 indicates that the model performs no better than a random classification (Hanley and McNeil 1982). To evaluate the variability (leverage) in tree characteristic selection for foraging across birds, I quantified the influence of each individual bird on the β coefficients and significance of tree characteristic variables in the most parsimonious model of each candidate set by calculating Cook's distances values and DFBETA statistics for each n groups (individual birds), and by refitting the models with n-i birds to compare significance ('influence' package; Nieuwenhuis *et al.* 2015). Cook's distance and DFBETA statistics are used to detect outliers in a model. I used 4/n as a cut-off for Cook's distance and $2/\sqrt{n}$ for DFBETAs (Belsley *et al.* 1980, Van der Meer *et al.* 2010). Cook's distance describes the influence of each individual bird on all parameters combined in the model, while DFBETAs are calculated for each variable-group combination (n*k).

Selection ratio for diameter at breast height (dbh)

To further explore the size (dbh) of live Douglas-fir trees preferred for foraging by breeding WISA, I performed a selection ratio analysis (Design III for sample of available resource units; Manly *et al.* 2002). To represent the used habitat (n_{μ}), I included Douglas-fir trees that were used by either member of a pair (male or female) during the nestling stage only. I combined observations from both members of a pair to avoid repeated measures, given that the availability of habitat was the same for both birds in the area surrounding the nest (nesting territory). The available habitat (πij) consisted of all the available (or non-used) Douglas-fir for which the dbh had been measured within a given territory. Dbh categories were preferred or avoided when the 95% confidence interval of the selection ratio did not overlap one. Selection ratios between zero and one indicated avoidance while values above one indicated preference (Manly *et al.* 2002). I compared the values of the selection ratios with Bonferroni-corrected χ^2 tests for multiple comparisons ($\alpha = 0.05$).

One nesting territory in the MS zone was excluded from the analysis because there were only measurements for six available Douglas-fir, as little sampling was done and hybrid spruce was dominant on the nesting territory. I only included Douglas-fir that were used at least five minutes apart from each other to reduce the potential effects of temporal and spatial correlation across tree uses, given that dbh could be spatially correlated. I included trees that were used at least once for any of the three foraging modes (gleaning, pecking and sap feeding), excluding reutilizations (unique trees within foraging mode only). I used Mann-Whitney-Wilcoxon and Kruskal-Wallis tests to assess whether to pool data by biogeoclimatic zone or foraging mode. I found differences in dbh of used live Douglas-fir between the MS and IDF zones, and across foraging modes in the MS zone (Table A1.2); therefore, I analysed the data for both biogeoclimatic zones and sap feeding (MS zone only) separately. I separated the dbh categories following the sampling categories of the nested plots used in Drever *et al.* (2015), *i.e.* small trees (≤ 22.4 cm dbh), large trees (22.5 - 57.4 cm dbh) and very large trees (≥ 57.5 cm dbh). I further separated the large and very large trees into three categories (22.5-33.9, 34.0-45.4 and ≥ 45.5cm dbh), to get more precision for the large tree category as it contained most of the foraging observations, and because very large trees were rare, therefore associated with a high variance.

Reutilization of trees

Quantifying the reutilization of trees (used for foraging multiple times) and their characteristics constitutes valuable information on habitat selection for foraging, as trees used more than once are likely to be of higher importance for foraging. For the reutilization analysis, I considered only foraging observations collected during the nestling stage and observations that were separated by at least five minutes, as the birds were more likely to return to the same tree within a short period of time. I pooled the observations of both members of a pair to obtain the number of utilizations of each tree. I tested the effect of year on the reutilization rate ($\frac{\#\ \text{uses of tree}}{\#\ observations\ for\ the\ bird}$) with a Mann-Whitney-Wilcoxon test to determine whether pooling the data was acceptable. The observations were more aggregated in time in 2015 than in 2014, since the battery life of the radio-transmitters was reduced and birds were tracked for longer consecutive periods. I compared some of the characteristics (dbh, tree species and live or dead) of reutilized foraging trees with trees that were used only once for foraging in the MS and IDF zones and overall, using χ^2 and Mann-Whitney-Wilcoxon tests. For tree species, I compared the proportion of western larch (*Larix occidentalis*) and ponderosa pine (separately) to reduce the degrees of freedom used in the χ^2 tests, as they were the most reused tree species overall. To obtain an accurate measure of the dbh of dead trees (highly reused trees), I 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 that were used for foraging during all four nesting stages (with replacement; Efron 1979). Bootstrapping provides a more robust estimate of the true population mean, requires no assumption of normality when computing the confidence intervals and is more appropriate for small sample size.

2.4 Results

2.4.1 *Foraging and communication behaviour*

During the summers of 2014 and 2015, I observed 1 669 behaviours during 1 387 substrate use observations, from 29 radio-tagged adult Williamson’s Sapsuckers (16 in 2014 and 13 in 2015; Table 2.2). Among the 1 387 observations, 1 132 (82%) included at least one occurrence of foraging for 27 birds (few observations were made for two of the 29 birds, and none included foraging). Gleaning was the most frequent behaviour and sap feeding was the most used behaviour when considering duration (Table 2.3). The most frequent communication behaviour was drumming (35%), followed by territorial calls (28%; ‘Chyah’ sound in Gyug 2009). I observed WISA gleaning on needles 91 times (n=71 trees, 17 birds), which occurred intensively in late June. The food item that was gleaned from conifer needles has yet to be confirmed, however I climbed one of the trees immediately after an observation and found a western spruce budworm (*Choristoneura sp.*) within the needles. I observed aerial foraging 28 times by 12 birds, but I did not consider it as foraging in the statistical analyses as I suspect it is not tied to preference for any tree characteristic.

The frequency of foraging modes differed with the gender (χ^2 = 17.32, df = 2, p = < 0.001) and nesting status of the birds (χ^2 = 121.83, df = 6, < 0.001; Figure 2.1). Gleaning increased by 44 % for both genders combined between the pre-nestling and nestling stage, and females gleaned 10% more often than males overall (Figure 2.1). I found no difference in the proportions of use of the foraging modes by age categories (second year and after second year; χ^2 = 3.88, df = 2, p = 0.14). During the nestling stage, birds foraged significantly less often at the top section (27%) of trees compared to birds in the pre-nesting (39%) and post-breeding stages (50%; χ^2 = 70.81, df = 6, p = < 0.001; Figure 2.2a). Second year birds foraged 7% less often on the top section of trees (χ^2 = 8.73, df = 2, p = 0.01) and 8% more often on trunks than older birds (χ^2 = 7.10, df = 1, p = 0.01), which foraged significantly more often on the top section and on branches (Figure 2.2b). The foraging height and location (branch and trunk) did not differ with gender (height: χ^2 = 3.75, df = 2, p = 0.15; location: χ^2 = 0.84, df = 1, p = 0.36), and the foraging location did not differ with nesting status (χ^2 = 3.34, df = 3, p = 0.34).

2.4.2 Characteristics of trees used for foraging and drumming by individual traits

Of the 1 387 substrate use observations, 1 122 (81%) were on live trees (n = 786 trees), 241 (17%) on dead trees (n = 112 trees), 12 on wooden utility poles, six on the ground, four on fallen logs, one on a stump and one in a shallow creek. The observations on the ground, fallen logs and stump were all associated with gleaning, the shallow creek was used for bathing and the wooden utility poles were used for drumming 11 times, but also involved preening five times and pecking one time. There were insufficient data to test for differences in characteristics of dead trees across individual traits, therefore I tested for differences in live tree characteristics (Table 2.4a-b), but included dead trees when reporting tree characteristics (Figures 2.3, 2.4; Tables 2.4, 2.5, A2.2). The characteristics of live trees used for foraging significantly differed by foraging mode and nesting status of the birds, while gender and age had no significant effect (Table 2.4). Given the lack of variation in tree substrate selection by gender and age categories, I dropped these variables in the remaining analyses.

In this section, I describe the characteristics of trees used for each foraging modes and nesting status, the test statistics are presented in Table 2.4 (unless specified) and more detailed information on tree characteristics are presented in Table 2.5 and Figure 2.3. In the Montane Spruce zone, WISA used a significantly higher proportion of Douglas-fir for sap feeding (84%) than gleaning (52%), while pecking was chiefly observed on western larch (49%). The mean dbh of trees used for sap feeding (28.9 ± 1.6 cm) was significantly smaller than gleaning (35.9 ± 1.3 cm) and pecking trees (40.1 ± 2.0 cm). The proportion of decay class for live trees also differed for sap feeding (median = 1) compared to gleaning (median = 2A) and pecking (median = 2A; χ^2 = 3.90-14.01, df = 1, $p < 0.001$, $\alpha = 0.02$). The proportion of dead trees used for pecking (17%) was higher than for gleaning (3%) and sap feeding (0%; χ^2 = 63.15-173.32, df = 1, $p < 0.001$, $\alpha = 0.02$). Drumming occurred chiefly on dead (median decay class 5) western larch (85.9%) of 45.3 ± 3.4 cm mean dbh.

In the Interior Douglas-fir zone, the proportion of use of tree species was not significantly different for gleaning (88%) and sap feeding (99%), while trees used for pecking were mostly ponderosa pine (54%). The mean dbh did not significantly 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 proportion of use of decay classes did not significantly differ for live trees among foraging modes, however 43% of pecking trees were dead, significantly more than for gleaning (4%) and sap feeding (0%; χ^2 = 226.93-277.76, df = 1, $p < 0.001$, $\alpha = 0.02$). Drumming was observed mostly on dead (median decay class 4) ponderosa pine (55.2%, 50.6 ± 6.9 cm dbh) and Douglas-fir (44.8%, 48.9 ± 10.1 cm dbh). Overall, WISA that were not feeding nestlings (pre-nestlings, post-breeding and non-breeders) used trees with significantly larger dbh than during the nestling stage (Figure 2.4, Table A1.3).

2.4.3 Selection of trees for foraging

I fitted GLMMs to determine how tree characteristics influenced the probability of use by foraging WISA in each biogeoclimatic zone. I only used unique trees that adult radio-tagged WISA foraged on during the nestling stage (the largest sample), because the selection of dbh for foraging varied by nesting status in both biogeoclimatic zones (Table 2.4). I pooled the data for sites within each biogeoclimatic zone, even though the characteristics of live trees used for foraging differed (only decay class in the MS zone), because the model outcomes were qualitatively the same when fitted separately.

The characteristics of live trees that were relevant to WISA for foraging in both the Montane Spruce and Interior Douglas-fir zones were tree species, dbh and blistering and resin exudation (MS zone only), larger live Douglas-fir exuding resin being preferred (Figure 2.5a-b; Tables 2.6a-b, 2.7a-c and 2.8a-c). The models representing both biogeoclimatic zones (overall) did not perform as well as the separate models for each zone (using AUC values), therefore I decided to present the results separately for each biogeoclimatic zone. The odds of a live tree being selected for foraging were higher for Douglas-fir (MS zone: odds ratio [O.R.] = 2.41; IDF zone: O.R. = 6.23), larger dbh (MS zone: O.R. = 1.05 per 1 cm increase; IDF zone: 1.07 per 1 cm) and blistering and resin exudation (MS zone: O.R. = 2.27; Table 2.8a-b). The effects of tree species included in the model were compared with the reference group (avoided tree species). Thus, Douglas-fir is only preferred over lodgepole pine and deciduous trees in the MS zone, or ponderosa pine and deciduous trees in the IDF zone. Live western larch was used in higher proportion to its availability (Table 2.6a), although the preference was not significant in the multivariate models. None of the interactions between variables improved the model fit (Likelihood ratio tests: χ^2 range = 2.32-12.22 and P values range = 0.16-1). One bird was considered to have high leverage with a Cook's distance of 0.44 (cut-off = 0.37) in the MS zone, but none in the IDF zone (cut-off = 0.44). The DFBETA values indicated variability across birds in tree characteristic selection for foraging in the MS zone only, with six of 11 birds having at least one value above the cut-off (0.60 MS zone; 0.67 in the IDF zone). 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 Montane Spruce, Interior Douglas-fir and overall candidate model sets.

2.4.4 Selection ratios for dbh of live Douglas-fir

I used selection ratios to examine the selection of dbh categories of live Douglas-fir used for foraging in the MS (sap feeding separately) and IDF zones. In both biogeoclimatic zones, small Douglas-fir trees (< 22.5 cm dbh) were used for foraging less often in proportion to their availability, while larger dbh were preferred (Figure 2.6). For sap feeding in the MS zone, WISA preferred Douglas-fir live trees of 34.0-45.4 cm dbh and avoided live Douglas-fir trees of $\geq$ 45.5 cm dbh, although the sample size was small.

2.4.5 Reutilization of foraging trees

Of the 772 trees (live or dead) used for foraging, 177 (23%) were reutilized for foraging (both biogeoclimatic zones combined), considering only observations that were obtained during active telemetry tracking throughout the breeding season. The reutilization rate of individual trees between years did not differ, therefore I pooled the data from 2014 and 2015 (W = 9967.5, P= 0.18). Overall, reutilized trees were larger in dbh by 4.4 cm than trees that were used only once, and were more often dead (used once: 7.7% dead; reused: 13.0%; Tables 2.6a-b, 2.9). Western larch and ponderosa pine were not reutilized more often for foraging than other trees, but represented most (81%) of the 112 dead trees used once or more for foraging. The bootstrapped mean dbh of dead western larch and ponderosa pine used for foraging was 46.0 cm (42.0-50.2 cm dbh 95% bootstrapped conf. int., n = 70 trees).

2.5 Discussion

I identified the main foraging modes of breeding Williamson's Sapsuckers to be gleaning, pecking and sap feeding. Pecking for subcortical larvae was not reported previously as an important foraging mode for WISA, representing only 0.4% of the foraging modes used during the breeding season in Colorado, mostly during cold temperatures (Crockett 1975). My study is the first to provide WISA foraging habitat requirements that account for different foraging modes and individual traits. Foraging behaviour (foraging mode and use of foraging trees) varied by gender and nesting status, but the selection of foraging substrate characteristics varied mostly with foraging modes and nesting status, not gender. Birds that were not constrained to feeding nestlings (pre- and post-breeding and non-breeders) used larger trees on average. In the Montane Spruce biogeoclimatic zone, sap trees were smaller (dbh) than trees used for gleaning or pecking. Overall, WISA foraged on a wide range of tree types, but preferred large live Douglas-fir ($\geq$ 22.5 cm dbh). Larger dead trees (mostly western larch and ponderosa pine) were used mostly for pecking and drumming, especially outside of the nestling stage, and were reutilized in higher proportions for overall foraging.

Gleaning, pecking and sap feeding appeared as essential foraging modes for WISA when considering the frequency of use and time spent on each activity. My results showed that pecking was more important during the pre-nestling stage (mostly April and May), when temperatures are also generally colder. Pecking may be more important for WISA breeding in Canada, at the northern limit of their range, because of more frequent periods of insect inactivity due to cold temperatures. Aerial foraging and gleaning on conifer needles have also been described as opportunistic behaviours of WISA Crockett (1975), consistent with my findings. I found that females used gleaning as a foraging mode more often than males, however I found no difference between genders in tree characteristics use. Since females were generally captured later than males, it is possible that I recorded more observations for females later in the breeding season, when ants were more abundant. Crockett (1975) found that females foraged 4.9% more often on the upper section of the trunk and used trunks 5.8% more often than males, which used branches and the ground more frequently, although he used a larger sample size (22 222 behavioural observations). I observed that the frequency of use of the foraging modes varied across nesting status, following the same patterns as observed in Colorado (Crockett 1975), i.e. gleaning was significantly more frequent during the nestling stage, during which non-breeders continued sap feeding at similar frequencies. Sap feeding was common for adults that were not feeding nestlings, especially in the spring (Crockett 1975). Higher rates of sap feeding in the spring could be explained by the increased sap flow of conifers as temperatures rise (Wang *et al.* 2005). Pecking and sap feeding may be critical for the survival of adults particularly during periods when ants are not abundant (Crockett 1975, J. St-Amand pers. obs.), but could still be required for nestlings. Overall, during the breeding season, gleaning ants is likely the most important foraging mode for WISA adults and nestlings, occurring mostly on large live Douglas-fir.

Douglas-fir was preferred by foraging WISA, contrasting with the closely related Red-naped Sapsuckers (*Sphyrapicus nuchalis*; sympatric to WISA) and Red-breasted Sapsuckers (*Sphyrapicus rubens*; sympatric) that forage on deciduous and coniferous trees, and the Yellow-bellied Sapsuckers (*Sphyrapicus varius*; allopatric) that forage mostly on deciduous trees (Rushmore 1969, Raphael and White 1984, Walters 1996). WISA may prefer Douglas-fir because it is possibly preferred as a foraging substrate by ants, the main food item in their diet during the breeding season. In western Oregon, ant species such as *Camponotus sp.* and *Formica sp.* 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 a smoother trunk facilitating gleaning. Live Douglas-fir was also used for pecking, probably for feeding on bark-beetle larvae (*Scolytinae*), especially the Douglas-fir bark-beetle (*Dendroctonus pseudotsugae*) which I observed on several occasions on the sites. While I have limited data on this tree species, hybrid spruce was almost a significantly preferred tree species for foraging in territories close to the altitudinal limit of the range of WISA, between 1400 m and 1560 m A.S.L. At these altitudes, hybrid spruce starts to replace Douglas-fir in forest stands where WISA breed (Meidinger and Pojar 1991). Western larch was used in higher proportion to its availability, but was not significantly preferred in the model sets containing dbh, meaning that the selection of western larch as a foraging tree was driven by its large size in relation to other trees on site. Overall, Douglas-fir are the most preferred tree species for foraging and are likely to have a significant influence on WISA fitness.

Tree size was the most important predictor of WISA foraging. The models and analysis of reutilized trees showed that WISA select larger trees for foraging than other trees available in the vicinity, with a preference for live Douglas-fir of $\geq$ 22.5 cm dbh. WISA foraged on smaller trees during the nestling stage, probably because they were spatially constrained by having to return to the nest regularly to feed nestlings, preventing long-distance trips to reach better quality (larger) foraging trees. Larger trees may provide more food resources to foraging sapsuckers because they provide a larger foraging surface with more bark furrows and fungi that favour arthropod abundance (Grove 2002, Miller *et al.* 2007). Also, larger trees are likely to provide shelter to foraging WISA from adverse weather (rain and wind), as well as from aerial predators such as Cooper's Hawks (*Accipiter cooperii*) and Northern Goshawks (*A. gentilis*; Crockett 1975, Tozer *et al.* 2011).

Combining the MS and IDF zones, trees that were used for the three main foraging modes (gleaning, pecking and sap feeding) had similar dbh, excluding sap feeding in the MS zone, which involved significantly smaller trees. In a previous study in British Columbia, sap trees had a larger mean dbh in the Okanagan (MS zone; $\bar{X}$=37.7 cm dbh, range = 8-75 and n = 71 trees; Gyug *et al.* 2009a). Since the sample size was higher and the data covered more nesting territories, the results in Gyug *et al.* (2009a) are probably more representative of the mean dbh of sap trees in the MS zone, making the dbh of live Douglas-fir used for sap feeding similar compared to other foraging modes in the MS and IDF biogeoclimatic zones. My results suggest that tree size is not as important for sap feeding as for gleaning and pecking – other characteristics such as local injuries on the trunk of the tree might be more influential on sap tree selection (Eberhart 2000). Mancuso *et al.* (2014) suggested that the sap trees of Yellow-bellied Sapsuckers are good retention tree candidates, being often reused for several years and larger than the available trees; I suggest the same for WISA as they are generally easily identifiable (see Gyug *et al.* 2009a) and can also be used for gleaning and pecking.

Decay class and signs of decay did not seem to influence tree selection for foraging, except for signs of blistering and resin in the Montane Spruce zone. Blistering and resin exudations are a defense mechanism that can be caused by events in the life of the tree such as fires, drought, insect attacks and mechanical damage (Bois and Lieutier 1997). For WISA foraging, it means that the tree is stressed and might be experiencing an insect infestation. Bark-beetles can trigger the exudation of resin, which can provide a source of food for other insects (potential prey) such as ants (*Formicidae*), fruit flies (*Drosophilidae*), sap beetles (*Nitidulidae*) and rove beetles (*Staphylinidae*; Yoshimoto *et al.* 2005; Yoshimoto 2009). Also, blistering and resin can be associated with a wounded section of a tree, making it suitable for sap well excavation. Other signs of decay higher in the tree could be important for WISA foraging, but I was mainly able to observe the lower part of the tree. Ant nest presence had a positive, but non-significant effect on the odds of WISA foraging. Sometimes I suspected the presence of an ant nest, but I could only confirm it after seeing several ants penetrating the trunk of the tree, limiting my sample size and explaining the large confidence intervals.

Dead trees (mostly recently dead western larch and ponderosa pine) were used in high proportions for pecking and drumming, these were also used more often before and after the nestling stage and were reused more than live trees. Dead standing trees might have been reutilized more often because they were rare on the study sites. WISA selected recently dead trees for pecking probably because they generally hold the highest densities and diversity of arthropods, mostly bark beetle sub-cortical larvae that forage on the inner bark (Stokland *et al.* 2012). Larger dead trees offer optimal habitat for sub-cortical larvae because they have more heartwood and a thicker bark that regulates temperature and protect against several types of predators (Paine *et al.* 1981, Wilhelmsson *et al.* 2002). Drumming was also associated with dead western larch and ponderosa pine. During my study, WISA could drum on short dead limbs to respond to other birds drumming, but the main drumming trees that they used to mark their territory were often larger, therefore taller, than the surrounding trees (used and available) with little to no bark (generally decay class 4 or 5). These drumming trees were often exposed to the sun, therefore dry and probably more resonant. Very large and large partially dead western larch and dead ponderosa pine are also used by WISA as nesting substrates (Unpublished data, Gyug *et al.* 2009b). WISA used dead trees more often for foraging before and after the nestling stage probably because they were drumming more often during these stages and were foraging opportunistically (Crockett 1975, J. St-Amand Unpublished data).

Large live trees (Douglas-fir) are preferred for foraging overall, but dead standing trees could also be critical, especially before and after the nestling stage when ants are likely not as abundant and WISA rely on pecking. My results showed that sap feeding can be associated with different characteristics than gleaning and pecking, and yet most studies on foraging habitat of sapsuckers are limited to sap trees (Mancuso *et al.* 2014, Gyug *et al.* 2009a). My study underlines the importance of considering the influence of different foraging modes and individual traits on habitat selection when studying the foraging habitat of a species of conservation concern.

2.6 Tree-level management recommendations

I recommend adding live Douglas-fir and hybrid spruce to the biophysical characteristics of the critical habitat for foraging of Williamson's Sapsuckers (the latter in nesting territories $\geq$ 1400 m A.S.L.). Retention should prioritize live Douglas-fir of $\geq$ 22.5 cm dbh for overall foraging. I recommend the retention and recruitment of $\bar{x}$ = 46.0 cm dbh (range = 42.0-50.2 cm dbh) western larch and ponderosa pine to provide dead and dying trees for nesting, pecking and drumming. Overall, forest management should target the retention and recruitment of the largest trees possible to provide quality (preferred) WISA habitat, since large dbh was the best predictor that a tree would be selected for foraging.

Logging threatens the integrity of the habitat of many woodpecker species in North America and Europe (Angelstam and Mikusinski 1994, Imbeau *et al.* 2001, Nappi *et al.* 2015). Late-seral tree species such as Douglas-fir, large trees and dead trees are characteristics of mature forests, which typically decline in availability in managed landscapes. Mature forest characteristics can be maintained or restored with passive management strategies, including protecting portions of mature forest from anthropogenic disturbances. Active restoration strategies can accelerate the restoration of mature forest characteristics by creating small gaps to obtain vertical and horizontal heterogeneity, killing large live trees to create dead standing trees and coarse woody debris, and cutting smaller trees that compete with larger ones to increase the number of large trees (thinning; Franklin 2002, Keeton 2005). Selective and partial tree cutting could be compatible with WISA habitat, depending on the relationship between WISA and the side effects of disturbances, such as edges, gaps and open areas.

2.7 Chapter 2 figures

Fig. 2.1

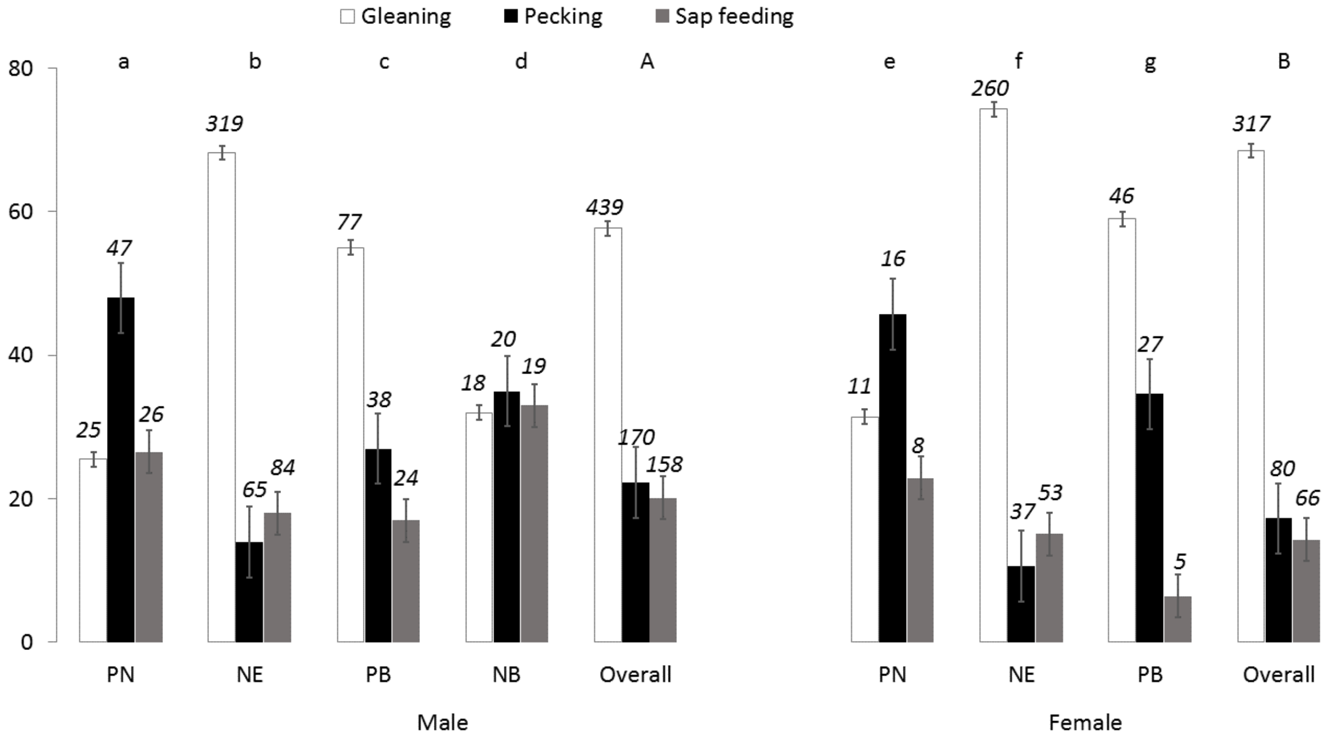
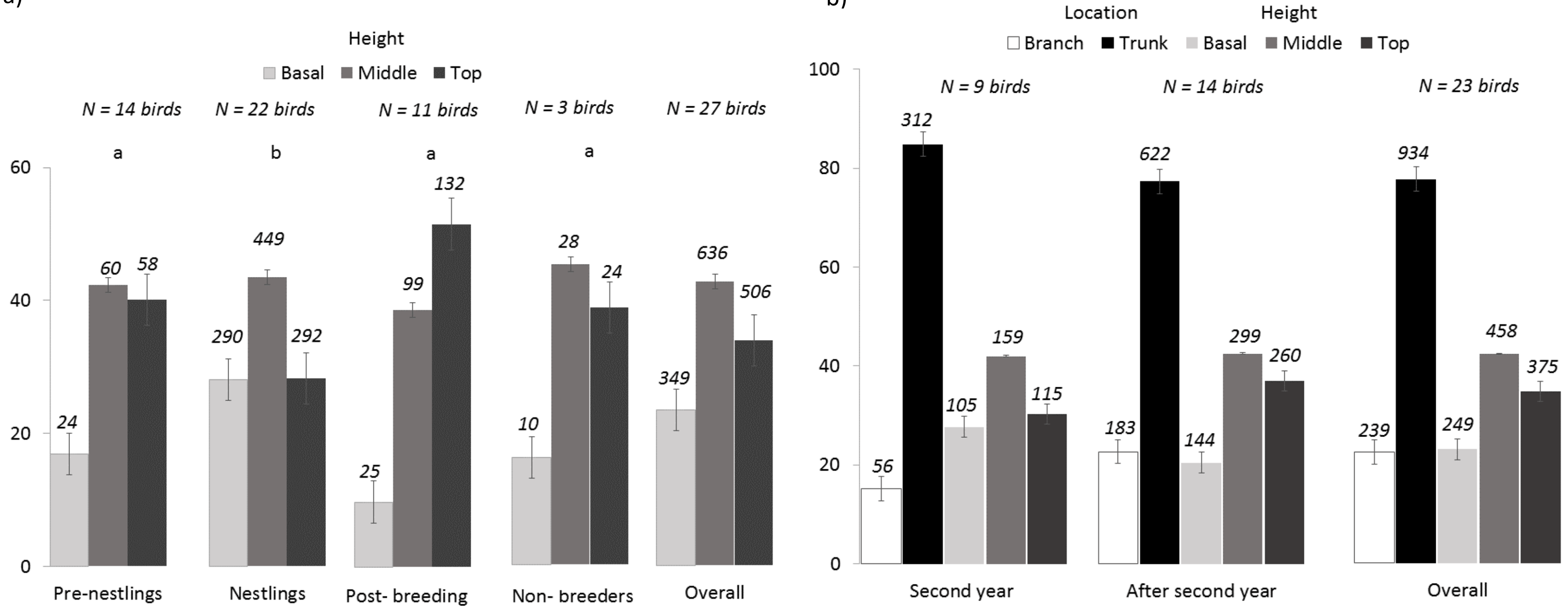


Figure 2.1. Frequency of use of the three main foraging modes of male and female 27 radio-tracked Williamson's Sapsuckers per nesting status stages, in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones in 2014-2015, based on 16 males including three non-breeders (median = 33 observations/male and range = 4-80) and 11 females (median = 22 observations/female and range = 1-78). Shared letters indicate no significant difference in foraging mode proportions with nesting status (males: α = 0.01, females: α = 0.017) and between male and female overall use (α = 0.05), using Bonferroni-corrected χ^2 tests. The number of observations is indicated above the bars. Error bars represent the standard error of the proportion. Nesting status classes are the following, PN = pre-nestlings, NE = nestlings, PB = post-breeding and NB = non-breeders.

Fig 2.2


a)

b)

Figure 2.2. Proportion of use for foraging of tree height sections (basal, middle, top) and location (branch, trunk) by a) nesting status and b) age class of 27 radio-tracked Williamson’s Sapsuckers in 2014-2015. The number of observations (uses of a section or location) is indicated above the bars. Individual radio-tagged WISA could be observed during several nesting stages and the age of four birds was missing. Shared letters mean no difference using Bonferroni-corrected χ^2 tests ($\alpha = 0.0125$) for nesting status comparisons.

Fig. 2.3

a) Montane Spruce zone

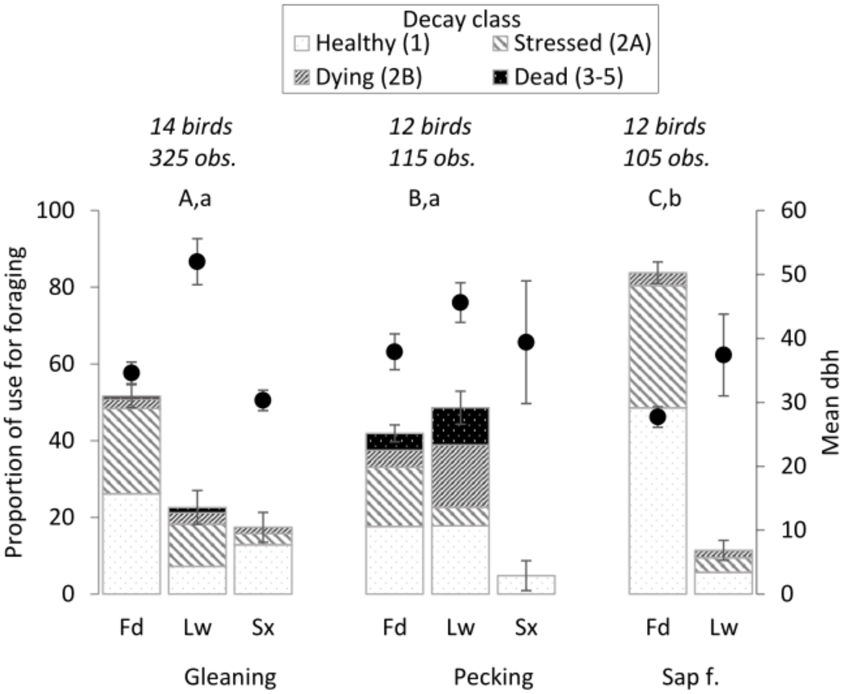


Fig. 2.3

b) Interior Douglas-fir zone

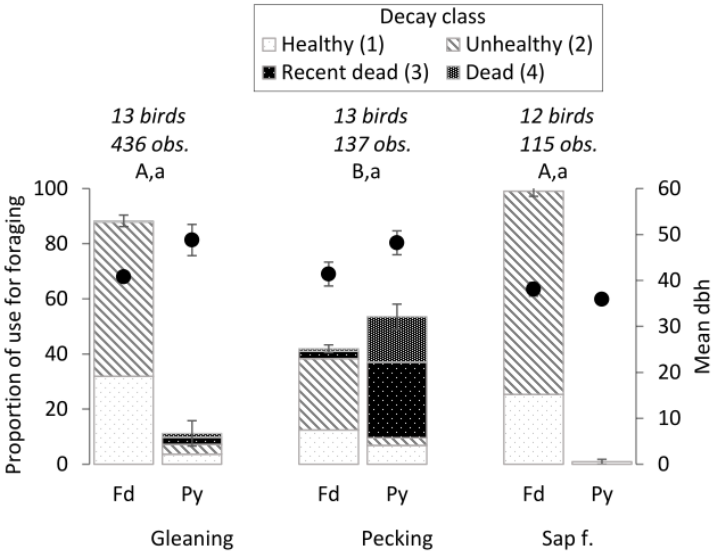


Figure 2.3. Proportion of tree species (full bars), mean dbh (circles) and decay categories (stacked bars) of live and dead trees used for gleaning, pecking and sap feeding by 27 radio-tracked Williamson's Sapsuckers in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones during the 2014-2015 breeding seasons in British Columbia. Shared letters mean no difference in the proportions 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 trees species do not total 100% because tree species that were used < 10% in total are not presented. Fd = Douglas-fir, Lw = western larch, Sx = hybrid spruce and Py = ponderosa pine.

Fig. 2.4

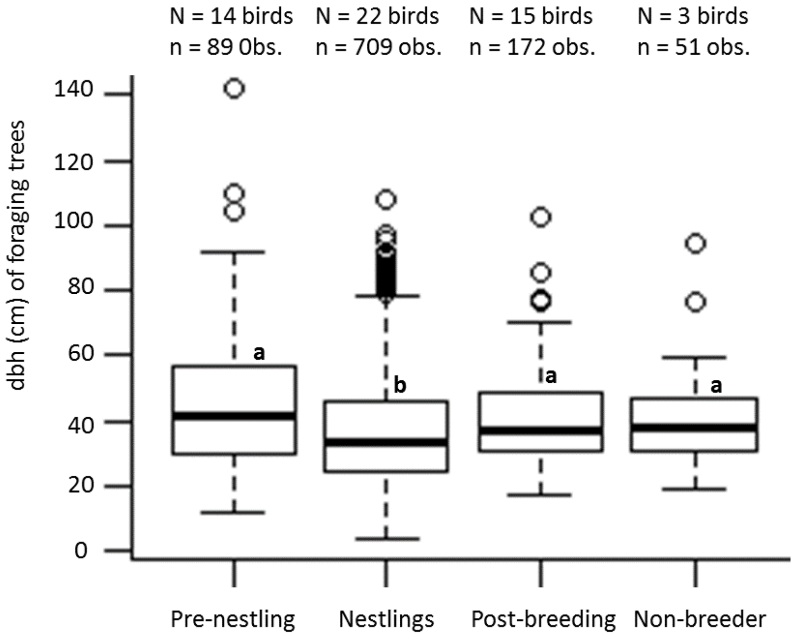


Figure 2.4. Dbh of live and dead trees that were used for foraging by Williamson's Sapsuckers according to their nesting status in southern British Columbia in 2014-15. Shared letters mean no significant difference using Bonferroni-corrected (α = 0.017) Mann-Whitney-Wilcoxon. Sample sizes are indicated above each boxplot and bar. Post-breeding includes birds that were observed foraging following a nest failure or predation, or > 4 days after the nestlings fledged.

Fig. 2.5

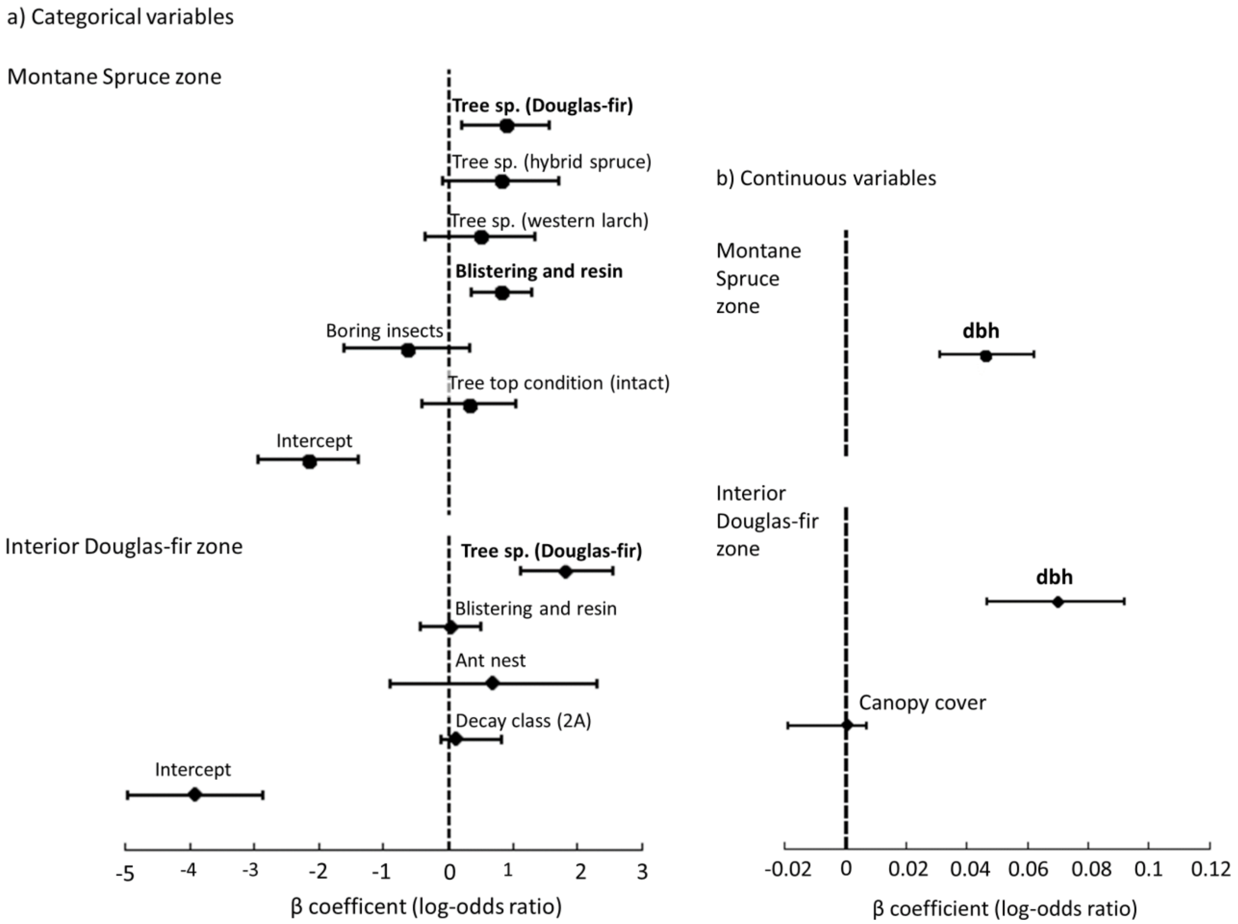


Figure 2.5. Generalized Linear Mixed-Models of the selection of tree characteristics for foraging by 20 radio-tracked Williamson's Sapsuckers during the nestling stage. Multi-model averaged β coefficients and 95% confidence intervals of a) categorical and b) continuous variables of the 95% confidence set are presented. Variables with confidence intervals that did not overlap zero are considered more important and are bolded. The data were collected during the summers of 2014-2015 in two biogeoclimatic zones in south-central British Columbia, the Montane Spruce (n = 299 foraging trees, 11 birds) and Interior Douglas-fir zones (232 foraging trees, 9 birds). Reference levels (intercepts) of the tree species factor were the avoided tree species groups (Montane Spruce zone: lodgepole pine and deciduous trees; Interior Douglas-fir zone: ponderosa pine and deciduous trees).

Fig. 2.6

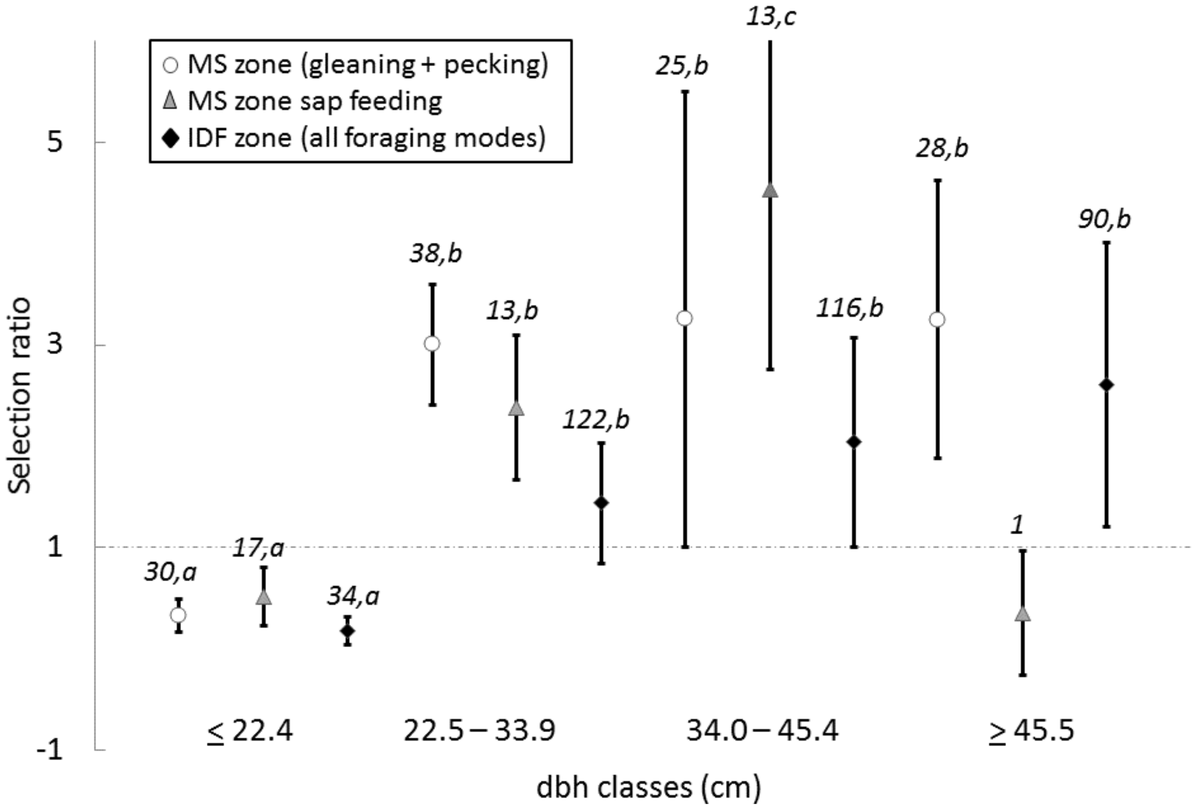


Figure 2.6. Selection ratios and 95% confidence intervals of dbh categories of live Douglas-fir used for foraging by Williamson's Sapsuckers during the nestling stage, in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones in south-central British Columbia (N = 7 nesting territories in each biogeoclimatic zone). Foraging observations from both members of the pair were pooled to avoid repeated measures of available habitat. A selection ratio of one indicates no selection and is represented by the broken line. Preference is indicated by a value above one and avoidance below one. The number of uses are indicated above the bars and shared letters indicate no significant differences across dbh categories within the same biogeoclimatic zone, using Bonferroni-corrected χ^2 tests.

2.8 Chapter 2 tables

Table 2.1. Description of measurements taken for the used and available substrates and their use in statistical analyses for Chapter 2 on substrate selection for foraging by Williamson's Sapsuckers in southern British Columbia.

Variable name	Description of the variable	Variable type (continuous, binomial or categorical)
Substrate use	WISA occurrence (response variable) 1. No use by WISA observed (0) 2. Used by a WISA (1)	Binomial
Tree species	1. Douglas-fir 2. Ponderosa pine 3. Deciduous 4. Western larch 5. Lodgepole pine 6. Hybrid spruce (Engelmann X White Spruce)	Categorical
Dbh	Diameter at breast height (dbh [cm]) of the tree	Continuous
Tree height	Height of the tree (m), measured with a clinometer	Continuous
Decay class	Decay stage of the tree: 1. Healthy tree, no visible signs of decay 2A. Healthy tree with minor signs of decay 2B. Live tree with one major or ≥ 3 minor signs of decay (Montane Spruce zone only) 3. Recently dead tree with needles or twigs still on and tight bark 4.Dead tree with no needles or fine twigs with ~50% of major branches lost 5. Dead tree with ≤ 2/3 of original height and sapwood/heartwood sloughing from the top	Categorical

Table 2.1. (continued)

Variable name	Description of the variable	Variable type (continuous, binomial or categorical)
Signs of decay (contribution in determining decay class)	A combination of: 1. Blistering/sap seeping or resin on the bark (minor) 2. Signs of boring insects (minor) 3. Mechanical damage (not considered decay) 4. Burnt (not considered decay) 5. Brown needles (minor or major) 6.Trunk gall (minor) 7. Fungus (major) 8. Hearth rot (major) 9. Signs of ants nesting (major) 10. Dead branches (minor or major) 11. No signs of injury or decay	Categorical (11 levels, although some levels were combined). Presence-absence (binomial) in models.
Tree-top form (contribution in determining decay class)	Tree top condition: 1. Intact 2. Broken top (major) 3. Forked top (major) 4. Dead top (major)	Categorical

Table 2.2. Number of behaviours observed, substrate use observations and standing trees used by radio-tracked Williamson's Sapsuckers during the 2014-2015 breeding season in south-central British Columbia. I collected 95 substrate use observations on banded birds with no radio-transmitter or with a radio-transmitter with a depleted battery within 60 m from the nest in 2015 (nest patch observations; see the Methods section for description).

	All behaviours				Foraging only			
Data type	Behaviour	Substrate use observations	Trees*	Birds	Behaviour	Substrate use observation	Trees*	Birds
MS zone								
Males	460	391	252	9	308	285	202	8
Females	286	240	182	6	232	215	166	6
Total	746	631	434	15	540	500	368	14
IDF zone								
Males	625	501	292	9	454	408	247	8
Females	298	255	172	5	231	224	157	5
Total	923	756	464	14	685	632	404	13
Overall								
Males	1085	892	544	18	762	693	449	16
Females	584	495	354	11	463	439	323	11
Total	1669	1387	898	29	1225	1132	772	27

* I excluded 21 substrates that were not trees, such as wooden utility poles, ground, logs, stumps and shallow creeks.

Table 2.3. Frequency (# of uses) and duration of behaviours observed while tracking 27 Williamson's Sapsuckers during the 2014-2015 summers in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones, in British Columbia. Other behaviours include perching, preening, sleeping, sunbathing and copulating.

	# of uses		Duration (minutes)*		
	% of use	n	$\bar{X}$ ± SE (range)	Proportion of time (%)	n
Gleaning	46	749	1.6 ± 0.1 (0-45)	24	1127
Pecking	15	246	3.9 ± 0.5 (0-45)	19	890
Sap feeding	13	217	5.2 ± 0.5 (0-65)	25	1170
Communication	13	219	4.5 ± 0.5 (0-38)	15	710
Other	13	205	3.0 ± 0.4 (0-65)	17	810
Total	100	1636	2.9 ± 0.2 (0-65)	100	4707

* One duration was recorded per substrate use observation even if multiple behaviours were observed.

Table 2.4. Differences in characteristics of live trees that were used for foraging by 27 radio-tracked Williamson's Sapsuckers by gender, nesting status, age and site, in southern British Columbia in 2014-2015. The sample size represents the number of substrate use observations, except for foraging mode where behaviour observations are used. The significance thresholds were Bonferroni-corrected (α = 0.017) because three tests were performed per individual trait (or biogeoclimatic zone). Statistical significance is bolded.

a) MS zone	Foraging mode			Gender			Nesting status*				Age			Site within b. zone		
	χ^2 (W)[†]	df	P	χ^2 (W)	df	P		χ^2 (W)	df	P	χ^2 (W)	df	P	χ^2 (W)	df	P
Charact.																
Tree sp.[‡]	**11.15**	**2[§]**	**<0.001**	1.43	2	0.49		0.69	1[§]	0.41	0.18	1[§]	0.68	0.56	1[§]	0.46
dbh	**13.50**	**2**	**0.002**	(11574)	1	0.70		**27.16**	**3**	**<0.001**	(12192)	1	0.08	(32058)	1	0.52
Decay cl.	**15.59**	**4**	**0.004**	0.29	2	0.87		6.68	2	0.04	3.52	2	0.17	**2.20**	**2**	**<0.001**
Sample[¤]	*GL*	*PE*	*SF*	*m.*	*f.*		*PN*	*NE*	*PB*	*NB*	*SY*	*ASY*		*Oliver*	*O.Falls*	
N birds	14	12	12	8	6		7	11	8	1	4	8		8	6	
n obs.	306	88	105	251	201		45	314	66	27	89	281		219	233	

b) IDF zone	Foraging mode			Gender			Nesting status*				Age			Site within b.zone		
	χ^2 (W)[†]	df	P	χ^2 (W)	df	P		χ^2 (W)	df	P	χ^2 (W)	df	P	χ^2 (W)	df	P
Charact.																
Tree sp.[‡]	**11.45**	**2**	**0.004**	<0.001	1	1		<0.001	1	1	1.20	1	0.06	**30.69**	**1**	**<0.001**
dbh	6.79	2	0.03	(39616)	1	0.74		8.8	3	0.03	(22012)	1	0.28	**(43844)**	**1**	**<0.001**
Decay cl.	2.2	2	0.33	0.01	1	0.91		3.26	3	0.35	2.13	1	0.15	**13.44**	**1**	**<0.001**
Sample[¤]	*GL*	*PE*	*SF*	*m.*	*f.*		*PN*	*NE*	*PB*	*NB*	*SY*	*ASY*		*Princ.*	*Merritt*	
N birds	13	13	12	8	5		7	11	7	2	5	6		8	5	
n obs.	405	67	115	374	195		44	395	106	24	199	249		416	153	

*Only two nesting status - nestling stage and post-breeding - were compared with the χ^2 tests because there was insufficient data for the pre-nestling and non-breeder status (except for decay class in the Interior Douglas-fir zone).

[†] χ^2, Mann-Whitney-Wilcoxon (W) and Kruskal-Wallis (χ^2) test statistics.

[‡] Douglas-fir and hybrid spruce were pooled since 66% of all hybrid spruce was used by one male (see text for description).

[§] The χ^2 test was performed to compare the use of Douglas-fir and hybrid spruce group (pooled) and western larch only since the group of avoided tree species (lodgepole pine and deciduous) was not used in sufficient numbers for comparison.

[¤] Foraging modes: GL = gleaning, PE = pecking and SF = sap feeding. Nesting status: PN = pre-nestling, NE = nestling, PB = post-breeding and NB = non-breeder. Age: SY = second year and ASY = after second year. The age is missing for four birds. Observations can comprise several foraging modes

Table 2.5. Proportion of use and measurements of tree species characteristics using substrate use observations of 27 radio-tracked Williamson's Sapsuckers for the three main foraging modes and drumming, in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones in 2014-2015. The mean and median statistics are presented for the diameter at breast height (dbh) and decay class, respectively. Standard error of the mean and standard error of the proportion are presented accordingly. The bolded values represent the characteristics of the tree species that were used in higher proportions for each foraging mode (using substrate use observations). Trembling aspen, lodgepole pine and water birch were included in the statistics, but their characteristics are not presented in the table (because use < 10%), overall proportions of tree species do not sum to 100%. Blistering includes resin exudation.

a) MS zone	Tree species	Douglas-fir	Western larch	Hybrid spruce	Overall
	Charact.	Value ± SE (range)	Value ± SE (range)	Value ± SE (range)	Value ± SE (total)
Gleaning *n = 325 obs.,* *236 trees*	% Tree sp.	**51.6 ± 3.0**	22.6 ± 4.4	17.4 ± 3.9	(91.6)
	dbh (cm)	**34.6 ± 1.7 (4.5-91.8)**	52.0 ± 3.6 (6.2-108.0)	30.3 ± 1.6 (13.4-56.0)	35.9 ± 1.3
	Decay cl.	**1 (1-4)**	2A (1-5)	1 (1-2B)	2A
	% alive	**98.4 ± 3.4**	93.6 ± 5.7	100	97.5 ± 2.5
	% Blistering	**51.6 ± 4.7**	25.5 ± 6.3	16.7 ± 4.4	40.3 ± 1.7
Pecking *n = 115 obs.,* *75 trees*	% Tree sp.*	**41.9 ± 2.2**	**48.6 ± 4.3**	4.8 ± 3.9	(95.3)
	dbh (cm)	**37.9 ± 2.8 (12.2-80.9)**	**45.6 ± 3.1 (15.4-85.2)**	39.4 ± 9.6 (29.4-58.5)	40.1 ± 2.0
	Decay cl.	**1 (1-4)**	**2B (1-5)**	1	2A
	% alive	**89.5 ± 2.5**	**80 ± 5.4**	100	82.7 ± 2.0
	% Blistering	**50.0 ± 3.6**	**23.3 ± 6.2**	0	36.0 ± 2.7
Sap feeding *n = 105 obs.,* *57 trees*	% Tree sp.*	**83.8 ± 2.8**	11.4 ± 2.6	0	(95.2)
	dbh (cm)	**27.7 ± 1.6 (12.4-76.5)**	37.4 ± 6.4 (20.9-62.5)	NA	28.9 ± 1.6
	Decay cl.	**1 (1-2B)**	1 (1-2B)	NA	1
	% alive	**100**	100	NA	100
	% Blistering	**50.0 ± 4.0**	50.0 ± 2.8	NA	50.6 ± 2.0
Drumming *n = 71 obs.,* *25 trees*	% Tree sp.*	14.1 ± 6.5	**85.9 ± 6.9**	0	(100)
	dbh (cm)	40.6 ± 4.9 (19.2-55.3)	**45.3 ± 3.4 (15.0-68.9)**	NA	43.8 ± 2.8
	Decay cl.	3 (1-5)	**5 (2A-5)**	NA	4
	% alive	25 ± 13.8	**29.4 ± 14.2**	NA	28.0 ± 3.3

Table 2.5.

b) IDF zone (Princeton and Merritt)

	Tree species	Douglas-fir	Ponderosa pine	Overall
	Characteristics	Value ± SE (range)	Value ± SE (range)	Value ± SE (total)
Gleaning	% Tree sp.	**88.3 ± 2.1**	11.2 ± 4.6	(99.5)
n = 436 obs.,	dbh (cm)	**40.8 ± 1.0 (10.0-141.8)**	48.8 ± 3.4 (19.2-90.8)	44.6 ± 1.0
271 trees	Decay cl.	**2A (1-4)**	2A (1-4)	2A
	% alive	**99.6 ± 2.5**	64.5 ± 6.7	95.6 ± 3.0
	% Blistering	**63.4 ± 3.0**	6.5 ± 6.0	56.5 ± 1.4
Pecking	% Tree sp.	**41.9 ± 1.4**	**53.5 ± 4.6**	(97.4)
n = 137 obs.,	dbh (cm)	**41.4 ± 2.6 (16.3-109.5)**	**48.2 ± 2.6 (27.1-104.4)**	43.8 ± 1.8
89 trees	Decay cl.	**2A (1-4)**	**3 (1-4)**	3
	% alive	**91.5 ± 1.8**	**17.9 ± 6.7**	57.3 ± 2.5
	% Blistering	**41.8 ± 2.2**	**5.1 ± 6.1**	27.0 ± 2.9
Sap feeding	% Tree sp.	**99.1 ± 1.9**	0.9 ± 0.9	(100)
n = 115 obs.,	dbh (cm)	**38.1 ± 1.5 (18.7-59.0)**	35.9	38.0 ± 1.5
44 trees	Decay cl.	**2A (1-2B)**	1	2A
	% alive	**100**	100	100
	Blistering	**62.8 ± 2.4**	0	61.4 ± 1.4
Drumming	% Tree sp.	**44.8 ± 6.3**	**55.2 ± 4.2**	(100)
n = 29 obs.,	dbh (cm)	**48.9 ± 10.1 (24.4-114.7)**	**50.6 ± 6.9 (29.1-87.6)**	49.6 ± 6.6
18 trees	Decay cl.	**4 (2A-5)**	**4 (3-5)**	4
	% alive	**36.4 ± 13.8**	**0**	22.2 ± 2.9

Table 2.6. 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 two biogeoclimatic zones in south-central British Columbia. Two sites are grouped in the a) Montane Spruce biogeoclimatic zone, while b) Princeton and c) Merritt (Interior Douglas-fir zone) are presented separately because of differences in tree characteristics. The mean and median values are presented for the diameter at breast height (dbh) and decay class respectively. The sample sizes represent the number of unique trees that were measured as available, foraging or reused, and the percentage of tree species is calculated with the number of trees for each category as the denominator. Trembling aspen, lodgepole pine and water birch were included in the statistics, but their characteristics are not presented in the table (< 10% use), therefore overall proportions of tree species do not sum to 100%. Blistering includes resin exudation.

a) MS zone (Oliver and Okanagan Falls), *N = 14 birds*

		Available *n = 368 trees*	Foraging (used) *n = 368 trees*	Foraging ≥ 2x *n = 74 trees*
	Characteristics	Value ± SE (range)	Value ± SE (range)	Value ± SE (range)
Douglas-fir	% Tree sp.	50.3 ± 2.6	58.7 ± 2.5	54.1 ± 2.6
	dbh (cm)	19.5 ± 1.2 (4.0-99.3)	33.6 ± 1.2 (4.5-91.8)	36.6 ± 2.6 (12.2-76.5)
	Decay class	1 (1-3)	1 (1-4)	1 (1-4)
	% alive	96.7 ± 2.7	97.2 ± 2.6	97.5 ± 6.0
	% Blistering	23.9 ± 3.0	51.0 ± 3.4	55.0 ± 7.4
Western larch	% Tree sp.	18.9 ± 2.0	22.6 ± 2.2	28.4 ± 4.8
	dbh (cm)	26.8 ± 2.5 (3.6-86.0)	48.6 ± 2.4 (6.2-108.0)	53.3 ± 3.4 (29.8-85.2)
	Decay class	1 (1-5)	2A (1-5)	2A (1-5)
	% alive	95.7 ± 2.1	89.2 ± 2.2	71.4 ± 5.1
	% Blistering	18.8 ± 2.3	26.5 ± 2.9	14.3 ± 5.5
Hybrid spruce	% Tree sp.	12.6 ± 1.7	12.2 ± 1.7	12.2 ± 6.0
	dbh (cm)	22.8 ± 1.6 (4.7-51.0)	30.9 ± 1.6 (13.4-58.5)	35.9 ± 3.7 (19.8-58.5)
	Decay class	1 (1-5)	1 (1-2B)	1 (1-2B)
	% alive	95.7 ± 1.8	100	100
	% Blistering	6.5 ± 2.1	15.6 ± 1.7	44.4 ± 4.8
Overall	% Tree sp.	81.8	93.5	94.7
	dbh (cm)	20.6 ± 0.8 (3.6-99.3)	35.7 ± 1.0 (4.5-108.0)	40.2 ± 2.1 (12.2-85.2)
	Decay class	1 (1-5)	2A (1-5)	2A (1-5)
	% alive*	94.9	94.9	90.5 ± 4.9
	% Blistering	21.6 ± 1.9	41.0 ± 2.0	40.5 ± 5.1

* The overall proportion of live used and available trees are the same because of the sampling design.

Table 2.6.

b) Princeton (IDF), *N = 8 birds*		Available	Foraging	Foraging ≥ 2x
		n = 286 trees	*n = 286 trees*	*n = 71 trees*
	Characteristics	Value ± SE (range)	Value ± SE (range)	Value ± SE (range)
Douglas-fir	% Tree sp.	70.3 ± 2.7	85.0 ± 2.1	85.9 ± 2.5
	dbh (cm)	26.2 ± 1.0 (8.1-75.0)	38.5 ± 0.8 (10.0-103.0)	37.8 ± 1.4 (11.0-58.9)
	Decay class	2A (1-4)	2A (1-4)	2A (1-2B)
	% alive	97.0 ± 2.6	98.8 ± 1.3	100
	% Blistering	41.3 ± 2.2	62.6 ± 1.1	65.6 ± 2.4
Ponderosa pine	% Tree sp.	29.0 ± 2.7	15.0 ± 2.1	14.1 ± 4.1
	dbh (cm)	27.4 ± 1.6 (8.4-66.9)	44.5 ± 2.6 (19.2-104.4)	50.0 ± 7.7 (27.1-104.1)
	Decay class	1 (1-5)	3 (1-4)	3 (3-4)
	% alive	65.1 ± 2.6	27.9 ± 4.9	0
	Blistering	4.8 ± 3.5	7.0 ± 1.1	10.0 ± 8.4
Overall	% Tree sp.	99.3	100	100
	dbh (cm)	26.6 ± 0.8 (8.1-75.0)	39.4 ± 0.8 (10.0-104.4)	39.5 ± 1.7 (11.0-104.1)
	Decay class	2A (1-5)	2A (1-4)	2A (1-4)
	% alive*	87.8	87.8	85.9 ± 2.5
	Blistering	30.4 ± 2.0	54.2 ± 1.0	57.7 ± 2.2

c) Merritt (IDF), *N = 5 birds*		Available	Foraging	Foraging ≥ 2x
		n = 118 trees	*n = 118 trees*	*n = 30 trees*
	Characteristics	Value ± SE (range)	Value ± SE (range)	Value ± SE (range)
Douglas-fir	% Tree sp.	58.8 ± 4.5	72.0 ± 4.1	59.4 ± 4.5
	dbh (cm)	23.2 ± 2.4 (4.5-107.2)	46.4 ± 2.3 (16.3-141.8)	52.0 ± 6.3 (26.0-141.8)
	Decay class	2A (1-5)	2A (1-3)	2A (1-2A)
	% alive	91.4 ± 4.8	97.6 ± 3.9	100
	% Blistering	31.4 ± 5.2	56.5 ± 2.0	57.9 ± 8.0
Ponderosa pine	% Tree sp.	24.4 ± 3.9	23.7 ± 3.9	34.4 ± 8.4
	dbh (cm)	31.4 ± 3.8 (4.5-85.5)	54.1 ± 3.2 (27.4-90.8)	57.2 ± 5.8 (30.8-90.8)
	Decay class	2A (1-5)	2A (1-4)	2A (1-4)
	% alive	69.0 ± 3.9	57.1 ± 3.6	54.5 ± 8.3
	Blistering	13.8 ± 4.6	3.6 ± 2.0	9.1 ± 8.0
Overall	% Tree sp.	83.2	95.7	93.8
	dbh (cm)	23.7 ± 1.8 (4.5-107.2)	47.2 ± 1.9 (16.3-141.8)	52.3 ± 4.4 (26.0-141.8)
	Decay class	2A (1-5)	2A (1-4)	2A (1-4)
	% alive*	85.9	85.9	81.3 ± 7.0
	Blistering	21.8 ± 4.3	40.5 ± 1.8	42.2 ± 7.6

* The overall proportion of live used and available trees are the same because of the sampling design.

Table 2.7. Candidate model sets in Akaike Information Criterion (AICc)-based model selection of live tree characteristic selection for foraging by 27 radio-tracked Williamson's Sapsuckers in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones, and overall, in southern British Columbia, Canada. The AICc is a measure of the quality of the model (goodness of fit) and models are ranked from lowest to highest ΔAICc - the difference in AICc values between model *i* and the top model in the candidate set. Wi is the probability of the model to be the best within the model set and the weight used to calculate weighted multi-model averaged parameters. Only the 95% confidence AICc model sets are presented and models that are ≤ 2 ΔAICc are bolded, having the most support. The Area Under the Curve (AUC) is a measure of performance for the model - a value of one indicates that the model can perfectly classify foraging trees and unused trees. Blistering includes resin exudation.

	Model variables	Rank	AICc	ΔAICc	W_i	W	AUC
a) MS zone (Oliver and O. Falls)	**Tree sp., dbh, blistering**	**1**	**499.9**	**0**	**0.43**	**0.43**	**0.78**
	Tree sp., dbh, blistering, boring insects	**2**	**500.2**	**0.3**	**0.37**	**0.8**	**0.78**
	Tree sp., dbh, blistering, boring insects, tree top condition	**3**	**501.5**	**1.6**	**0.19**	**0.99**	**0.78**
b) IDF zone (Princeton and Merritt)	**Tree sp., dbh**	**1**	**514.7**	**0**	**0.38**	**0.38**	**0.79**
	Tree sp., dbh, canopy cover	**2**	**515.8**	**1.17**	**0.21**	**0.60**	**0.79**
	Tree sp., dbh, ant nest	**3**	**516.0**	**1.30**	**0.20**	**0.80**	**0.79**
	Tree sp., dbh, decay class, canopy cover	4	517.6	2.96	0.09	0.89	0.79
	Tree sp., dbh, ant nest, blistering	5	518.0	3.33	0.07	0.96	0.79
c) Overall	**Tree sp., dbh, blistering, boring insects**	**1**	**1067.5**	**0**	**0.39**	**0.39**	**0.77**
	Tree sp., dbh, blistering	**2**	**1068.4**	**0.9**	**0.25**	**0.64**	**0.77**
	Tree sp., dbh, ant nest, blistering, boring insects	**3**	**1068.8**	**1.23**	**0.21**	**0.85**	**0.77**
	Tree sp., dbh, ant nest, blistering, boring insects, burn	4	1070.4	2.84	0.09	0.95	0.77

Table 2.8. Relative influence (W_+), multi-model averaged parameter estimates (β) and odds ratios (with 95% confidence intervals) of variables in the 95% confidence set of generalized linear mixed-effects models used to identify important characteristics of live trees for foraging by 27 radio-tracked Williamson's Sapsuckers in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones, and c) overall. Variables are considered significant (bolded) when the 95% confidence intervals on their parameter estimates do not overlap zero and the 95% confidence intervals on their odds ratios do not overlap one. Variables with a negative effect are italicized. Decay class and signs of decay were fitted in exclusive models to avoid collinearity. Only signs of decay that were present on at least 5% of the foraging trees were fitted.

Parameter	W_+	β (95% conf. Int.)	SE	Odds ratio (95% conf. Int.)
a) MS zone				
Intercept	***0***	***-2.17 (-2.94 - -1.39)***	***0.39***	***0.11 (0.05-0.25)***
Douglas-fir*	**1**	**0.88 (0.20 - 1.55)**	**0.34**	**2.41 (1.22-4.71)**
Western larch	1[†]	0.49 (-0.36 - 1.35)	0.44	1.63 (0.70-3.86)
Hybrid spruce	1[†]	0.82 (-0.07 - 1.73)	0.46	2.27 (0.93-5.64)
dbh (cm)	**1**	**0.05 (0.03 - 0.06)**	**0.08**	**1.05 (1.03-1.06)**
Blistering and resin	**0.99**	**0.82 (0.34 - 1.29)**	**0.24**	**2.27 (1.40-3.63)**
Boring insects	*0.46*	*-0.65 (-1.63 - 0.32)*	*0.50*	*0.52 (0.20-1.38)*
Top condition	0.39	0.33 (-0.39 - 1.06)	0.37	1.39 (0.68-2.89)
b) IDF zone				
Intercept	***0***	***-3.93 (-4.98 - -2.88)***	***0.54***	***0.02 (0.01 – 0.06)***
Douglas-fir*	**1**	**1.83 (1.11- 2.54)**	**0.36**	**6.23 (3.03 – 12.68)**
dbh (cm)	**1**	**0.07 (0.05 – 0.09)**	**0.01**	**1.07 (1.05 – 1.09)**
Decay 2A	0.78	0.12 (-0.58 – 0.34)	0.24	1.13 (0.56 – 1.40)
Blistering and resin	0.16	0.04 (-0.43 – 0.51)	0.04	1.04 (0.65 – 1.67)
Ant nest	0.26	0.69 (-0.92 – 2.29)	0.69	1.99 (0.40 – 9.87)
Canopy cover (%)	0.36	0.006 (-0.006 – 0.02)	0.006	1.00 (0.99 – 1.02)
c) Overall				
Intercept	***0***	***-2.22 (-2.78 - -1.66)***	***0.28***	***0.11 (0.06 – 0.19)***
Douglas-fir	**1**	**0.72 (0.17 – 1.28)**	**0.28**	**2.05 (1.19 – 3.60)**
Western larch	1[†]	0.56 (-0.19 – 1.3)	0.38	1.75 (0.83 – 3.67)
Hybrid spruce	1[†]	0.80 (-0.01 – 1.61)	0.41	2.23 (0.99 – 5.00)
Ponderosa pine	*1*[†]	*-0.82 (-1.71 – 0.07)*	*0.45*	*0.44 (0.18 – 1.07)*
dbh (cm)	**1**	**0.05 (0.04 – 0.06)**	**0.01**	**1.05 (1.04 – 1.06)**
Blistering and resin	**1**	**0.47 (0.15 – 0.79)**	**0.16**	**1.60 (1.16 – 2.20)**
Boring insects	*0.73*	*-0.59 (-1.26 – 0.08)*	*0.34*	*0.55 (0.28 – 1.08)*
Ant nest	0.44	0.62 (-0.77 – 2.01)	0.62	1.86 (0.46 – 7.46)
Burn	0.31	0.23 (-0.45 – 0.90)	0.35	1.26 (0.64 – 2.46)

* Reference levels (intercepts) of the tree species factor were the avoided tree species group (MS zone: lodgepole pine and deciduous trees; Princeton: ponderosa pine and deciduous trees; Overall: deciduous trees).

[†] The weight of the variable in the 95% confidence set (W_+) is calculated for the tree species categorical variable, of which each tree species is a level.

Table 2.9. Differences in characteristics of trees that were used once or reutilized (≥ 2X) in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones. I used Mann-Whitney-Wilcoxon tests (W; nonparametric) and χ^2 tests. Significant differences are bolded. Lw = western larch, Py = ponderosa pine.

Biogeoclimatic zone		$\bar{x}$ ± SE				
	Tree characteristic	Used 1X	Reused ≥ 2X	χ^2 (W)	df	P
MS zone	**dbh**	**35.7 ± 1.0**	**40.2 ± 2.1**	**(8245.5)**	**1**	**0.001**
n = 294 used 1X,	% dead tree	4.1 ± 2.1	9.5 ± 11.1	NA*	NA	NA
74 reused	% Western larch	21.1 ± 2.3	29.7 ± 4.8	2.04	1	0.15
IDF zone	dbh	41.1 ± 0.9	43.5 ± 1.9	(14696)	1	0.43
n = 301 used 1X,	% dead tree	11.3 ± 2.7	15.5 ± 7.9	0.91	1	0.34
103 reused	% Ponderosa pine	16.6 ± 2.8	20.4 ± 6.5	0.52	1	0.47
Overall	**dbh**	**37.8 ± 0.7**	**42.2 ± 1.4**	**(44364)**	**1**	**0.001**
n =772 used 1X,	**% dead tree**	**7.7 ± 1.6**	**13.0 ± 5.7**	**4.02**	**1**	**0.04**
177 reused	% Lw+Py	19.2 ± 1.7	24.3 ± 3.6	1.91	1	0.17

* The proportions of dead trees in the Montane Spruce zone could not be tested because of low sample size.

Chapter 3 - Selection of forest stand-level composition, structure and configuration for foraging and nesting of Williamson's Sapsuckers.

3.1 Introduction

Birds that are foraging in forest habitats are expected to cue on (forest) stand characteristics that are associated with high concentrations of preferred foraging substrates (feeding sites) and adequate environmental conditions for prey items. For forest bird species, key characteristics of stand-level foraging habitat 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). In forest management, 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). Stands and forest patches are often used as similar concepts, therefore to avoid confusion I only use the word "patch" in the context of subsections of stands that are used by birds - the foraging and nest patch. Partial logging is one way of managing stands, whereby groups of trees called retained groups, are left unharvested (Franklin *et al.* 1997). Habitat selection studies at the stand scale can inform forest management on stand-level foraging habitat characteristics, assuming that birds select habitats (stand characteristics) that increase their fitness (Hall *et al.* 1997). Stand characteristics that are selected in higher proportion than their availability by a bird species are considered preferred (Johnson 1980) and, in most cases, represent high quality habitat. The main driver in stand-level foraging habitat selection is the concentration of food resources (foraging substrates), but other factors might be influential such as concealment, avoidance of competition and proximity to nesting site (Orians and Pearson 1979, Lima and Dill 1990).

The distribution of groups of trees can affect the quality of foraging opportunities for birds. Optimal foraging theory predicts that birds maximize their fitness by choosing resources that provide high food intakes with low constraints such as travel distance (Schoener 1971). Central place foraging theory predicts that birds are more likely to be affected by the distribution of foraging patches when they are breeding (and subject to the spatial constraints of returning to a nest) than when they are not breeding (Orians and Pearson 1979). According to central place foraging theory, breeding birds should select nest sites with nearby foraging areas in a circular distribution around the nest to minimize travel distances. Flight cost and travel distances to foraging patches determine the profitability of foraging and transporting food over a certain distance, and can make provisioning from distant patches economically unsustainable (Pennycuick *et al.* 1984). Birds that must travel longer distances during the nestling stage can suffer from a decrease in reproductive success (Ens *et al.* 1992, Frey-Roos *et al.* 1995, Boersma and Rebstock 2009).

Stand-level configuration characteristics are key elements in maintaining foraging habitat for species of conservation concern. I refer to stand configuration characteristics as the spatial arrangement of resources (trees) within stands (*e.g.*, open, dispersed and agglomerated). The spatial arrangement of stands and groups of trees determine the amount of edges and gaps (open areas) that can influence the quality of foraging habitat for birds (Turchin 1998). An edge effect element occurs at the interface of two ecosystems that strongly contrast in composition and structure – such as where clear-cuts adjoin old forest (Matlack and Litvaitis 1999). Abiotic conditions (*i.e.*, temperature, humidity and exposure to light and wind) can differ between forest edges and the rest of the stand (Esseen and Renhorn 1998, Rheault *et al.* 2003, Esseen 2006). Such altered microclimate can change the composition of understory plant and insect communities, affecting foraging opportunities for birds (Whitcomb *et al.* 1981, Harper and Macdonald 2001). Small gaps in the forest can benefit certain bird species; however, others avoid gaps by moving in forested areas when possible (Bélisle and Desrochers 2002). Gap avoidance may be linked to avoidance of increased predation risk, limitations in perceptual range at which birds can identify habitat and the absence of adequate forested habitat used for foraging and perching (Lima and Zollner 1996).

Birds that nest in cavities (cavity nesters) are among the most sensitive bird species to forest management, because they use trees for nesting and, in many cases, foraging (Imbeau *et al.* 2001). 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 (Berg *et al.* 1994, Imbeau *et al.* 2001). Stand-level forest management that favours woodpecker species is gaining popularity 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, Drever *et al.* 2008). In North America, the cavity nester community includes approximately 85 species of birds such as some passerines, ducks, diurnal raptors and owls, and managing forest management practices that benefit woodpecker species are likely to benefit the entire community (Scott *et al.* 1977).

Sapsuckers (*Sphyrapicus sp.*), a group of woodpeckers, are best known for their sap feeding behaviour, even though they also glean insects (mostly ants) on the trunk of trees, peck in wood for subcortical larvae and consume fruits and seeds (Tate 1973, Crockett 1975, Morrison *et al.* 1987). Information on stand-level foraging habitat characteristics of sapsuckers comes primarily from studies using nesting territory occurrence rather than direct foraging observations to determine habitat preferences. Stand-level habitat selection for foraging habitat varies with species, ranging from preferences for young forest (Yellow-bellied Sapsuckers [*S. varius*; Tozer *et al.* 2012]) to mature forest (Red-breasted Sapsuckers [*S. rubens*; Kissling and Garton 2008]). Sapsucker species also vary in their responses to changes in stand configuration and foraging patch distribution caused by logging, although the number of studies is limited. Stand configuration does not seem to influence foraging behaviour for Yellow-bellied Sapsuckers, the best-studied sapsucker. Foraging trip orientation, provisioning bolus size and provisioning rates did not differ between pairs of Yellow-bellied Sapsuckers nesting in managed forest (linear forested strips between harvested strips) and those nesting in unharvested continuous mixed forest (Bédard 2013). Also, the distances from the nest and characteristics of sap trees did not differ between unmanaged and partially logged (20-30% of trees harvested) stands (Mancuso *et al.* 2014). Conversely, nests of Red-breasted Sapsuckers were found only in buffers of mature forest ≥ 100 m wide in managed coastal rainforest, suggesting that large stands of contiguous mature forest are likely required for foraging (Kissling and Garton 2008).

Williamson's Sapsuckers (*S.thyroideus* [WISA]) have been designated as Endangered in Canada under the Species at Risk Act (SARA; 2006) and are Blue-listed in British Columbia (BC Conservation Data Centre 2015), because they breed at the northern periphery of their range and habitat alteration caused by human activities (primarily logging) could affect the already low population numbers. WISA are the least studied of the sapsuckers because they are found only in montane forests that often have limited road access.

The number of studies on stand-level habitat selection, including composition, structure, distribution of foraging patches and within-stand configuration is limited for Williamson's Sapsuckers. Drever *et al.* (2015) used stand-level characteristics to predict WISA nesting territory occurrence, assuming that WISA select their nest locations according to nesting requirements, but also quality of foraging habitat. Overall, nesting territory occurrence was best explained by stand characteristics that are directly related to the presence of suitable nest trees, however some characteristics were linked to potential foraging opportunities such as densities of very large stumps and large hybrid spruce trees (*Picea engelmannii* X *Picea glauca*), surface area of 80-119 years old Douglas-fir dominated stands (*Pseudotsuga menziesii* var. *Glauca*) and crown closure of

>15m tall trees. One of the limitations of the Drever *et al.* (2015) study was that it was not able to make a clear distinction between nesting and foraging habitat. The productivity of late-stage nests was significantly lower in nesting territories with tree densities of < 85 live trees/ha, suggesting that foraging habitat could be insufficient below this threshold (Gyug *et al.* 2010). Coarse woody debris and stumps are possibly a key element of WISA habitat since they are required by colonies of the two ant groups that are preferred by WISA, *Camponotus spp*. and *Formica rufa sp*. group (Gyug *et al.* 2014b). Only two studies on WISA have addressed spatial use of habitat, and these provide insights on the importance of foraging patch distribution. Gyug *et al.* (2007) used the mean distance to the nearest-neighbour to infer that WISA home ranges probably extend to a radius of 225 m around the nest. Also, one radio-tagged male WISA had a home range of 54.2 ha and was detected at a maximum distance of 500 m from the nest (Manning and Cooper 1996). Habitat selection of within-stand configuration characteristics for foraging have yet to be studied. However, WISA nesting territory occurrence has been associated with forests disturbed by fire (Hutto *et al.* 2015, Hutto and Patterson 2016) and logging (Whitcomb *et al.* 1981, Keller 1992, Drever *et al.* 2015), suggesting that stand configuration characteristics such as presence of forest edge might be preferred for nesting or foraging.

A study on WISA foraging habitat selection at the stand level is required to provide tools for forest managers and to fill current knowledge gaps regarding critical habitat, as outlined by the WISA Recovery Strategy (Environment Canada Recovery Strategy 2014). A study on the selection of stand-level characteristics, such as tree and stump densities and CWD volumes, is needed to facilitate the connection between previous studies on foraging substrate selection (tree level) and landscape-level nesting territory selection, giving a more comprehensive portrait of the foraging ecology of WISA. Data on foraging trip distances, using quantitative observations, are required to promote more effective design of conservation 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 WISA foraging habitat.

3.2 Objectives

In this chapter, I use observations of radio-tracked birds to identify the characteristics of forest stands that should be considered by forest managers to conserve WISA foraging habitat. I have three objectives related to WISA 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 WISA and propose conservation and management zones to protect active breeding habitat and 3) evaluate the selection of within-stand configuration characteristics for foraging. Questions 2 and 3 focus on the nestling stage because foraging patch distribution and stand configuration are most likely to affect birds at this stage, when they must return frequently to the nest to feed nestlings.

3.3 Methods

3.3.1 Sites, capture and telemetry

I monitored Williamson's Sapsucker foraging trips and movement during the breeding season at four sites in managed landscapes (two in each of two Areas of Occupancy or biogeoclimatic zones) in 2014 and 2015 (see Chapter 1 General Methods section for details). The Oliver (2014) and Okanagan Falls (2015) sites were located in the Montane Spruce biogeoclimatic zone (MS zone), and the Princeton (2014) and Merritt (2015) sites were located in the Interior Douglas-fir biogeoclimatic zone (IDF zone). All sites contained a proportion of protected intact forest, older clear-cut (≥ 20 years old), stands that have been affected by an insect outbreak (likely mountain pine beetle), forestry and paved roads, clearings for powerlines or pipelines (except Okanagan Falls) and history of low to moderate intensity wildfire (BC Vegetation Resource Inventory [VRI, 2016], Les Gyug [Okanagan Wildlife Consulting], Brian Drobe [Weyerhaeuser Company], pers. comm.). Recent clear-cuts (< 20 years old) were only present at the sites in the MS zone (Oliver and Okanagan Falls), and partial harvesting (with retained groups) were only present at the Okanagan Falls site. I located breeding adults using call-playbacks and a database of WISA detections in recent years (Gyug *et al.* 2014a). I caught adults during the pre-incubation until mid-nestling stage using 1) a combination of mist-nets, call-playbacks and a male decoy as a lure, 2) dip nets and 3) aerial mist-nets supported by poles (up to ~9m; see General Methods section for details). I banded WISA with a numbered aluminium and three coloured plastic bands and I sutured a radio-transmitter (BD-2, 1.2g, detection range 1 km; Holohil systems, Ltd., Carp, Ontario, Canada) to the two central rectrices following Tremblay *et al.*, (2009). I monitored nest contents to confirm nest status, using a camera mounted on an extendible pole (maximum height 14m).

I radio-tracked foraging adults during bouts of 0.5 to 4 hours during all time periods of the day (morning, afternoon and evening) and tried to obtain visual observations of their behaviour, following a homing tracking protocol (Mech 1983). I 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 I lost the signal, noting the distance. Detection range was on average 427 ± 182 m (range = 160-592 m) and seemed to vary with the terrain conditions. Also, I tried occasionally to detect radio-transmitters that had been deployed on birds at far away distances and once obtained a signal from a lower elevation (~ 100m) over a partially open area at 1.1 km from the nest tree of the nestling-feeding adult (likely to be around the nest). Most of the relocations were associated with a behavioural observation (62% of total). However, in some cases a spatial relocation (GPS point; 38% of total) was recorded if the observer could identify the tree or group of trees that the bird used based on observations of a WISA in flight, auditory cues (pecking, calls, etc.) or a strong and clear telemetry signal for several minutes.

3.3.2 Sampling of stand characteristics

I sampled the characteristics of used and available stands in sets of two circular nested plots of 9.77 m radius (0.03 ha) and 17.84 m radius (0.1 ha). I recorded the number of all standing (alive and dead) trees by species according to the following: 22.5-57.4 cm diameter at breast height (dbh) live trees and 22.5 cm diameter at stump height (dsh) stumps (in the 0.03 ha plot), ≥ 57.4 cm dbh live trees and ≥ 22.5 cm dbh dead conifer trees (in the 0.1ha plot; Figure 3.1). Also, I measured coarse woody debris ≥ 7.5 cm diameter at intersect (CWD) in 2 X 11.28 m line transects, following the Vegetation Resources Inventory Ground Sampling Procedures of the British-Columbia Ministry of Forests and Range (2007). The “used” plots were centered on a used substrate (tree: n = 47, fallen log: n = 1) to overlap with the highest concentration of behavioural observations, representing the foraging patches that were used the most often in each nesting territory. The plots representing “available” habitat were paired with nested plots for used habitat and positioned systematically in a way not to overlap with any WISA detections (visual or foraging sign), at the same distance from the nest as the paired nested plot for used habitat, in a random direction and centered on the same substrate type (*i.e.,* tree or fallen log). I sampled two to four and six to ten nested plots and CWD transects per territory in 2014 and 2015, respectively. I sampled only two plots per nesting territory (used and available) in 2014 originally, but increased to four for the nesting territories on the Princeton site during the spring of the following year (the habitat was comparable to 2014). In 2015, six plots were measured 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 nested plots were measured in a territory, I positioned one pair of plots in the nest patch (< 60m from nest; used and available) and another at the furthest relocation where a visual detection occurred, while I positioned the remaining in between, in the nesting territory of the birds. I positioned one plot at the furthest (most distant) relocation, assuming that central place foraging birds will travel long distances only if the benefits of the foraging patch can overcome the energetic costs of travelling.

I converted the sampled densities of trees and stumps to get a count per one hectare, by multiplying the count by the conversion factor that is specific to each plot size. I calculated the volume-density of CWD (m^3/ha) in the plots from the two transect lines, using the formula $y_i \left(\frac{m^3}{ha}\right) = \frac{\pi^2}{8 \times L} \times \sum_{j=1}^{m_i} {d_{ij}}^2$, where L is the length of the transect (11.28 x 2 = 22.56 m) and d_{ij} is the diameter at intersect of each CWD pieces that 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. I excluded all bark pieces and live downed trees to obtain an estimate of dead wood volume per hectare for each tree species (logs and branches), as a proxy for potential ant nesting habitat.

3.3.3 Characterization of stand configuration

To estimate the availability of predefined stand configuration categories in WISA nesting territories, I created a polygon layer using ArcGIS 10.2.2 (ESRI, Redlands, California, United-States) 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, United-States), 2) a GIS database on stand characteristics maintained by the British Columbia Ministry of Forests, Lands and Natural Resource Operations (VRI), and 3) ground validation. I 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. I delimited stands based on the distribution of trees, dividing them into five categories: 1) Areas of open habitat and 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 10% crown closure with trees clustered in groups (natural or because of logging), 3) forest edges, which was continuous forest within 15m from an open area, 4) open stands, which was contiguous forested areas with ≤ 30% crown closure with trees in a scattered configuration (usually not clustered; determined with VRI data) and 5) closed stand, which was contiguous forested areas with > 30% crown closure (determined with VRI data). To characterize the spacing of retained groups, I measured the smallest distance between two randomly selected distinct adjacent non-contiguous groups and calculated the mean and standard error (n = 20 comparisons). All stands were dominated by

Douglas-fir, western larch (*Larix occidentalis*) or ponderosa pine (*Pinus ponderosa*). I excluded from the layer, paved roads (never used by WISA) and stands that were dominated by lodgepole pine (*Pinus contorta*; 2 uses out of 358), because they were different from other categories and had low use. I calculated the availability of each stand configuration category, for each nesting territory of radio-tracked birds, using a buffer corresponding to a distance from the nest that I determined during the foraging trip distance analysis (95th percentile, more details in results section), in each biogeoclimatic zone.

3.3.4 Statistical analysis

Selection of stand-level composition and structure for foraging

I identified the relevant stand-level characteristics of foraging patches by comparing used patches (nested plots) to available patches (unused) in the MS and IDF biogeoclimatic zones separately, since the composition of tree species in stands differed. I 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. Mixed-effects models incorporate both fixed effects, which explain variation in the response variable, and random effects, which serve as additional error terms to account for correlations among plots from the same nesting territory (lme4 package in R; Gillies *et al.* 2006, Bates *et al.* 2015). The variables that are more likely to influence foraging patch selection by Williamson's Sapsuckers were determined *a priori* from all the stand-level variables measured, based on the tree-level preferences identified in Chapter 2. I used six explanatory variables (fixed effects) representing the density of: 1) very large Douglas-fir, 2) large Douglas-fir, 3) western larch (MS zone) or ponderosa pine (IDF zone), 4) dead standing trees, 5) stumps and 6) the volume-density of CWD. Density of live and dead trees and stumps included trees with $\geq$ 22.5cm dbh (dsh for stumps), except for live Douglas-fir, which is divided in two categories large (22.5-57.4cm dbh) or very large ($\geq$ 57.5cm dbh). Hybrid spruce was pooled with Douglas-fir and included in a separate analysis, but the outcome was qualitatively the same, therefore I excluded it to reduce potential noise in the data and because it was present in four plots only. I divided the six explanatory variables by one hundred before fitting the data to avoid convergence problems due to high eigenvalues, and divided the model outputs by the same number (one hundred) when I presented them. I 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. I used a Pearson's correlation matrix to assess collinearity across variables, considering $r \geq 0.70$ as correlated.

Using backward stepwise model selection, I removed the least significant variables one by one until I obtained a model that included only significant variables. I identified the most parsimonious models using the Akaike Information Criterion corrected for small sample sizes (AICc) 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, I used multi-model averaging to calculate the averaged-weighted parameters of the variables (Burnham & Anderson 2004). I 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 in 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 WISA foraging patches, while a value of 0.5 indicates that the model performs equivalently to a random classification (Hanley and McNeil 1982). I 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 sampled tree density (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. I did not estimate thresholds using model-based techniques, taking into account the probability of foraging occurrence, because the probability of occurrence was set to 0.5 by my used-available sampling design (see Guénette *et al.* 2005, Toms *et al.* 2015). As a post-hoc analysis, I used t-test to evaluate the potential differences in the availability of trees of $\geq$ 22.5cm dbh between the MS and IDF zones to compare the two habitat types.

Tree density in foraging and nest patches

I used multiple analysis of variance (MANOVA) tests to compare the stand characteristics between nest patches ($\leq$ 60 m from nest) and foraging patches (> 60 m from nest) to test the hypothesis that Williamson's Sapsuckers select nest patches based on foraging opportunities. MANOVAs are appropriate to compare the sample means of multiple numerical dependent variables between two different groups (independent variable; Bock and Haggard 1968). The independent variable was whether the plot was in the nest patch (0) or used for foraging further in the nesting territory (1). Tree density of nest patches was represented by nested plots centered on trees that were used or not (available) for foraging, located within 60 m from the nest tree. Foraging patches were located in the rest of the nesting territory (> 60m from the nest tree). I assumed that plots of used and unused habitat within the nest patch represented the nest patch adequately, even though they were not randomly distributed. The *a priori* selected dependent variables were: density of large Douglas-fir, density of very large Douglas-fir, density of dead conifer trees and total tree density (trees/ha). The total tree density includes all tree species, such as Douglas-fir, western larch, ponderosa pine, hybrid spruce, lodgepole pine, trembling aspen (*Populus tremuloides*) and water birch (*Betula occidentalis*). Trees of < 22.5cm dbh were excluded from the analysis because they are not considered a preferred foraging tree and are not likely to influence the nesting environment (*e.g.*, nest cavity concealment) because of their low height. I 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). There was a departure of the assumption of independence across observations of MANOVA tests, since a mean of 2.8 pairs of used and available plots (range = 1-5) were measured 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 (Dixon 2003). An alpha level of 0.05 was used and significance means that the covariance matrices are different, causing a departure from homogeneity. I 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. If the MANOVA test revealed a difference between nest patches and foraging patches, I tested the density of different types of trees using one-way ANOVA tests. To counteract the problems associated with multiple testing, I applied a Bonferroni correction on the alpha threshold for significance of the T-tests by dividing it by the number of comparisons (m).

Foraging distances

I examined the distances from the nest at which WISA were detected to obtain an estimate of the area in which WISA travel for foraging during the nestling stage. I only used relocations that were statistically independent, determined using the time to statistical independence (TTSI) tool in the rhr package in R (Signer and Balkenhol 2015). The TTSI tool calculates the time interval at which the spatial autocorrelation between two subsequent relocations becomes negligible (calculations presented in Swihart and Slade 1985). The TTSI were calculated for each bird (N = 20), but I used the mean value for each biogeoclimatic zone (MS zone: mean ± SE = 31.7 ± 10.8 minutes, range = 9.3-93.1 minutes; IDF zone: mean ± SE = 37.3 ± 13.8 minutes, range = 3.1-111.1 minutes). I calculated the Euclidian distances from the nest of the statistically independent WISA foraging trips using UTMs (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. I plotted the trip distances against the percentiles and used the 50th, 90th and 95th percentiles to support recommendations for nest reserve zone and nest management zones to protect active and recent nesting territories. These percentiles are commonly used in studies that are reporting home range sizes and utilization distributions (e.g. Ostfeld 1986, Murgatroyd *et al.* 2016). I also verified, using the plot, that there were no important distance gaps ($\geq$ 50m) between consecutive percentiles within the recommended distances.

Selection of stand-level configuration for foraging

To evaluate the selection of stand configuration, I calculated selection ratios ($\hat{W}i$, Design III for census of available resource units; Manly *et al.* 2002), using the statistically independent WISA relocations combined by nesting territory (use: n_{μ}) and the GIS layer of stand configuration categories (availability: π_{ij}). I considered stand configuration categories to be preferred (value > 1) or avoided (value < 1) when the 95% confidence interval of the selection ratio did not overlap one, which would mean that proportions of use equal availability (Manly *et al.* 2002). I compared the values of the selection ratios with Bonferroni-corrected χ^2 tests for multiple comparisons ($\alpha = 0.05$). As a post-hoc analysis, I 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 Montane Spruce and Interior Douglas-fir zones to compare the two habitat types. For all analyses, I first considered the data for each biogeoclimatic zone separately and then pooled them if the patterns were qualitatively the same. I also described qualitatively the gap-crossing behaviour (crossing of open habitat) of WISA during foraging trips. I obtained a threshold of the proportion of open and single trees habitat area at which the selection of higher tree densities ($\geq$ 22.5cm dbh) in foraging plots becomes more important. I identified the threshold fitting a Locally Weighted Least Squares Regression (LOESS) curve to a scatter plot of the mean density in foraging plots per nesting territory. The LOESS curve is a non-parametric locally-weighted regression line that provides more flexibility than a parametric regression, not being limited by an assumed distribution (Atkeson *et al.* 1997). All the analyses in this chapter are for adult WISA that were feeding nestlings (nestling stage) except for the stand characteristics analysis (GLMM) which included nested plots measured for three non-breeding males and one for which I only have pre-nestling stage data.

3.4 Results

3.4.1 Selection of foraging patch characteristics

To characterize stands, I measured 48 sets of nested plots that were centred on a foraging tree used by Williamson's Sapsuckers during all nesting stages (foraging patch; $\bar{x}$ ± SE = 2.9 ± 1.0 relocations, range = 1-8 relocations), and 48 sets of nested plots that were centered on a tree for which I observed no WISA, or sign of use (available patch; Table 3.1). In the Montane Spruce zone, no model explained the selection of stand-level characteristics by WISA significantly better than the null model ($\leq$ 2 ΔAICc, Table 3.2). Multi-model averaging revealed no significant habitat variables at the stand level in the MS zone, although CWD volume (m^3/ha) almost had a significant positive effect (Table 3.3, Figure 3.2). In the IDF zone, two models best predicted WISA foraging at the stand level, the three influential variables being density (trees/ha) of large live Douglas-fir (22.5-57.4 cm dbh), density of very large live Douglas-fir ($\geq$ 57.5 cm dbh) and density of dead conifer trees ($\geq$ 22.5 cm dbh; $\leq$ 2 ΔAICc, Table 3.2). The odds of a foraging patch being used increased with each increase of one tree in density for large live Douglas-fir (0.7%), very large live Douglas-fir (9.4%) and dead conifer trees (4.4%; Table 3.3, Figure 3.2). Although the effect of dead conifer density was not significant, I suggest considering their importance because foraging patches that did not contain $\geq$ 22.5cm dbh live Douglas-fir contained high densities of dead conifer trees (Figure 3.3). The bootstrapped mean densities 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. Mean densities of used plots should become the retention targets, keeping in mind that heterogeneity is required and that there is a cumulative effect of the presence of these three elements (Figure 3.3). The overall densities of $\geq$ 22.5cm dbh standing trees in available habitat did not differ between the MS and IDF biogeoclimatic zones, however WISA selected denser foraging patches (by 115.5 trees/ha on average) in the Interior Douglas-fir zone than in the Montane Spruce zone (Table 3.4).

3.4.2 Tree density in foraging and nest patches

I assessed whether Williamson's Sapsuckers select nest patches (patch characteristics measured $\leq$ 60 m from nest) based on characteristics that are related to foraging opportunities using MANOVA tests. The homogeneity in variance assumption was respected in both biogeoclimatic zones (MS zone: F = 0.0021 and p = 0.96; IDF zone: F = 1.11 and p = 0.30), however there was a departure from the multivariate normal assumption. In the Montane Spruce zone, nest patch ($\leq$ 60 m) characteristics did not differ from foraging patches that were in the rest (> 60 m) of the nesting territory (F = 0.50 and p = 0.73; Table 3.5). In the Interior Douglas-fir zone, WISA selected nest patches that had a lower mean density (231.7 trees/ha of trees $\geq$ 22.5 cm dbh of all species; Douglas-fir = 90%) than the foraging patches (Figure 3.4). When pooling both biogeoclimatic zones, a non-significant trend suggests that nest patches had lower mean density of trees than the foraging patches overall (F = 2.42, p = 0.06).

3.4.3 Foraging distances

To describe foraging trip distances, I used 358 WISA relocations that were considered statistically independent (no spatio-temporal correlation) from 20 birds that were feeding nestlings. Of the total number of relocations, 209 (58%) were based on visual observations (96% were foraging observations including 59% gleaning, 23% sap feeding, 18% pecking), the remaining 42% were spatial relocations (foraging or other behaviour unknown). WISA that were feeding nestlings were detected more often foraging in the distance category between 50m and 150m from the nest in the MS zone (49% of total relocations) and 0 to 100m in the Interior Douglas-fir zone (38% of total relocations), respectively (Figure 3.5). The farthest distance from the nest at which I observed WISA was 556 m in the MS zone and 831 m in the IDF zone. Considering that foraging trips of the last ten or five percentiles were unusual (cut-offs = 90th and 95th percentiles), the area used by WISA extended from 300 to 340 m radius (28 to 36 ha) from known nest trees in the MS zone and 340 to 410 m (36 to 53 ha) in the IDF zone (Figure A2.1). About half of the relocations were included in the first 140 m (6.2 ha) from the nest in the MS and IDF biogeoclimatic zones (MS zone: 53th percentile, IDF zone: 50th percentile; core areas).

3.4.4 Stand configuration for foraging

With Montane Spruce and Interior Douglas-fir zones combined, or analysed individually, WISA significantly avoided areas of open habitat and single tree (30% use of available area; Figure 3.6, Table 3.6). Areas containing retained groups were preferred in the MS zone, although the preference was non-significant, because of large 95% confidence intervals that could be explained by the low number of nesting territories containing retained groups (n = 2 territories; Figure 3.7d). The mean minimal distance between retained groups was 16.4 m ± 0.9 m (range = 2-54 m). In the Interior Douglas-fir biogeoclimatic zone, forest edges and stands with > 30% crown closure were significantly preferred, 65% and 15% more often than available, respectively. Stands with > 30% crown closure were the most used stand configuration category overall with 195 foraging uses. The proportion of open and single tree area was 21% higher on average in nesting territories of the IDF zone compared to the MS zone, as the IDF zone contained more area of open habitat and single trees (t = 6.89, p = 0.003). The longest crossing of open and single trees area in the MS zone was 174 m across a 5.9 ha seed tree cut, one which WISA were only seen crossing on the way back to the nest after foraging on the other side several times (Figure 3.7a). In the IDF zone, the longest crossing of open and single trees area was 160 m across a 12.1 ha pasture, which was crossed in both directions every time WISA foraged on that side of the territory (Figure 3.7g). For this opening, there was no possibility of using forest edges to go around, forcing the crossover, as the opening extended almost beyond the limits of the nesting territory on either side. In nesting territories with ≥ 17% open and single trees, WISA seemed to select foraging patches with higher tree densities (Figure A2.2).

3.5 Discussion

This study was the first to investigate the selection of stand-level characteristics, including composition, structure and configuration, for foraging by Williamson's Sapsuckers using observational data. I did not find any forest stand characteristics significantly associated with WISA foraging or nesting in the MS zone. Conversely, WISA preferred foraging patches with high densities of foraging substrates in the IDF zone (≥ 22.5cm dbh large live Douglas-fir and large dead conifer trees). In both biogeoclimatic zones, nest patches tended to have lower densities of large trees (≥ 22.5cm dbh) than foraging patches, with a larger and significant difference in the IDF zone. WISA feeding nestlings were relocated 50% of times within 140m of their nest (core area) and 95% of relocations within 340 m (MS zone) and 410 m (IDF zone). In both biogeoclimatic zones, open and single tree areas were avoided, while forest edges and forest with >30% crown closure were preferred in the IDF zone. There was a higher proportion of open and single tree areas in the IDF zone compared to the MS zone, but foraging patches had higher densities of large trees.

Multi-scale habitat selection may involve hierarchical selection patterns in which birds select habitat from broad to fine scales (top-down; Mayor *et al.* 2009). Studies of multi-scale habitat selection showed that woodpeckers can forage in hierarchical patterns selecting foraging patches first, and then foraging substrates (Hutto 1985). For example, Black-backed Woodpeckers (*Picoides arcticus*) selected foraging patches with high tree densities before selecting foraging trees with larger diameter within those patches (Dudley *et al.* 2012). My results showed that WISA select foraging patches with higher tree density in the IDF, but not the MS zone, while preferences at the foraging substrate level were detected in both biogeoclimatic zones (MS and IDF; Chapter 2). Contrary to what was expected in the MS zone, WISA may have selected foraging habitat in a non-hierarchical pattern, meaning that the foraging substrates (trees) are selected regardless of foraging patch characteristics. In the IDF zone, WISA possibly selected foraging resources in a hierarchical pattern by selecting foraging patches with high concentrations of foraging substrates (trees), before selecting individual foraging substrates.

Patches with higher concentration of foraging substrates (benefit) are selected by central-place foraging birds to compensate for increasing travel distance to foraging sites (cost; Orians and Pearson 1979, Cezilly and Benhamou 1996). The nesting territories in the IDF zone contained higher proportions of open habitat (non-foraging) and thus longer foraging trips were necessary compared to the MS zone. WISA may select foraging habitat in a hierarchical pattern to compensate for the cost of increased travel distances caused by higher proportions of non-foraging area. Hierarchical habitat selection could represent an adaption of WISA to survive and reproduce in heterogeneous nesting territories that contain high proportions of open non-foraging habitat and fragments of suitable foraging habitat. This relationship would need to be examined further, incorporating more data to relate foraging distance to multi-scale habitat characteristics.

In a previous study, CWD and stumps were identified as important for the ant species consumed by WISA (Gyug et al 2014b). My results did not support the hypothesis that CWD and stumps are important for WISA foraging, because abundance of CWD and stumps were not significant variables in the models that predicted foraging patch selection. However, the scale at which I sampled stand characteristics might have been insufficient to detect the importance of CWD and stumps in foraging habitat. I rarely observed WISA foraging directly on an ant colony (n = 2; Chapter 2) and the ants that WISA forage on can travel up to 200 m from the colony (Brian 1983). A few productive ant colonies within a nesting territory could be sufficient to provide food for a breeding pair of WISA. In Canada and in northwestern United-States, WISA 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 rotting CWD and stumps (Thomas *et al.* 1979, Sanderson *et al.* 1980). Old forests, which typically include significant amounts of dead standing and downed CWD, are also preferred by most woodpecker species in North America (Lemaître, 2005, Tremblay *et al.*, 2009, 2010, 2015, Nappi *et al.* 2015).

I observed WISA foraging in locations up to 556 m away from the nest in the Montane Spruce zone and 831 m in the Interior Douglas-fir zone, further than the 500-m maximum distance traveled by one radio-tracked male WISA that was feeding nestlings in a previous study in BC (Manning and Cooper 1996). The nesting territory sizes I identified (340 m and 410 m radius; 95% percentile) are larger than the 225 m that was identified by Gyug *et al.* (2007) using the nearest-neighbour distance. In a similar telemetry study on Red-naped Sapsuckers (*S. nuchalis*) in the Interior Douglas-fir biogeoclimatic zone in British Columbia, nesting territory radius was 205.2 ± 58.2 m during the nestling stage - determined by the Minimum Convex Polygon method (Walters 1990). To my knowledge, no other studies have reported space use data for other sapsucker species. In concordance with Gyug *et al.* (2007), I found that WISA used larger nesting territories in the IDF zone than in the MS. Space use can be explained by demographic traits such as bird age and mass (Lorenz *et al.* 2015a), but most studies report the availability and distribution of quality foraging habitat as the main predictor of space use (Dixon 1995a,b, Tremblay *et al.* 2009, Rota *et al.* 2014, Tingley *et al.* 2014). WISA may travel longer distances in the IDF zone because of the higher proportion of open areas (natural grasslands or artificially maintained pastures), a hypothesis that could be examined in future studies. My ability to detect WISA at greater distances was limited because of the difficulties associated with following birds quickly over rugged terrain, therefore I suspect that the maximum foraging distances are larger than I reported here. I temporarily lost the radio-signal of birds six times while tracking during the nestling period, meaning that the birds were too far to be detected. During those events, I suspect that the birds could have traveled more than one kilometer away from the nest, since the signal did not come back after I moved closer and away from potential obstacles that could have caused interference with the radio-telemetry signal, such as boulders and hills. Red-naped Sapsuckers were detected at 1.1km from their nest during the nestling stage in British Columbia (Walters 1990) and this could easily be the case for WISA. More advanced technologies such as GPS trackers could give unbiased estimates of maximum and average foraging trip distances for WISA (*e.g.,* Pinpoint 8, Lotek Wireless, Newmarket, ON, Canada).

My results suggest that WISA can forage and nest in habitat surrounding forest openings, possibly preferring forest edges for foraging and lower tree density in nest patches than foraging patches. Previous studies in managed landscapes also suggested that WISA prefer establishing their nesting territory in proximity with forest openings created by fire or logging (Whitcomb *et al.* 1981, Keller 1992, Hutto *et al.* 2015, Drever *et al.* 2015). A similar pattern of habitat selection has been reported in several other North American woodpecker species (Drever *et al.* 2008, Tremblay *et al.* 2009, Tozer *et al.* 2012, Lorenz *et al.* 2015a). These woodpecker species may choose stands previously disturbed by harvesting, insects or wildfire to establish their nesting territories because of the increased number of decayed trees suitable for nesting and foraging. Internal decay is required for nest excavation, being the only nest tree characteristic that is consistently selected by primary cavity excavators, along with dbh (Kilham 1971, Conner *et al.* 1976, Lorenz *et al.* 2015b). The preference for nesting in forest openings could also be related to the enhanced visibility in low tree density areas, which has been correlated with higher reproductive success for some cavity-nesters, possibly because of nest defence behaviours (Li and Martin 1991). Active nest defence by adult woodpeckers against rodents, other bird species and mustelids has been reported for several species including WISA (Crockett and Hansley 1975, Paclik *et al.* 2009).

Foraging and nesting in proximity to openings could decrease predation risk and increase foraging habitat quality for WISA. The main predators of adult WISA that have been identified are Cooper's hawks (*Accipiter cooperii*) and Northern goshawks (*Accipiter gentilis*), which hunt using close range surprise attacks and ambush, and prefer hunting in forest interior patches more than in forest edges and open areas (Crockett 1975, Beier and Drennan 1997, Roth II and Lima 2003). Predation risk might be higher for adult WISA in large patches of dense forest, driving selection for foraging in more open habitat such as forest edges (Lima and Dill 1990, Götmark and Post 1996). Trees in stands with openings are more likely to be stressed, injured and decayed (U.S. Department of Agriculture 1981), thus having higher diversity and abundance of insects (Yoshimoto *et al.* 2005), and being more suitable for sap feeding (Gyug *et al.* 2009a, see Chapter 2). The abundance of ants preferred for foraging by WISA might increase close to forest openings, because of the improved solar radiation that is used to regulate the temperature of ant colonies, and higher abundance of CWD (Punttila *et al.* 1991, Chen *et al.* 2002, Kadochova *et al.* 2014).

While small openings in the forest canopy could increase the amount of suitable habitat for ants (Brian and Brian 1951), large openings should be considered as habitat loss and may even reduce the access to suitable foraging habitat within the nesting territory. I observed that WISA avoided crossing large areas of open habitat and single trees when possible during gap-crossing, by following the edge of the forest. Woodpeckers the size of WISA are known to be less affected by predation risk when crossing open areas, compared to smaller woodpeckers (Götmark and Unger 1994, Grudd and Doherty 1999, Bélisle and Desrochers 2002). Therefore, WISA likely avoided open areas because they represent unsuitable foraging habitat (tree density too low), and flyovers could cause an additional energetic cost to foraging trips, flight being one of the most energetically expensive animal activities (Pedley 1977, Norberg 1990). Multiple small retained groups of 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. The areas of open habitat and single trees in the MS zone were mostly clear-cuts and seed tree cuts, while in the IDF zone they were grasslands that were sometimes artificially maintained by cattle grazing and herbicides. Other common sources of openings in both biogeoclimatic zones were roads, powerlines and pipelines. Little information is available on WISA habitat selection in unmanaged landscapes. It is not clear whether or how habitat selection patterns would differ in unmanaged forest, where there may also be abundant openings, caused by fire, windthrow, insect outbreaks and senescence of large trees (Herman and Lavender 1990, Arno 1991).

3.6 Stand-level management recommendations

The association that WISA have with forest openings for foraging and nesting is key to their persistence in managed landscapes. However, given the results in this Chapter, Chapter 2 and other studies, timber harvesting should conserve some old forest characteristics, including large trees, standing dead trees, decaying trees, large CWD and large stumps (Gyug *et al.* 2014b). I recommend the minimal overall retention of > 85 large live trees/ha for foraging in active and previously active nesting territories (based on Gyug *et al.* 2010), preferably live Douglas-fir ($\geq$ 22.5cm dbh), as shown in Chapter 2. I recommend a no-harvest reserve zone in a 140-m radius around recent (standing) or active nest trees (nest reserve zone). I recommend partial logging, leaving trees with characteristics of preferred foraging trees (large Douglas-fir) as retained groups in the nest management zone, extending from the no-harvest area (140 m from the nest) out to 340 m from the nest in the MS and 410 m in the IDF biogeoclimatic zones. In cases where open areas (roads, power lines, clear-cuts, seed tree cuts, etc.) cover more than 17% of the nesting territory, retained groups should be left in densities of approximately 250 large live Douglas-fir (22.5-57.4 cm dbh) per hectare and 25 very large live Douglas-fir of $\geq$ 57.5cm dbh or dead conifer trees of $\geq$ 46cm dbh (chiefly western larch and ponderosa pine, see Chapter 2). Clear-cuts and seed tree cuts should be avoided in WISA nest management zone and not exceed 160 m in length (diameter; 2 ha) in WISA Area of Occupancy to reduce habitat loss and constraints associated with gap-crossing. The 160-m length threshold is based on the maximum distance of open area and single tree area crossed by WISA without evidence of gap-crossing avoidance (longer distances of open habitat were avoided). Clear-cuts with an elongated shape may be easier to cross than similar size circular clear-cuts, making the resources available on the opposite side, thus reducing the effects of habitat loss on a single nesting territory. More research is required on gap-crossing and use of retained groups designs by WISA to further validate these recommendations.

3.7 Chapter 3 figures

Fig 3.1.

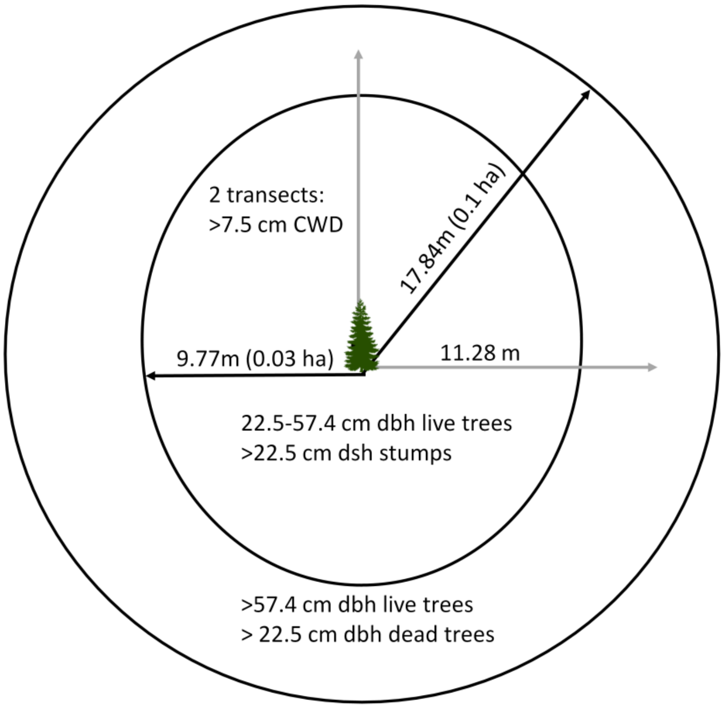


Figure 3.1. Design of nested plots used to measure forest stand characteristics that could be relevant to foraging for Williamson’s Sapsuckers. Nested plots were centered on a foraging substrate (n = 47 trees, 1 log) or a randomly selected similar substrate on which WISA, or signs of WISA foraging, were not observed (available habitat; total = 96 use and available nested plot sets).

Fig.3.2

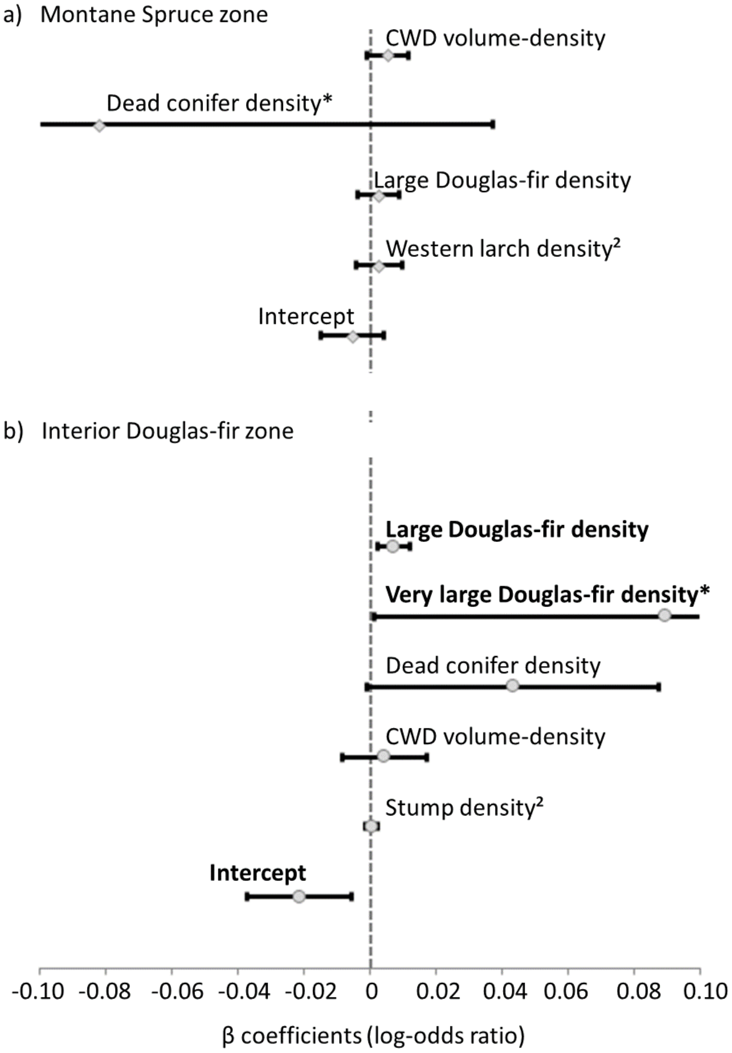


Figure 3.2. Selection of stand-level characteristics for foraging by Williamson's Sapsuckers in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones in British Columbia, Canada. The multi-model averaged coefficients of variables in the 95% confidence set of Generalized Linear Mixed Models (GLMM) are presented with their 95% confidence intervals. Positive β coefficients represent preference 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 interval (-0.20 – 0.038) of dead conifer trees in the Montane Spruce biogeoclimatic zone was too large to display.

Fig. 3.3

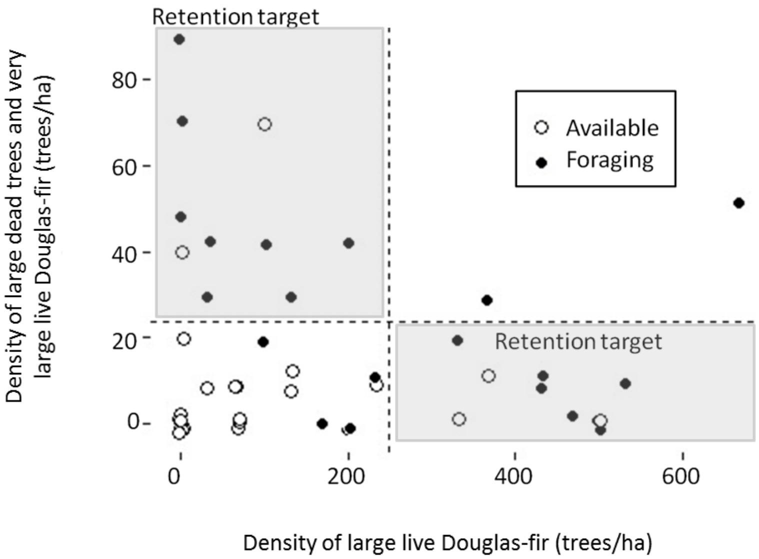


Figure 3.3. Stand composition and structure of patches used and unused (available) for foraging by Williamson's Sapsuckers in the Interior Douglas-fir biogeoclimatic zone in southern British Columbia, Canada. The dashed lines represent bootstrapped (10 000 replicates) means and are presented to show retention targets. Foraging patches were selected for their high density of large live Douglas-fir (22.5-57.4cm dbh) or their high density of very large live Douglas-fir ($\geq$ 57.5cm dbh) and $\geq$ 22.5cm dbh standing dead conifer trees. I combined very large live Douglas-fir density with dead conifer tree density to facilitate the interpretation of foraging patches for forest management.

Fig. 3.4

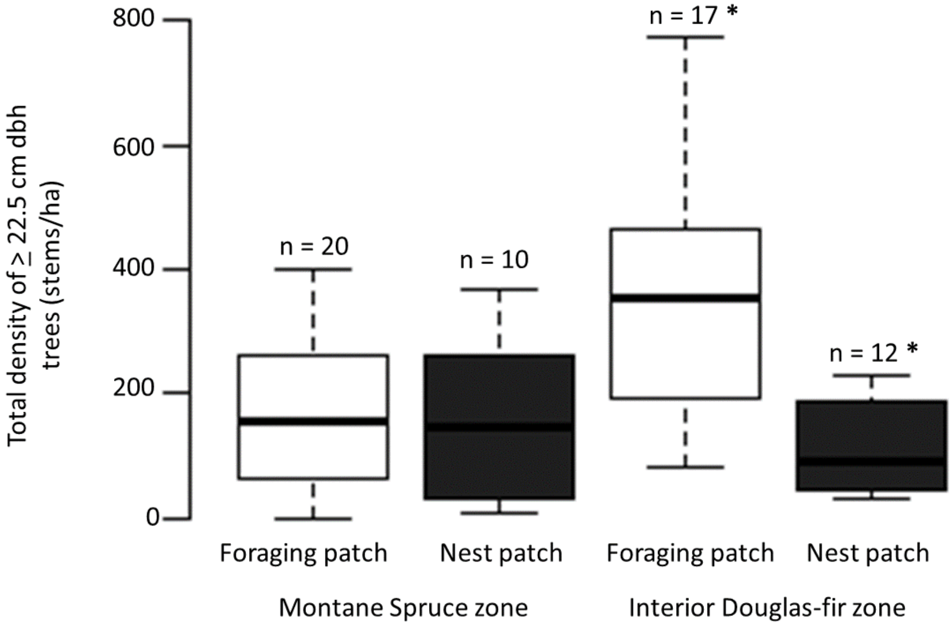


Figure 3.4. Total tree (> 22.5cm dbh) density in foraging patches (> 60m radius from the nest tree, white boxes) and nest patches (< 60m radius, dark boxes) in both the Montane Spruce and Interior Douglas-fir habitats of Williamson's Sapsuckers in southern British Columbia, Canada. The foraging patches were used during the pre-nestling and nestling stages for any foraging mode. Differences were tested between foraging and nest patches in each biogeoclimatic zone using MANOVA and significant differences are indicated by '*'.

Fig. 3.5

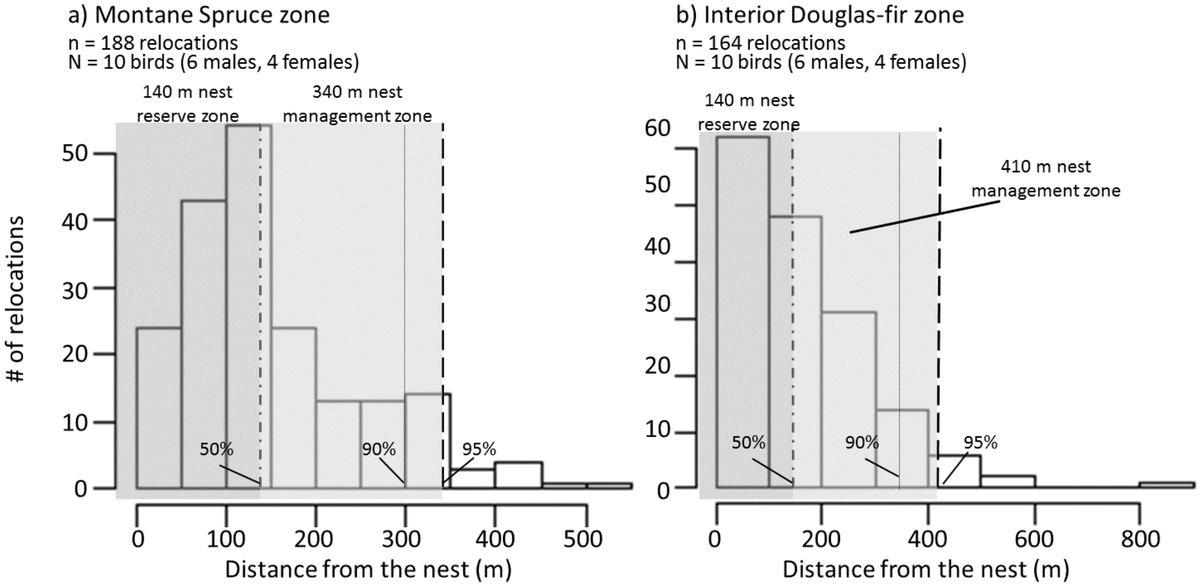


Figure 3.5. Distance from the nest of telemetry relocations of Williamson's Sapsuckers during statistically independent foraging trips to feed their nestlings (no spatio-temporal autocorrelation) in a) the Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones, in 2014-2015.

Fig. 3.6

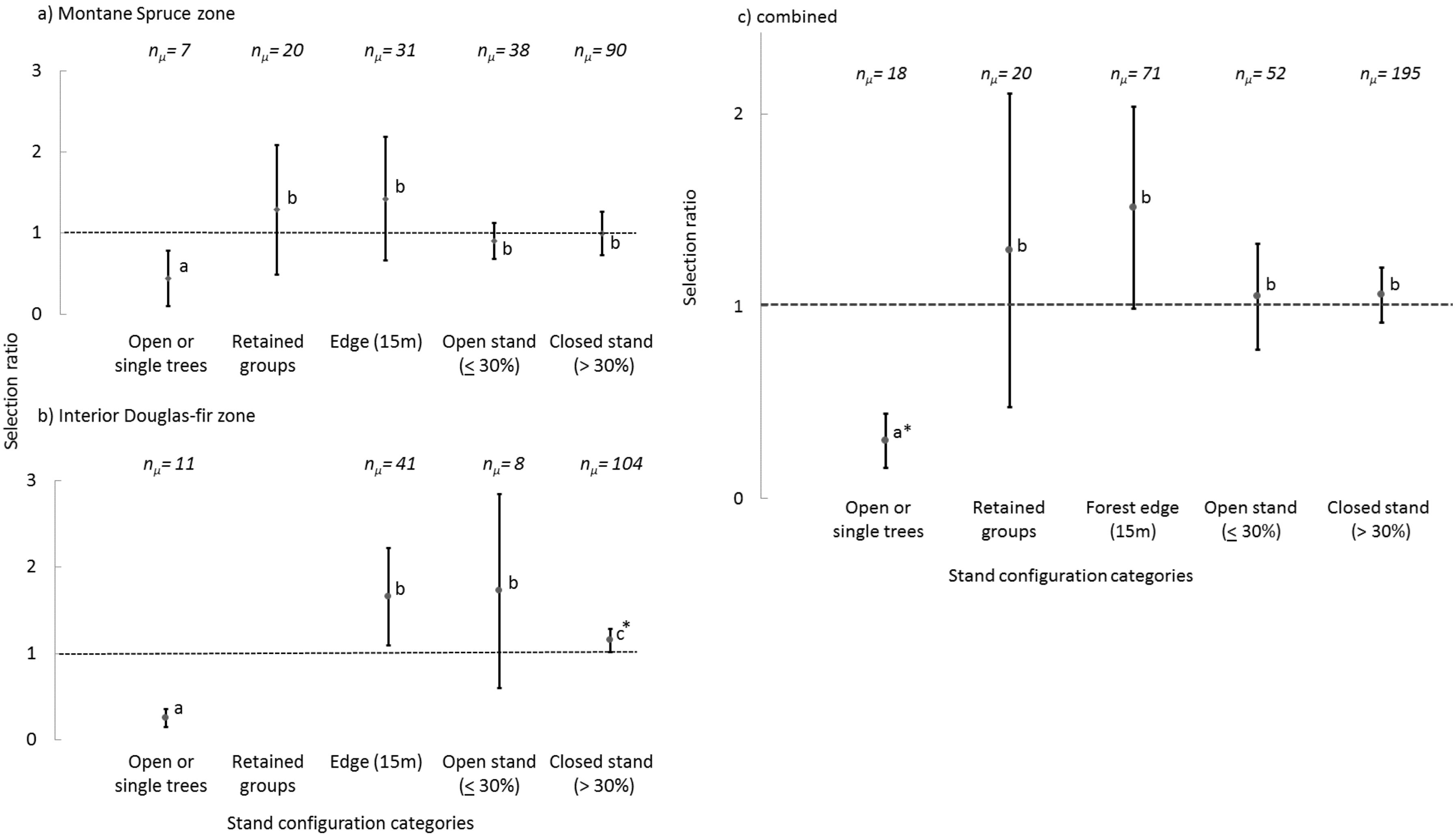

a) Montane Spruce zone
nμ= 7
nμ= 20
nμ= 31
nμ= 38
nμ= 90
3
2
1
0
a
b
b
b
b
Open or single trees
Retained groups
Edge (15m)
Open stand (≤ 30%)
Closed stand (> 30%)
Selection ratio
b) Interior Douglas-fir zone
nμ= 11
nμ= 41
nμ= 8
nμ= 104
3
2
1
0
a
b
b
c*
Open or single trees
Retained groups
Edge (15m)
Open stand (≤ 30%)
Closed stand (> 30%)
Stand configuration categories
c) combined
nμ= 18
nμ= 20
nμ= 71
nμ= 52
nμ= 195
2
1
0
Selection ratio
a*
b
b
b
b
Open or single trees
Retained groups
Forest edge (15m)
Open stand (≤ 30%)
Closed stand (> 30%)
Stand configuration categories

Figure 3.6. Selection ratios and 95% confidence intervals of stand configuration categories used (n_{μ}) by foraging Williamson's Sapsuckers during the nestling stage, in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones, and c) combined, in 2014-2015. Dominant tree species in all categories were either Douglas-fir, western larch or ponderosa pine. Open and closed stands have $\leq$ 30% and > 30% crown closure, respectively. Fourteen sapsucker nesting territories were used and foraging observations from both members of a pair were pooled for the territory 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 preferential 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 dbh classes using Bonferroni-corrected χ^2 tests.

Fig. 3.7

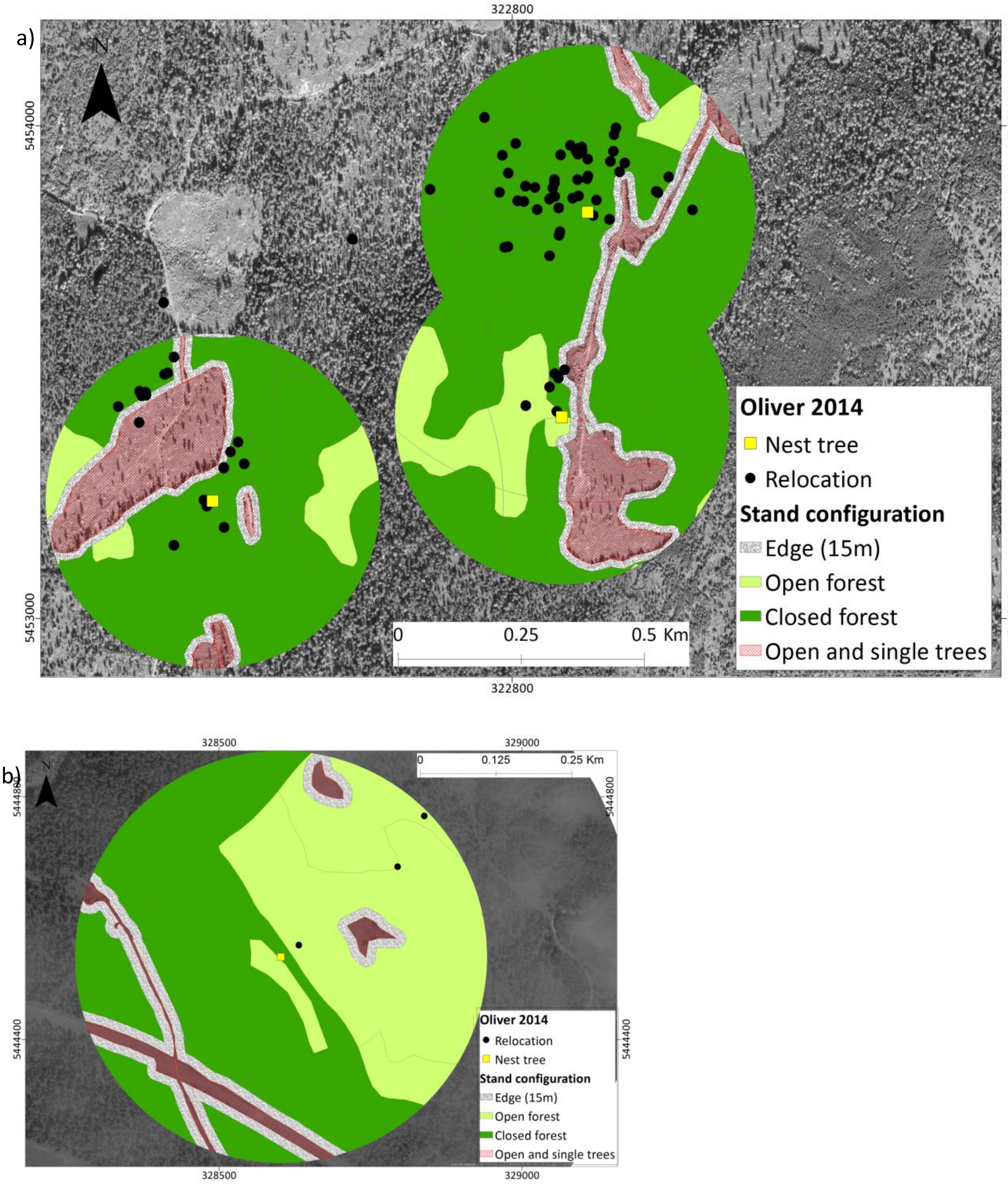

a)
N
322800
5454000
5453000
0
0.25
0.5 Km
Oliver 2014
Nest tree
Relocation
Stand configuration
Edge (15m)
Open forest
Closed forest
Open and single trees
b)
N
328500
329000
5444800
5444400
0
0.125
0.25 Km
Oliver 2014
Relocation
Nest tree
Stand configuration
Edge (15m)
Open forest
Closed forest
Open and single trees

Fig. 3.7

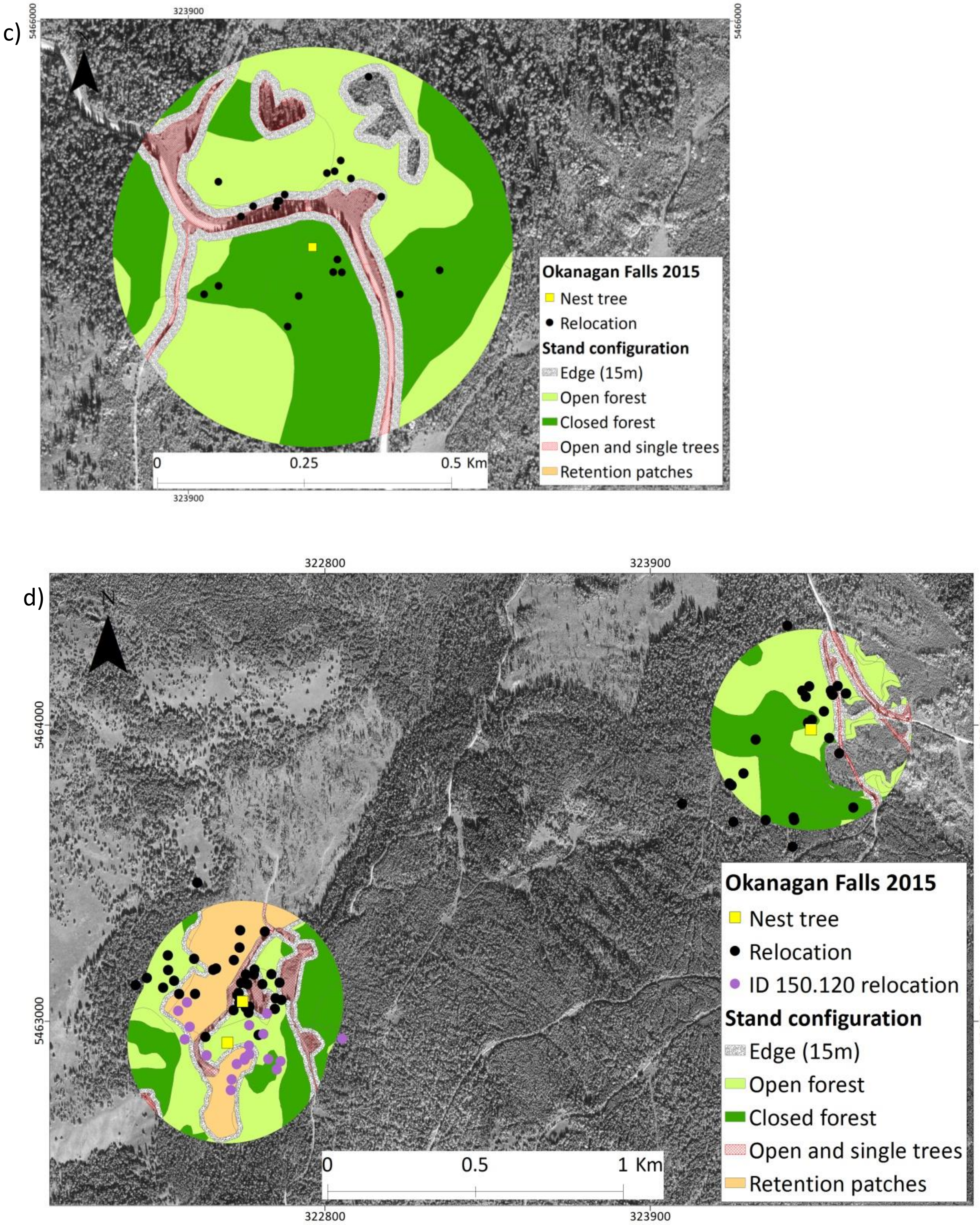

c)
323900
5466000
N
Okanagan Falls 2015
Nest tree
Relocation
Stand configuration
Edge (15m)
Open forest
Closed forest
Open and single trees
Retention patches
0
0.25
0.5 Km
d)
322800
323900
5464000
5463000
N
Okanagan Falls 2015
Nest tree
Relocation
ID 150.120 relocation
Stand configuration
Edge (15m)
Open forest
Closed forest
Open and single trees
Retention patches
0
0.5
1 Km

Fig 3.7

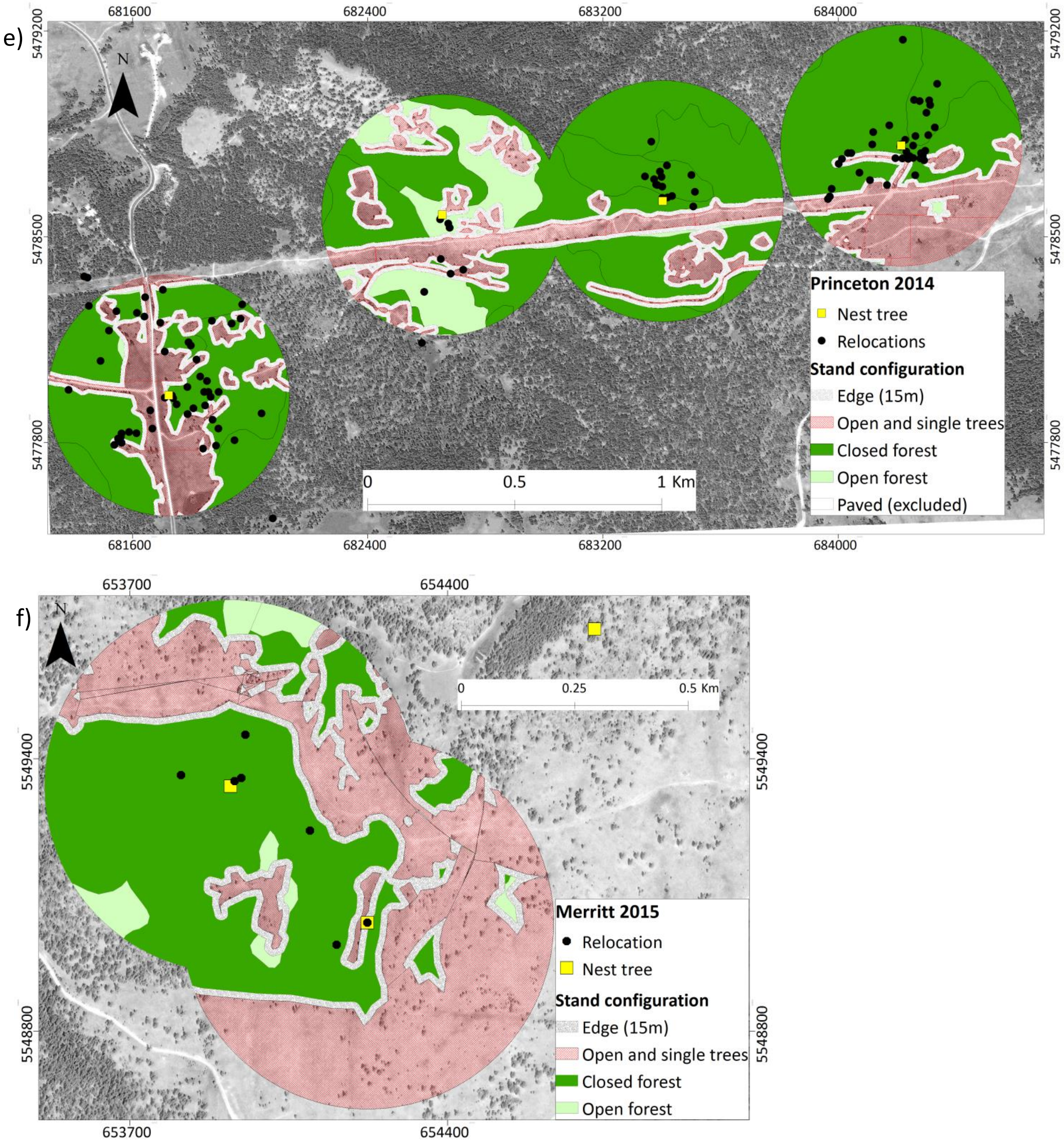

e)
681600
682400
683200
684000
5479200
5478500
5477800
N
0
0.5
1 Km
Princeton 2014
Nest tree
Relocations
Stand configuration
Edge (15m)
Open and single trees
Closed forest
Open forest
Paved (excluded)
f)
653700
654400
5549400
5548800
N
0
0.25
0.5 Km
Merritt 2015
Relocation
Nest tree
Stand configuration
Edge (15m)
Open and single trees
Closed forest
Open forest

Fig. 3.7

g)

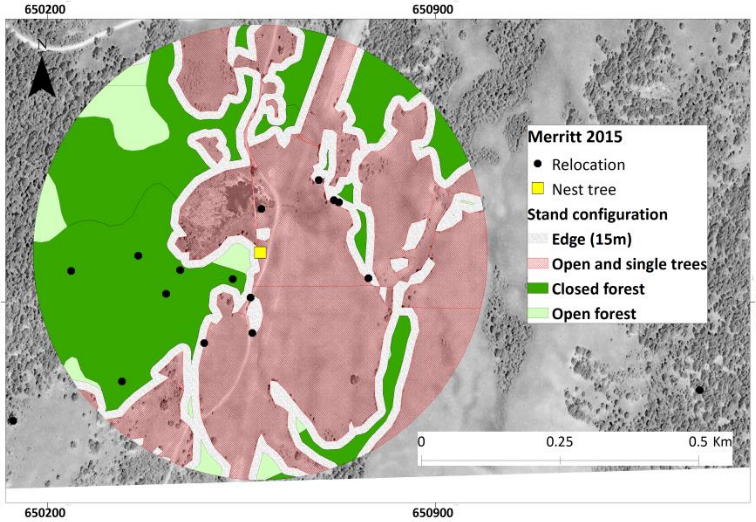


Figure 3.7. Available stand configuration categories, nest location and foraging trip relocations in 14 Williamson's Sapsucker nesting territories at the a-b) Oliver, c-d) Okanagan Falls, e) Princeton and f-g) Merritt sites. The availability of stand configuration categories is defined in buffers of 340 m in the Montane Spruce (a-d) and 410 m in the Interior Douglas-fir biogeoclimatic zones (e-g). Edges represent the ecotone between open and forested areas in a 15-m buffer. Open and single tree areas include clear-cuts, seed tree cuts, forestry roads, power line and pipeline clearings, fields, grasslands and pastures. Closed stand is for > 30% canopy cover while open stand is for $\leq$ 30% canopy cover. At the Okanagan Falls site d), two breeding pairs nested in proximity and shared foraging patches, this behaviour was abnormal during the study. Also, at the Merritt site f) a female nested in two nest cavities simultaneously with two different males (polyandry). The longest observed crossings of open and single trees areas were a) 174 m in the Montane Spruce (a-d) and 160 m in the Interior Douglas-fir biogeoclimatic zones.

3.8 Chapter 3 tables

Table 3.1. Number of nested plots (0.03 and 0.1 ha) measured to contrast stand-level differences between patches used (foraging) and available (unused) by Williamson's Sapsuckers in a telemetry study in the Montane Spruce (MS) and Interior Douglas-fir (IDF) biogeoclimatic zones 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 used/available ratio.

		Vegetation plots			
Year	Biogeoclimatic zone	Used	Available	Nest patch†	WISA nesting territories*
2014	MS	5	5	2	5
	IDF	9	9	4	5
2015	MS	20	20	8	4
	IDF	14	14	8	4
	Total	48	48		
		96		22	18‡

* Include three territories of non-breeding birds and one territory of a pair for which only pre-nestling stage data were collected.

† The nest patch is ≤ 60 m from the nest tree and nest patch plots include used and available plots.

‡ The total number of nesting territories in which the nest patch was sampled was 15 (MS zone: n = 8, IDF zone: n = 7)

Table 3.2. 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) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones in British Columbia, Canada. All variables represent densities, such as trees/ha for standing trees, stumps/ha for stumps and m^3/ha for coarse woody debris (CWD).

	Model variables	Rank	AICc	ΔAICc	W_i	AUC
a) MS zone *n = 50 plots, 9 nesting territories*	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) IDF zone *n = 46 plots, 9 nesting territories*	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

Table 3.3. 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. 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.

		Densities $\bar{x}$ ± SE (range)					
a) MS zone	Variable	Foraging	Available	W_+	β (95% Conf. Int.)	SE	Odds-ratio (95% Conf. Int.)
n = 50 plots, 9 nesting territories	Intercept	-	-	0	-0.0051 (-0.015-0.0046)	0.0049	1.005 (0.985-1.005)
	CWD (m^3/ha)	144.6 ± 30.7 (0-583.5)	79.1 ± 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 ± 0.6 (0-10.0)	2.4 ± 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 ± 22.3 (0-366.7)	76.0 ± 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 ± 14.5 (0-360.0)	25.6 ± 6.6 (0-110)	0.07	0.0029 (-0.0040-0.0099)	0.0029	1.003 (0.996-1.010)
	Stumps^2	90.7 ± 17.5 (0-266.7)	110.7 ± 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 ± 3.4 (0-80)	4.8 ± 2.1 (0-30.0)	0.01	0.016 (-0.030-0.063)	0.024	1.016 (0.969-1.064)
b) IDF zone	**Intercept**	-	-	0	**-0.021 (-0.037--0.0052)**	**0.0081**	**0.979 (0.963-0.994)**
n = 46 plots, 9 nesting territories	**Large Doug.-fir**	**247.8 ± 42.2 (0-666.7)**	**94 ± 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 ± 3.4 (0-50.0)**	**2.6 ± 1.1 (0-20.0)**	**1**	**0.090 (0.0014-0.18)**	**4.50**	**1.094 (1.001-1.194)**
	Dead conifers	13.9 ± 3.8 (0-70.0)	6.1 ± 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 ± 12.7 (0-283.7)	41.8 ± 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 ± 17.4 (0-333.3)	76.8 ± 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 ± 10.7 (0-230.0)	24.3 ± 9.3 (0-166.7)	0.03	0.0055 (-0.014-0.025)	0.0098	1.006 (0.986-1.025)

Table 3.4. Densities of standing live and dead trees > 22.5cm dbh measured in foraging patches and available (unused) habitat patches in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones. T-tests were used to test the significance of the differences (α = 0.05; bolded if significant).

	X̄ ± SE (range)		t-test	
	Montane Spruce	Interior Douglas-fir	t	p
Foraging	**181.7 ± 24.4 (0-400.0)**	**297.2 ± 43.8 (50.0- 773.3)**	**2.35**	**0.02**
Available	134.1 ± 23.4 (0-373.3)	136. 8 ± 27.6 (0-500.0)	0.07	0.94
Overall	157.9 ± 17.1 (0-400.0)	217.0 ± 28.3 (0-773.3)	1.82	0.07

Table 3.5. Difference in stand composition and structure between nest and foraging patches of Williamson's Sapsuckers in the a) Montane Spruce, b) Interior Douglas-fir and c) pooled biogeoclimatic zones in southern British Columbia, Canada. Mean stand densities for different tree types are in trees per ha. Bolded text indicates significant differences. I used Bonferroni-corrected t-tests to identify differences among the nest and foraging patches for each variable.

		x̄ ± SE (trees/ha)			
	Test	Nest patch	Foraging	t (F)	p
a) MS zone	MANOVA			(0.50)	0.73
N = 8 pairs	t-test (α = 0.0125)				
	Large live Douglas-fir density	73.3 ± 27.6	120.0 ± 26.2	-1.11	0.28
	Very large Douglas-fir density	8.0 ± 3.3	8.5 ± 4.2	-0.08	0.94
	Dead conifer density	1.0 ± 1.0	1.0 ± 0.7	0	1
	Total density	161.0 ± 39.0	169.5 ± 28.3	-0.18	0.86
	Sample size (# of plots)	10	20		
b) IDF zone	**MANOVA**			**(3.65)**	**0.02**
N = 7 pairs	t-test (α = 0.0125)				
	Large live Douglas-fir density	**72.2 ± 20.0**	**303.9 ± 49.3**	**-3.78**	**0.008**
	Very large Douglas-fir density	8.3 ± 4.41	9.4 ± 3.69	-0.19	0.85
	Dead conifer density	15.8 ± 7.6	13.5 ± 3.4	0.3	0.76
	Total density	**94.2 ± 20.8**	**342.2 ± 53.4**	**-3.75**	**< 0.001**
	Sample size (# of plots)	12	17		
c) Overall					
N = 15 pairs	MANOVA			2.42	0.06

Table 3.6. Use and availability of stand configuration categories in Williamson's Sapsucker nesting territories (buffers around nests) in a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones, and c) overall, in southern British Columbia. The mean proportion represents the available stand configuration within the nesting territory, and $\hat{W}_i$ is the selection ratio for each category. A $\hat{W}_i$ value above one indicates preference for a category relative to its availability, and a value below one indicates avoidance. Bolded categories were significantly preferred (95% confidence intervals do not overlap with one) and bolded italics represent categories that were significantly avoided. The data are for birds that were feeding nestlings only (nestling period) and all bird relocations (uses) are statistically independent (no spatio-temporal correlation). All stands were dominated by Douglas-fir, ponderosa pine or western larch. Open and closed stands have < 30% and > 30% crown closure, respectively. The analyses were performed by nesting territory, because breeding pairs share the same available habitat.

	Configuration	# of uses	Mean proportion ± SE (range)	$\hat{W}_i$ (95% Conf. Int.)
a) MS zone	***Open and single trees***	***7***	***0.09 ± 0.04 (0.05-0.18)***	***0.43 (0.05-0.81)***
N = 8 territories, 11 birds, 192 relocations	Retained groups	20	0.06 ± 0.11 (0-0.27)	1.29 (0.38-2.20)
	Edge (15m)	30	0.11 ± 0.03 (0.07-0.15)	1.36 (0.49-2.23)
	Open stand (≤ 30%)	44	0.26 ± 0.14 (0.04-0.43)	0.98 (0.73-1.24)
	Closed stand (>30%)	91	0.47 ± 0.22 (0.21-0.83)	0.97 (0.67-1.28)
b) IDF zone	***Open and single trees***	***11***	***0.28 ± 0.14 (0.12-0.48)***	***0.25 (0.14-0.36)***
N = 6 territories, 10 birds, 164 relocations	**Edge (15m)**	**41**	**0.17 ± 0.05 (0.10-0.23)**	**1.65 (1.06-2.23)**
	Open stand (≤ 30%)	8	0.06 ± 0.10 (0-0.25)	1.72 (0.56-2.88)
	Closed stand (>30%)	**104**	**0.49 ± 0.18 (0.30-0.73)**	**1.15 (1.00-1.29)**
c) Overall	***Open and single trees***	***18***	***0.17 ± 0.13 (0.05-0.48)***	***0.30 (0.16-0.44)***
N = 14 territories, 21 birds, 356 relocations	Retained groups	20	0.03 ± 0.09 (0-0.27)	1.29 (0.48-2.10)
	Edge (15m)	71	0.14 ± 0.05 (0.07-0.23)	1.51 (0.99-2.04)
	Open stand (≤ 30%)	52	0.18 ± 0.16 (0-0.43)	1.05 (0.78-1.33)
	Closed stand (>30%)	195	0.48 ± 0.19 (0.21-0.83)	1.06 (0.92-1.20)

Chapter 4 - summary and conclusions

Foraging habitat selection studies investigate how animals select resources for foraging, assuming that habitat preferences are associated with increased survival and reproductive success (Hall *et al.* 1997). For effective management recommendations, habitat selection studies should try to incorporate all possible relevant individual traits in the subject population, including gender, nesting status and age, and investigate selection at different spatial and temporal scales. There are several knowledge gaps regarding the foraging habitat for Williamson's Sapsuckers (*Shyrapicus thyroideus;* WISA), which are Endangered in Canada and Blue-listed in British Columbia (BC) and which require critical habitat protection. My thesis addressed some of these knowledge gaps by examining the foraging behaviour and the selection of foraging habitat characteristics of WISA during the breeding season, at the foraging substrate (tree) and forest-stand scales. In Chapter 2, I described the foraging behaviour and examined the influence of individual traits (gender, nesting status and age) on foraging mode use (gleaning, pecking and sap feeding) and characteristics of foraging trees (tree species, diameter at breast height [dbh] and decay class). I modeled the selection of tree characteristics relative to their availability, using Generalized Linear Mixed-Models (GLMM) and selection ratios, to obtain the relative importance of tree characteristics for foraging, and identify preferences. In Chapter 3, I examined habitat selection at the stand level (composition, structure and configuration), using again GLMM and selection ratios. I compared the stand-level characteristics of forest patches that were selected for foraging vs. nesting using MANOVA tests. I investigated foraging trip distances of WISA that were feeding nestlings and recommended nest reserve and nest management zones to protect the foraging habitat around nest trees. In this chapter, I discuss the implications of my results for forest management and our understanding of the ecology of WISA. I also recommend management actions to be implemented to conserve WISA habitat for nesting, foraging and communication (drumming), incorporating knowledge from previous studies with my findings.

In the Montane Spruce biogeoclimatic zone (MS zone), I found that large ($\geq$ 22.5 cm dbh) live Douglas-fir and hybrid spruce (*Picea engelmannii* X *Picea glauca*) were important trees for foraging (gleaning, pecking and sap feeding), large dying western larch (*Larix occidentalis*) were important for pecking and drumming. Lodgepole pine (*Pinus contorta*) and deciduous trees were avoided for foraging by Williamson's Sapsuckers. Drever *et al.* (2015) investigated WISA nesting territory occurrence in British Columbia, using field measurements and GIS-derived data, with the assumption that WISA chose their nesting territories based on potential foraging opportunities. Drever *et al*. (2015) found that stand-level characteristics that were positively associated with nest occurrence were the area of Douglas-fir stands 80-119 years old, moderate densities of large hybrid spruce trees (17.5–57.4 cm dbh; quadratic), moderate densities of very large stumps (≥ 57.5 cm dbh; quadratic) and densities of very large dead trees and very large western larch (≥ 57.5 cm dbh). My study supports the results from Drever *et al*. (2015), regarding the importance of large Douglas-fir, hybrid spruce and western larch for foraging. However, I found that densities of large stumps and large dead trees were not significant characteristics of foraging patches in the MS zone. Stumps provide colony substrates for ant species that WISA consume and are more relevant when measured at the scale of the nesting territory, considering that ants may travel as far as 200 m from the colony (Brian 1983, Gyug *et al*. 2014b, Drever *et al*. 2015). Large dead trees can be used by WISA for nesting, pecking and drumming (Chapter 2, Gyug *et al*. 2009b) and as colony substrates for ants - I may have not detected their importance because of their rarity (low sample size). Drever *et al.* (2015) found that stand-level characteristics that were negatively associated with the probability of nest occurrence in the MS zone were higher densities of large Douglas-fir or lodgepole pine (>25 trees/ha, 17.5-57.4 cm dbh). Lodgepole pine was also avoided in my study, but it is surprising that large Douglas-fir (17.5-57.4 cm dbh) were negatively associated with nest occurrence in Drever *et al.* (2015), since my results indicated that they were preferred as foraging trees. Perhaps the wider dbh class used in Drever *et al.* (2015) included too many smaller Douglas-fir that were not of interest for foraging, since I found that < 22.5 cm dbh live Douglas-fir were avoided by WISA for foraging in my study.

In the IDF zone, I found that large live Douglas-fir were important trees for foraging (gleaning, pecking and sap feeding) and large recently dead ponderosa pine (*Pinus ponderosa*) were important for pecking and drumming. Live ponderosa pine and deciduous trees were avoided for foraging by Williamson's Sapsuckers. Drever et al. (2015) found that nesting occurrence was associated with stands with older age classes of ponderosa pine in moderate density and high density of large trembling aspen (*Populus tremuloides*; 17.5–57.4 cm dbh; Drever *et al.* 2015). My thesis showed that ponderosa pine can be used for pecking and drumming, while trembling aspen are tied to nesting requirements (Gyug *et al*. 2009b). Ponderosa pine trees are also used for nesting (Gyug *et al*. 2009b). Drever (*et al.* 2015) found a negative association between Douglas-fir stands aged ≥ 120 years old and nest occurrence. This result differs from my findings since I found that WISA preferred to forage on large and very large Douglas-fir trees, which are expected to occur in mature stands. The conditions (stand characteristics and size of trees) of those mature stands were not always known by the authors, thus it remains difficult to compare their results with my field measurements. In the IDF zone, the habitat characteristics examined at the nesting territory level remained mostly associated with characteristics of nesting trees rather than foraging trees (Drever *et al.* 2015). Overall, Drever *et al.* (2015) described the habitat of WISA at a broader scale (nesting territory) with some uncertainties regarding preferences for Douglas-fir and hybrid spruce as foraging habitat. I resolved these uncertainties by looking at foraging habitat within the nesting territory, using visual observations of WISA.

I found that WISA tend to select nesting patches ($\leq$ 60 m around nest) that have lower tree density than foraging patches, and can forage in a variety of within-stand configurations such as retained groups, forest edges, open and closed stands. WISA have been classified as a forest edge-associated species by Whitcomb *et al.* (1981), because of their tendency to establish their nesting territories in proximity to forest openings created by logging or fire (Whitcomb *et al.* 1981, Keller 1992, Hutto *et al.* 2015, Drever *et al.* 2015). In the Okanagan and East Kootenays Areas of Occupancy, WISA preferred to establish their nesting territory in forests containing 6-7 ha of area of canopy opening (17-19% of a typical 36 ha nesting territory in the MS zone; canopy opening is not necessarily contiguous) and within 200 m from < 40 years old logged areas (Drever *et al.* 2015). In the Western Area of Occupancy, WISA preferred 20-25 % non-forested cover and 25-30 % crown closure of > 15 m trees (Drever *et al.* 2015). In Wyoming, in a hybrid spruce-Douglas-fir-lodgepole pine forest (similar to my Okanagan or MS sites), breeding territory density was significantly higher in stands fragmented by logging compared to unlogged forest, although WISA were rare on the study site (Keller and Anderson 1992). In Arizona, in a Douglas-fir dominated habitat mixed with ponderosa pine (similar to my Western or IDF sites), breeding densities were similar between logged and unlogged areas (Franzreb 1977). In Montana, in a habitat similar to the Western or IDF zone, the probability of occurrence of WISA decreased immediately after a severe fire, but increased after six years and peaked after 11 years, reaching more than six times the probability of occurrence in unburned stands (13% vs 2%; Hutto *et al.* 2015). The study specified that WISA nests were generally located at the edge between severely burned and unburned stands. The increased probability of tree decay and mortality of large trees combined with the regeneration of live trees 11-years post-fire probably contributed to provide nesting and foraging habitat. Ant species that WISA consume are associated with forest openings, because of improved solar radiation that regulates the temperature of the colony (Punttila *et al.* 1991, Chen *et al.* 2002, Kadochova *et al.* 2014). Overall, small openings in the forest canopy possibly have negative short-term and positive long-term effects because of the senescence of edge trees and increased ant abundance - this could be tested in future research using productivity data or long term monitoring of habitat selection at logged sites.

My thesis aimed to identify habitat characteristics that promote the survival and reproduction of WISA in Canada, with the assumption that animals select resources that increase their fitness (Hall *et al.* 1997). Marginal habitat can sometimes be used by breeding birds when higher quality habitat is not available, and this can lead to a range of fitness outcomes or even source-sink population dynamics (Johnson 2007, Tremblay *et al.* 2014). Gyug *et al.* (2010) showed that WISA can reproduce effectively in managed landscapes in all three Areas of Occupancy in Canada, using late-stage nesting productivity data from 160 nests (# of fledglings). Gyug *et al.* (2010) found no significant differences in nest productivity across Areas of Occupancy, years or between nests located in open or forested areas. A more detailed analysis is required to examine the effects of different habitat selection strategies on nesting productivity, combining the results of my thesis on critical foraging habitat with reproductive data that represent the entire breeding season (egg laying, incubation and nestling stage). For example, I suspect that WISA nesting territories could have a lower productivity when they contain a high proportion of open habitat or smaller available trees (suboptimal foraging habitat), and these types of habitat could even represent a sink for the population.

Using my results, we can better understand the threats that WISA populations are facing in Canada. I showed that foraging WISA avoided smaller trees overall ($\leq$ 22.5cm dbh), live ponderosa pine, trembling aspen, lodgepole pine and open areas (Chapters 2 and 3). However, trembling aspen is used for nesting and ponderosa pine is used for nesting, pecking and drumming, and should be considered part of WISA critical habitat (Gyug *et al*. 2009b, Chapter 2). Assuming that avoided characteristics decrease the quality of WISA nesting territories, potential threats to WISA habitat are 1) changes in tree species composition, 2) the reduction of mature forest characteristics in managed stands and 3) the creation of large open areas. Large, decaying or dead trees are characteristic of mature forests and typically decline in availability in managed landscapes. Logging in WISA nesting territories could contribute to long-term decline in quality and quantity of foraging habitat, unless managers implement mitigation measures such as protection or passive and active restoration of mature forest characteristics. Firewood cutting targets large standing dead trees and which are more often reused for foraging and used for nesting by WISA. Large areas of low quality foraging habitat such as open and single trees areas and lodgepole pine dominated stands could also have a negative effect on nesting territory quality by increasing travel distances required for birds feeding nestlings (Boersma and Rebstock 2009).

Because WISA tend to nest near forest openings and can forage in many types of within-stand configurations, appropriate forest management practices can be compatible with conserving WISA habitat. In this section, I propose management practices and strategies to be applied within known WISA nesting territories and areas containing critical habitat, combining knowledge from my thesis with previous studies (Table 4.1). Forest management must maintain the preferred tree species composition within WISA Areas of Occupancy, and heterogeneity (Douglas-fir and nesting trees) is required to maintain habitat for all life history requirements (nesting, foraging and communication). The most difficult challenge for forest management will be to maintain sufficient densities of large trees (85-300 trees/ha; Gyug *et al.* 2010) in WISA Area of Occupancy (potential WISA habitat). Large dying and dead standing trees should be protected with a no-harvest buffer during logging operations – these trees were more often reused for foraging and can be used for nesting. I recommend to exclude dead standing Douglas-fir, western larch and ponderosa pine trees from firewood cutting permits in WISA Area of Occupancy, since these large standing dead conifers were rare in WISA Area of Occupancy and require a long time to grow and decay. Conservation efforts should focus on preserving foraging habitat that is used during the nestling stage, since the birds are constrained to a certain area around active nests, but should also aim to provide habitat for birds throughout all their life stages (*i.e.*, post-breeding and non-breeders). I suggest a no-harvest nest reserve zone 140 m from recent (standing) or active nest trees, and a nest management zone out from 140 m to 340 m from the nest in the MS zone and 410 m in the IDF zone. In the nest management zone, I suggest to avoid clear-cuts and leave retained groups (85-300 large trees/ha) in any configuration (patch, scattered, strips) with a maximum spacing of 50 m between trees or patches. In the nest management zone of nesting territories containing > 17% open areas, I recommend retaining groups with a higher density of large tree to mitigate possible negative effects associated with larger foraging trip distances (250-280 trees/ha; Chapter 3), because WISA possibly compensate energy (and time) expenses by traveling to higher quality foraging patches. In WISA Area of Occupancy, I recommend avoiding clear-cuts and seed trees cuts when possible, especially when larger than 2 ha (maximum length of 160 m). Adjacent clear-cuts (or other open areas) should be separated by a 15-m strip of trees (edge size, Chapter 3), to avoid contiguous areas of open habitat and single trees. The recommendations on open areas aim at reducing possible issues associated with gap-crossing and increased foraging trip costs, but more research might be required since I did not collect detailed data on these phenomena.

One strategy to facilitate WISA conservation in managed landscapes and optimize forest management outcomes is to identify potential conflicts between harvesting priorities and WISA habitat requirements

(Table 4.2). Forest management activities that promote rapid tree growth and mature forest structure could be beneficial for WISA conservation and the forest industry. Such activities include the partial harvest or thinning of small trees (≤ 22.5cm dbh), creation of canopy gaps (especially when density ≥ 300 trees\ha), partial harvesting in even-aged or overstocked stands and harvesting of live lodgepole pine stands. Lodgepole pine is usually the first tree species to establish after logging or fire (Brown 1975), but this pine species is avoided by WISA. Forest management practices should promote the regeneration and growth of Douglas-fir, hybrid spruce, western larch and ponderosa pine. During my study, all WISA nesting territories contained a proportion of mature forest, therefore a proportion of intact mature forest should be retained within active nesting territories, using nest reserve zones (≤ 140 m from nest) or within Wildlife Habitat Areas (protected areas). I found evidence that retained groups within harvested areas can provide adequate breeding habitat - the two pairs that nested on the edge of a partial harvest block at the Okanagan Falls site during my study each fledged two or more nestlings successfully. Using a mix of forest management and conservation strategies may be the best way to secure the persistence of WISA in Canada, since this would distribute the risk in the advent of one strategy failing.

4.1 Chapter 4 tables

Table 4.1. Habitat requirements for foraging, nesting and communication for Williamson's Sapsuckers in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones. I recommend using these habitat characteristics as habitat management targets in WISA Area of Occupancy to meet the SARA recovery objective of maintaining or increasing population numbers in Canada.

WISA habitat	Montane Spruce B. zone	Interior Douglas-fir B. zone
Tree species composition range (%)*	• Fd† 66-76 • Lw 19-27 • Other 3-9	• Fd 76-86 • Py 13-21 • Other 1-3
Mean tree dbh (cm)	≥ 22.5 overall. By tree species: • Fd 35 • Lw 50 (foraging), 70 (nesting‡) • Deciduous 35 (At, Ew)	≥ 22.5 overall. By tree species: • Fd 40 • Py 50 (foraging), 70 (nesting‡) • Deciduous 35 (At, Ew)
Tree decay (% of trees)	• Resin exudation (foraging): ≥ 38 % Fd, 23 % Lw, 11 % Sx § • Nesting: Internal fungal infection (Lw, At and Ew) and broken or dead top Lw.	• Nesting: Recently dead Py or live At with internal fungal infection
Tree density range¥	• 85-300 trees/ha	• 85-300 trees/ha
CWD and stumps range¤	• 110-180 m^3/ha	• 20-70 m^3/ha

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

† In higher elevations (1 400 m), hybrid spruce can replace Douglas-fir.

§ I consider resin exudation synonymous to pitching.

¥ 85 live trees/ha is based on Gyug *et al.* (2010).

¤ Includes CWD ≥ 7.5cm dbh. Recommendations are based on the mean volume-densities in foraging patches, and are not definitive.

Table 4.2. Conflicts between Williamson's Sapsucker habitat requirements and harvesting priorities and suggested management strategies for the most common tree species encountered in WISA Area of Occupancy in Canada. Fd = Douglas-fir, Sx = Hybrid spruce, Lw = Western larch, Py = Ponderosa pine, At = Trembling aspen, Ew = Water birch, Pl = Lodgepole pine, Bg = Grand fir (*Abies grandis*), Bl = Subalpine fir (*Abies lasiocarpa*) and Act = Black cottonwood (*Populus trichocarpa*).

Tree species	Importance for WISA	Conflict	Available for harvest	Suggested management strategy
Fd	High	X		Partial harvesting. Leave oversized and trees with decay as legacy trees. Promote abundance and growth.
Sx	High*	X		Partial harvesting. Leave oversized and trees with decay as legacy trees. Promote abundance and growth.
Lw	High	X		Partial harvesting. Leave oversized and trees with decay as legacy trees. Promote growth.
Py	High	X		Partial harvesting. Leave oversized and trees with decay as legacy trees. Promote growth.
At	Medium			Leave intact where present. Partially harvest groups with > 10 trees if needed.
Ew	Low			Leave intact where present. Partially harvest groups with > 10 trees if needed.
Pl	Negative		X	Harvest
Bg	None		X	Harvest
Bl	None		X	Harvest
Act	Low			Leave intact where it grows.

* Hybrid spruce is only important in higher elevations such as 1 400 m.

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Appendix 1 – Chapter 2 supplementary material

Table A1.1. Variables of foraging and available trees that were measured but not used in the analysis of Williamson's Sapsucker tree characteristics selection for foraging. The data were collected during a telemetry study in 2014-2015 in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones in British Columbia, Canada. Bark cover was not used in the analysis because there was little variability. Animal use index was judged irrelevant and ant presence will be used in a subsequent analysis.

Variable name	Description of the variable	Variable type
Bark cover	Bark cover estimated in 10% increments from 0 to 100%	Continuous
Animal use index	There can be more than one sign recorded 1: Woodpecker foraging 2: Bird bark scaling 3: Signs of squirrel feeding 4: Antler rubbing 5: No signs	Factor (five levels, although the levels can be combined)
Ant presence	1: Absent (0) 2: Present (1) 3: Many (2)	Ordinal (three levels)

Table A1.2. Comparison of size (dbh) of live Douglas-fir used for foraging by 27 radio-tracked Williamson's Sapsuckers during study in 2014-2015, for the nestling stage only. Mann-Whitney-Wilcoxon tests were used for all tests, except to compare the dbh of live Douglas-fir used by foraging mode (Kruskal-Wallis). I used only live Douglas-fir that were used at least five minutes apart to reduce the potential effects of spatio-temporal correlation in dbh with adjacent trees. All live Douglas-fir are unique (no replication or reutilization).

Biogeoclimatic zone	Subset	dbh $\bar{X}$ ± SE	# trees	Test	χ^2 (W)	df	P
Overall (both)	**MS zone**	**34.0 ± 1.6**	**128**	**MS-IDF**	**(9640.5)**	**1**	**<0.001**
	IDF zone	**38.4 ± 0.9**	**211**				
MS zone	**Foraging mode**			**GL-PE-SF**	**8.66**	**2**	**0.01**
	Gleaning	35.8 ± 1.9	114	GL-PE*	(860)	NA	0.13
	Pecking	48.3 ± 7.5	7	**PE-SF***	**(921)**	**NA**	**< 0.001**
	Sap feeding	**28.1 ± 1.7**	**44**	**SF-GL***	**(4165.5)**	**NA**	**0.001**
IDF zone	Foraging mode			GL-PE-SF	5.03	2	0.08
	Gleaning	38.9 ± 0.9	264				
	Pecking	42.5 ± 2.8	24				
	Sap feeding	35.1 ± 1.1	74				

* I used Bonferroni-corrected Mann-Whitney-Wilcoxon tests to account for multiple testing (three tests, α = 0.017). GL = gleaning, PE = pecking and SF = sap feeding.

Table A1.3. Proportion of use and measurements of characteristics of tree species using substrate use observations of 27 radio-marked Williamson's Sapsuckers according to their nesting status in southern British Columbia in 2014-2015 in the a) Montane Spruce and b) Interior Douglas-fir biogeoclimatic zones. The mean and median values are presented for the diameter at breast height (dbh) and decay class, respectively. Blistering includes resin exudation.

a) MS zone (Okanagan Falls and Oliver)

	Tree species	Douglas-fir	Western larch	Hybrid spruce	Overall
	Charact.	Value ± SE (range)	Value ± SE (range)	Value ± SE (range)	Value ± SE (total)
Pre-nestling	% tree sp.	56.9 ± 1.9	36.2 ± 3.3	3.4 ± 2.5	(96.5)
N = 7 birds	dbh (cm)	39.4 ± 4.2 (17.9-76.9)	57.6 ± 5.4 (29.6-92.3)	29.4	44.7 ± 3.7
n = 58 obs.,	Decay cl.	2A (1-2B)	2B (1-5)	1	2A
33 trees	% alive	100	61.5 ± 3.6	100	81.8± 1.4
	% Blistering	58.8 ± 2.7	7.7 ± 4.4	0	36.4 ± 2.5
Nestlings	% tree sp.	58.3 ± 2.7	25.4 ± 4.2	9.2 ± 6.7	(92.9)
N = 11 birds	dbh (cm)	32.4 ± 1.5 (4.5-91.8)	48.2 ± 3.3 (6.2-108.0)	28.5 ± 2.2 (13.4-58.5)	34.2 ± 1.3
n = 338 obs., 254 trees	Decay cl.	1 (1-4)	2A (1-2B)	1 (1-2B)	2A
	% alive	98.7 ± 3.0	100	100	98.4 ± 2.4
	% Blistering	55.4 ± 3.9	34.0 ± 6.3	24.0 ± 8.1	47.6 ± 3.2
Post-breeding[*]	% tree sp.	44.4 ± 1.9	23.6 ± 3.0	30.1 ± 6.6	(98.1)
N = 4 birds	dbh (cm)	36.9 ± 2.3 (17.0-61.9)	46.0 ± 4.7 (23.1-85.2)	34.1 ± 2.4 (17.2-56.0)	38.0 ± 1.7
n = 72 obs.,	Decay cl.	1 (1-4)	2B (1-5)	1 (1-2B)	1
62 trees	% alive	89.7 ± 2.3	84.6 ± 4.1	100	90.3 ± 2.0
	% Blistering	34.5 ± 2.7	23.1 ± 4.7	5.3 ± 8.1	22.6 ± 2.5
Non-breeders	% tree sp.	62.1 ± 1.5	13.8 ± 4.2	0	(75.9)
N = 1 bird	dbh (cm)	32.3 ± 2.6 (19.2-54.0)	33.9 ± 2.5 (26.9-39.0)	NA	32.5 ± 1.9
n = 29 obs.,	Decay cl.	1 (1-4)	2B (1-4)	NA	2A
19 trees	% alive	92.3 ± 1.6	50.0 ± 1.9	NA	84.2 ± 1.1
	% Blistering	23.1 ± 1.6	0	NA	21.1 ± 1.6

[*] Post-breeding includes birds that were observed foraging following a nest failure or predation, or > 4 days after the nestlings fledged.

Table A1.3.

b) IDF zone (Princeton and Merritt)

	Tree species	Douglas-fir	Ponderosa pine	Overall
	Charact.	Value ± SE (range)	Value ± SE (range)	Value ± SE (total)
Pre-nestling	% tree sp.	61.3 ± 1.2	37.1 ± 3.8	(98.4)
N = 7 birds	dbh (cm)	45.3 ± 4.8 (16.3-141.8)	54.7 ± 6.3 (27.4-104.4)	48.0 ± 3.9
n = 62 obs.,	Decay cl.	2A (1-4)	3 (2A-4)	2A
42 trees	% alive	90.0 ± 1.5	16.7 ± 4.9	69.0 ± 1.5
	% Blistering	46.7 ± 1.8	8.3 ± 4.5	35.7 ± 3.1
Nestlings	% tree sp.	83.8 ± 2.0	14.6 ± 1.7	(98.4)
N = 11 birds	dbh (cm)	39.0 ± 0.9 (10.0-87.4)	48.6 ± 3.1 (19.2-90.8)	40.0 ± 0.9
n = 426 obs., 252 trees	Decay cl.	2A (1-4)	2A (1-4)	2A
	% alive	99.5 ± 2.7	52.8 ± 7.5	92.1 ± 2.5
	Blistering	64.5 ± 3.3	2.8 ± 6.1	54.4 ± 3.0
Post-breeding*	% tree sp.	79.3 ± 1.7	20.1 ± 3.8	(100)
N = 7 birds	dbh (cm)	41.3 ± 1.7 (19.0-103.0)	44.4 ± 2.7 (29.6-77.1)	42.0 ± 1.4
n = 116 obs.,	Decay cl.	2A (1-3)	3 (1-4)	2A
89 trees	% alive	98.6 ± 2.3	26.3 ± 7.1	83.1 ± 2.2
	% Blistering	58.6 ± 2.9	5.3 ± 5.4	47.2 ± 2.8
Non-breeders	% tree sp.	82.6 ± 0.8	17.4 ± 1.7	(100)
N = 2 birds	dbh (cm)	48.6 ± 3.9 (31.0-94.3)	44.6 ± 9.1 (19.8-59.2)	47.8 ± 3.5
n = 23 obs.,	Decay cl.	2A (1-2B)	3 (1-4)	2A
21 trees	% alive	100	50.0 ± 3.2	90.5 ± 1.2
	% Blistering	52.9 ± 1.5	25.0 ± 2.5	47.6 ± 1.4

* Post-breeding includes birds that were observed foraging following a nest failure or predation, or > 4 days after the nestlings fledged.

Appendix 2 – Chapter 3 supplementary material

Fig. A2.1

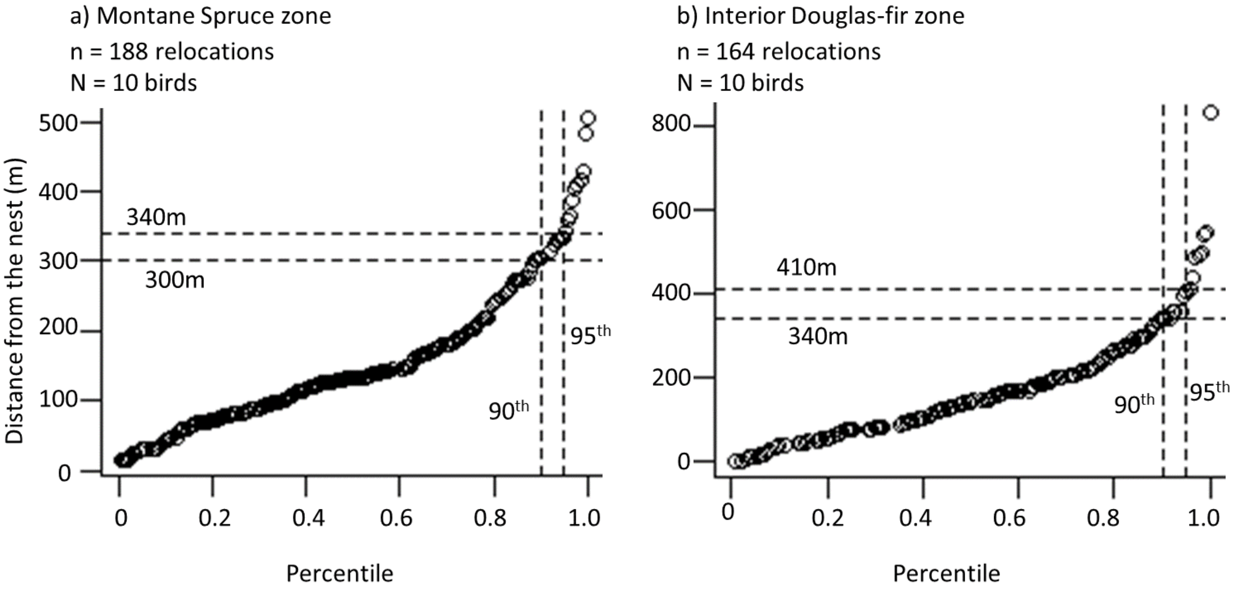

Figure A2.1. Distance from the nest against percentile distribution, used to identify gaps in relocation distances of Williamson's Sapsuckers and determine distance thresholds for conservation and management areas in the a) Montane Spruce and b) Interior Douglas-fir habitats of Williamson's Sapsuckers in southern British Columbia, Canada.

Fig. A2.2

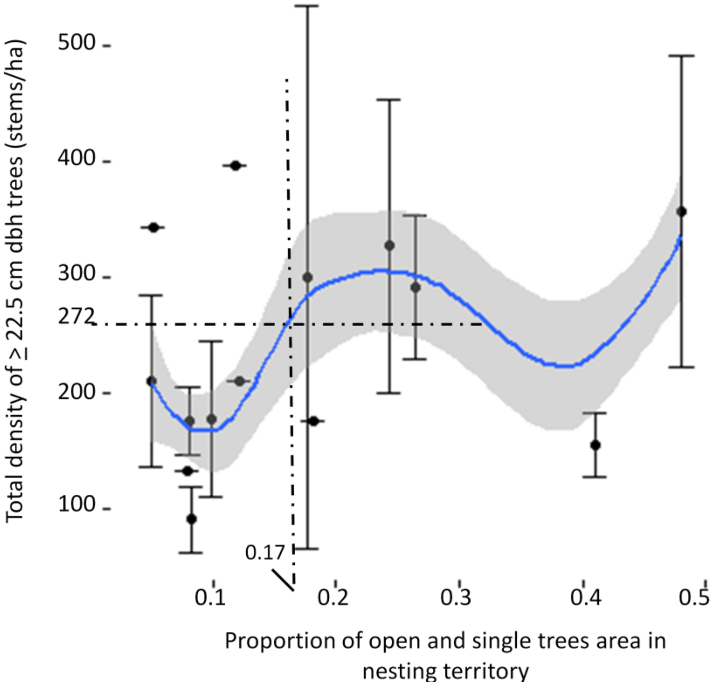

Figure A2.2. Density of foraging trees (> 22.5 cm dbh standing dead and alive) in forest stands that were used for foraging by Williamson's Sapsuckers in relation to the proportion of open and single trees area in the nesting territory. The data were collected in the Montane Spruce and Interior Douglas-fir biogeoclimatic zones in Canada in 2014-2015. The scatter points represent the mean tree density in each of 14 studied nesting territories in which data were available during the nestling stage, and the error bars represent the standard error. The mean density of trees for each nesting territory was estimated using 1 to 5 nested plots per nesting territory. The nested plots were centered on foraging trees in habitat that was highly used by WISA. I used a Locally Weighted Least Square Regression (LOESS) to obtain a locally weighted non-linear curve and its 95% prediction interval (shaded area). WISA only showed significant preferences for stand-level characteristics in the Interior Douglas-fir biogeoclimatic zone (see results), possibly because nesting territories contained higher proportions of area of open habitat and single trees. I used the mean density of foraging trees in the Interior Douglas-fir biogeoclimatic zone as a cut-off value (272 trees/ha) for the proportion of area of open habitat and single trees at which Williamson's Sapsuckers are likely to manifest stand-level preferences for foraging.