Habitat requirements of the Yellow-bellied Sapsucker, *Sphyrapicus varius*, in boreal mixedwood forests of northwestern Canada

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Abstract: Despite its role as a keystone species, few studies have investigated the habitat requirements of the Yellow-bellied Sapsucker (*Sphyrapicus varius* (L., 1766)) in the northwestern part of its range, where the current forest harvesting rotation schedule and targets for reducing the prevalence of old and mixedwood stands may reduce the optimal habitat for this species. We studied nesting and foraging habitat requirements of nesting sapsuckers in a boreal mixedwood forest of northwestern Canada by collecting data on nesting sites and foraging substrates on twenty-four 16- to 56-ha plots distributed among four habitat types in 1998 and 2002. Nests (n = 68) were generally found in large (≥22 cm diameter at breast height) trembling aspen (*Populus tremuloides* Michx) that were alive but declining and that showed high incidence (81.1%) of heartwood rot infection (*Phellinus tremulae* (Bondarzev) Bondarzev & Borisov in Bondarzev). Nest-site use by sapsuckers was predicted mainly by the presence of external fungal conks and tree diameter. Among tree species used as foraging substrates, paper birch (*Betula papyrifera* Marsh.) (65.6%) and green alder (*Alnus viridis* (Vill.) Lam. & DC.) (21.3%) were used most frequently. The use of birch was strongly correlated with its availability. Mature forests had higher densities of nesting sites and foraging substrates than immature aspen stands. In addition to reconfirming the importance of mature mixedwood forests for Yellow-bellied Sapsuckers, our study also indicates that forest harvest rotations in northwestern Canada should exceed 90 years to promote the keystone role of this species.

Résumé : Bien que le pic maculé (*Sphyrapicus varius* (L., 1766)) soit considéré comme une espèce-clée dans plusieurs écosystèmes forestiers nord-américains, il existe peu d'études récentes sur l'écologie de l'espèce dans les forêts du nord-ouest canadien où les objectifs de récolte des peuplements mixtes parvenus à maturité ainsi que le temps de rotation entre les récoltes menacent de réduire l'habitat optimale de cette espèce. Nous avons étudié l'utilisation de l'habitat pour la nidification et l'alimentation du pic maculé dans la forêt boréale mixte du nord-ouest canadien en décrivant les sites de nidification et les substrats utilisés pour l'alimentation dans vingt-quatre parcelles de 16–56 ha distribuées dans quatre types d'habitat en 1998 et 2002. Les cavités de nidification (n = 68) sont creusées principalement dans les peupliers faux-trembles (*Populus tremuloides* Michx), généralement vivants mais en sénescence, de grand diamètre (≥22 cm diamètre à hauteur de poitrine) et avec une forte incidence (81,1 %) d'infection du coeur par *Phellinus tremulae* (Bondarzev) Bondarzev & Borisov in Bondarzev. L'utilisation d'un site de nidification par le pic maculé peut être prédite surtout par la présence de carpophores du champignon ainsi que par le diamètre des arbres. Six espèces d'arbres sont utilisées comme substrat d'alimentation, principalement le bouleau blanc (*Betula papyrifera* Marsh., 65,6 %) et l'aulne crispé (*Alnus viridis* (Vill.) Lam. & DC., 21,3 %). La densité du bouleau blanc comme substrat d'alimentation est fortement corrélé avec la disponibilité du bouleau. À l'échelle du peuplement forestier, nos résultats indiquent que les peuplements de forêts matures ont des densités de nids et de substrats d'alimentation significativement plus élevées que les peuplements immatures décidus. En plus de confirmer l'importance de la forêt boréale mixte mature pour les besoins en habitats du pic maculé, notre étude suggère que le temps de rotation dans la récolte de matière ligneuse dans le nord-ouest canadien devrait être supérieur à 90 ans afin de promouvoir le rôle d'espèce-clée du pic maculé.

Introduction

In North America, 70% of the breeding population of Yellow-bellied Sapsuckers (*Sphyrapicus varius* (L., 1766)) is found in the boreal mixedwood forest ecosystem (Blancher 2003), where this species is the most common woodpecker species (Erskine 1977; Machtans and Latour 2003). Due to the importance of its range in Canada, this species has received the status of high national responsibility in Canada (Dunn et al. 1999). Generally, this species is considered a double keystone species in deciduous and mixed-forest ecosystems because it provides nesting and foraging habitat for a diversity of species (Kilham 1971; Erskine and McLaren 1972; Sutherland et al. 1982; Miller and Nero 1983; Daily et al. 1993; Rissler et al. 1995; Martin and Eadie 1999). Despite its high abundance in most of its range in northern Canada, the species' habitat requirements and its role in the boreal forest ecosystem are not well understood (see Walters et al. 2002).

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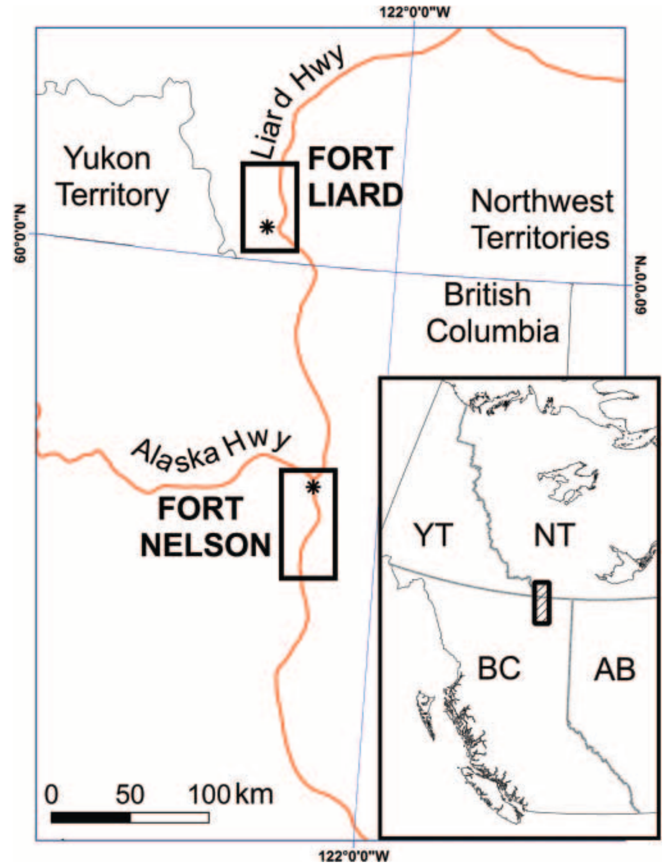
Recent forest songbird surveys conducted in northern Canada suggest that Yellow-bellied Sapsuckers reach higher abundance in mature and old deciduous and mixedwood forests (Schieck et al. 1995; Schmiegelow et al. 1997; Hobson et al. 2000; Schieck and Hobson 2000; Machtans and Latour 2003). Evidence from eastern North America also suggests that this species shows high habitat specificity for nesting and foraging substrates (Kilham 1971; Tate 1973; Runde and Capen 1987; Daily 1993). The specificity in habitat requirements could make the Yellow-bellied Sapsucker susceptible to anthropogenic changes to its habitat. In northwestern Canada, the current harvest regime for mature and old aspen stands is clear-cut harvesting with retention patches (Merkens and Booth 1998) and a rotation of 60–70 years (Stelfox 1995). Such large-scale conversion of mature and old forest stands to younger forests may decrease the availability of suitable nesting habitat for sapsuckers — particularly large aspen trees with fungal infection. Although sapsuckers will nest in cutover areas (when nest trees are retained), reproductive success in these habitats is not known (Walters et al. 2002). However, large aspen trees are usually removed from retention patches within clear-cuts, leaving poplar trees, which sapsuckers will not use as nest substrates (Merkens and Booth 1998). The growth of paper birch (*Betula papyrifera* Marsh.) and other shrub species is generally higher after harvesting, which could provide suitable foraging habitat for sapsuckers, but current silvicultural practices to control deciduous plant growth, such as herbicide use and thinning in cutover areas, could have detrimental effects on the availability of suitable feeding substrates. Detailed studies of the habitat requirements of Yellow-bellied Sapsuckers in the boreal forest are therefore needed to better understand potential impacts of timber harvesting on breeding populations.

The purpose of our study was to determine whether current forest harvesting practices will negatively affect the nesting and foraging requirements of Yellow-bellied Sapsuckers in a boreal mixedwood forest of northwestern Canada. To meet our purpose, we used a descriptive study approach based on data from numerous nest and comparison sites. Our first objective was to describe the characteristics of trees used for nesting activities and the occurrence of such nest trees in relation to typical harvest schedules. We predicted a high selectivity of Yellow-bellied Sapsuckers for large-diameter aspen trees with heartrot decay (i.e., infection with *Phellinus tremulae* (Bondarzev) Bondarzev & Borisov in Bondarzev), based on existing literature. Our second objective was to describe the tree species used for foraging. We predicted that Yellow-bellied Sapsuckers would be selective toward paper birch, considering the affinity for this tree species in other parts of the sapsucker range (i.e., eastern North America) and given the abundance of this tree species in the understory of boreal mixedwood stands (Stelfox 1995). Our third objective was to compare densities of nest trees and feeding substrates among four habitat types: mature (>90 years old) mixedwood stands, mature spruce stands, mature deciduous stands, and immature (<40 years old) deciduous stands. We predicted that mature mixedwood stands would have higher densities of nest trees and feeding substrates than other forest types, thereby being optimal habitat and putting the keystone role at greatest risk given mixedwood harvest practices (Hobson and Bayne 2000). Our final objective was to evaluate the relationship between nest tree density and the density of paper birch used for feeding activities. We predicted a positive and significant relationship between densities of active nest trees and feeding substrates (i.e., paper birch).

Fig. 1. Location of the study area and sampling sites near Fort Liard, Northwest Territories, and Fort Nelson, British Columbia, in northwestern Canada. Yellow-bellied Sapsucker (*Sphyrapicus varius*) nesting sites were surveyed in the entire study area, while foraging substrates were sampled only from the Fort Liard area.



Methods and materials

Study area

Two areas were included in the study design. The first was in the Liard River valley, in the southwest corner of Northwest Territories, Canada (60°15′N, 123°30′W, Fig. 1). The area is in the Boreal Taiga Plains ecoprovince. The region is dominated by mixed stands composed principally of trembling aspen (*Populus tremuloides* Michx), balsam poplar (*Populus balsamifera* L.), and white spruce (*Picea glauca* (Moench) Voss). The area also has a significant amount of coniferous stands, which are dominated by white spruce in uplands and riparian areas and by black spruce (*Picea mariana* (Mill.) B.S.P.) in wet areas (i.e., forest bogs), and pure deciduous stands (dominated by *P. tremuloides* and *P. balsamifera*) of varying ages. Old stands (i.e., with broken canopies and >120 years old) are characterized by tall (>30 m) and large-diameter (>50 cm) trees, a high cover of tall-shrub layers (dominated by *Alnus* spp. and willow, *Salix* spp.), and high structural heterogeneity (Machtans 2000; Machtans and Latour 2003). Major natural disturbances affecting forest structure include infrequent fire, blowdown, and insect outbreaks. Timber harvesting is infrequent in the area. A detailed description of the study area and avifauna can be found in Machtans (2000) and Machtans and Latour (2003).

The second sampling site was located ~250 km south of Fort Liard, along the Prophet River near Fort Nelson, British Columbia (Savignac 1998; Fig. 1). Temperature and climate in the Fort Nelson area are similar to those in Fort Liard, with mean July and January temperatures of 16.7 °C and –22.0 °C, respectively. Forests are similar to those in Fort Liard and are dominated by mature and old-growth mixedwood and spruce stands in riparian areas and by black spruce bog–fen wetlands in upland areas.

Methodology

Habitat description

In the Fort Liard study area, we measured habitat variables in four habitat types: mature and old mixedwood stands (n = 9), mature and old white spruce stands (n = 5), mature deciduous stands (n = 5), and immature deciduous stands (n = 5). These habitat types were selected based on availability at both sampling sites. Vegetation was sampled in sixteen 0.04-ha plots placed at 100 m intervals along every second transect of twelve 12.3-ha grids. In each 0.04-ha plot, we counted trees (stem ≥2 m tall and ≥8 cm in diameter at breast height (dbh)), poles (stem ≥2 m tall and 3–7 cm in dbh), and saplings (stem ≥2 m tall and 0–2 cm in dbh) of all species. Three dominant tall-shrub species (willow, green alder (*Alnus viridis* (Vill.) Lam. & DC.), and river alder (*Alnus tenuifolia* Nutt.)) were counted within two quarters (NE and SW) of the 0.04-ha plots, and canopy height, tall-shrub height, and percent canopy cover were also measured. Canopy height was measured with a clinometer and tall-shrub strata were visually estimated. Percent canopy cover was measured with an ocular tube; readings (i.e., cover [hits] or no cover [misses]) were taken every third step along four 350 m long transects in each 12.3-ha grid.

In a previous study conducted in the study area (Machtans and Latour 2003), two methods were used to age forest stands. The first method was based on the 1994 forest inventory for the area completed by the territorial government. The age of stands was inferred from stand heights, ground-truthed for the classification, and lumped into the following age categories: >200, 150–199, 110–149, 90–109, 70–89, 50–69, and 30–49 years. The second method used to age stands was to take tree cores at breast height from the largest specimens in a stand and calculate age directly. Specimens were chosen so that they clearly represented the cohort of trees in the stand (i.e., were not a fire residual), were among the tallest trees, and had strong lateral branching lower down (indicating that they grew in more open conditions than surrounding trees or were dominant all along the growth curve of the stand). We sampled 3–5 trees from each stand that fit these characteristics and averaged their age to get stand age.

Nesting habitat

Variables related to availability of Yellow-bellied Sapsucker nesting habitat were estimated for each habitat type: percent canopy cover, canopy height, tall-shrub height, mean tree diameter, total tree density (stems/ha), and density of large (≤30 cm in dbh) aspen trees.

Nest searches were conducted in 24 plots. In the Fort Liard region, 12 plots (30.3 ha) were visited 11–15 times between 15 May and 30 July 2002. In the Fort Nelson study area, nests were found by visiting 12 plots (16–56 ha) a minimum of five times between 23 May and 30 June 1998. Nest sites were also found opportunistically along access routes to the study plots. Nest tree density was estimated for all habitat types. Observers walked along transects and looked and listened for visual and aural cues that would indicate the presence of an active cavity, such as (*i*) noise from an adult excavating, (*ii*) presence of mating pairs, (*iii*) presence of fresh wood chips at the base of suitable nest trees, and (*iv*) nestling begging calls at a nest cavity. A minimum of five visits in any of our plots was thought to be sufficient to detect all active nests given the ease of detecting nests when nestlings are vocalizing from the cavities. Nest searching was conducted only on rain-free days with winds <20 km/h.

For each nest tree found we recorded tree species, tree height, tree dbh, presence or absence of fungal conks, presence or absence of old nest cavities, and decay class. To describe decay class, we used a variation of Chesterman and Stelfox’s (1995) classification that included live and declining trees: (*i*) alive, ≥95% foliage; (*ii*) declining, 95% > x ≥ 20% foliage; (*iii*) recently killed, hard wood, firm bark cover, 0% foliage; (*iv*) hard wood, no more small twigs; (*v*) hard wood, loose bark cover, broken top; (*vi*) soft, decomposed wood, broken trunk; (*vii*) stump. We also measured these tree characteristics on random trees of the same species. Random trees were selected within the boundaries of plot stands and ≤100 m from the nest tree by using a random distance and compass bearing from a nest tree.

Foraging habitat

For each habitat type, the number and density of available foraging substrates (i.e., stems with no apparent signs of sapsucker feeding) were estimated for paper birch (trees and poles), green alder, and river alder. These three species represent most trees used for feeding activities by sapsuckers in the study area.

We also measured feeding substrate characteristics on stems showing old or fresh signs of feeding. No data were collected directly on individual feeding birds. Each plot was surveyed for forage trees by searching for stems that had either inactive or recent sap holes. For each used stem found we recorded tree species, dbh, tree height (m), sap hole type (recent, ≤1 year old; inactive, ≥1 year old), tree defects (i.e., leaning, frost crack, broken top, broken branches), and sap hole height (m). Recent sap holes were identified by the presence of fresh sap and by the pale coloration of wood surrounding the holes. Sap holes classified as inactive had no sap flow and were surrounded by wood of a darker color. We estimated forage tree density per 12.3-ha plot by averaging values obtained from all 16 vegetation plots surveyed within a study plot.

Table 1. Summary of vegetation characteristics measured at four habitat types surveyed for Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in the Fort Liard area.

	Mature mixed (n = 96)		Mature white spruce (n = 32)		Mature deciduous (n = 32)		Immature deciduous (n = 32)	
Variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Canopy height	27.5	0.5	27.1	0.4	24.4	1.0	19.3	0.7
Mean tree dbh	25.1	0.5	25.9	0.7	21.7	1.3	13.9	0.5
Density of aspen trees ≥30 cm in dbh (stems/ha)[a]	73.2	7.5	71.1	12.2	60.2	15.7	14.1	4.3
% canopy cover[b]	46.3	1.5	57.0	5.2	39.9	2.7	69.9	2.2

[a]Average densities were calculated by averaging densities for all 0.04-ha circular plots per 12.3-ha grid.

[b]All variables were tested with one-way ANOVA except for percent canopy cover, which was tested using the Kruskal–Wallis test.

Statistical analysis

Habitat description

All habitat variables were tested using a one-way ANOVA with a Tukey HSD test for multiple comparisons (Zar 1984), with the exception of percent canopy cover, which was tested using a Kruskal–Wallis test.

Nesting habitat

Characteristics of nest versus random trees were compared using t tests (Zar 1984). For qualitative variables (decay class, percentage of trees with external conks, and percentage of trees with other nest cavities), a nonparametric likelihood ratio test was used instead. We tested the relationship between nest height and dbh of nest trees using a Pearson correlation analysis.

Habitat variables that best differentiated nest trees from randomly selected trees were tested using a backward-elimination stepwise logistic regression (SLR, SPSS Inc. 1997). Variables entered in the model were tree height class, dbh, decay class, presence or absence of fungal conks, presence or absence of another nest cavity, and the interaction between study area and each of the above-mentioned variables. The significance of the final models and of the contribution of each variable was tested by the change in deviance (–2 log-likelihood ratio, LR) between the saturated model (all variables included) and models with variables of interest removed. Entry and removal probabilities for each step of the stepwise procedure were set at 0.05 and 0.1, respectively. We compared nest density (no. of nests/ha) among habitat types using a two-way ANOVA.

Median diameter of aspen trees in forest stands of various ages was plotted for a range of forest types using data from Machtans and Latour (2003) and additional unpublished data (C.S. Machtans). This data represented a much broader age sample than that obtained from the plots searched intensively for nests. The relative abundance of Yellow-bellied Sapsucker from point-count surveys in stands of various ages in the study area was used to assess the relationship between the species' relative abundance and forest age (Machtans and Latour 2003).

Foraging habitat

We compared the proportion of forage substrates per habitat type as well as for the entire study area using χ^2 tests. Characteristics of forage substrates were tested using the Kruskal–Wallis test followed by Dunn's method for multiple comparisons (Zar 1984). Sap hole type on forage substrates was compared for each species using a χ^2 test. Mean stem density of forage substrates was compared among the four habitat types using a one-way ANOVA with Tukey's test for multiple comparisons (Zar 1984). The relationship between the density of paper birch stems used as foraging substrates and the number of available birch stems was tested with the Pearson correlation analysis (Zar 1984).

The relationship between nest density and the density of forage substrates was tested using the Pearson correlation analysis. We pooled the data from substrates with recent, recent and old, and old sap well cavities prior to performing this analysis. Correlation analysis was performed only on paper birch, as this species was the main forage substrate.

Data from Machtans and Latour (2003) and unpublished data (C.S. Machtans) were used to describe the size distribution of aspen for a range of stand ages wider than that available on the nest-searching plots. Data from the same sources were also used to show detection rates of sapsuckers for the broader range of forest age classes in the area.

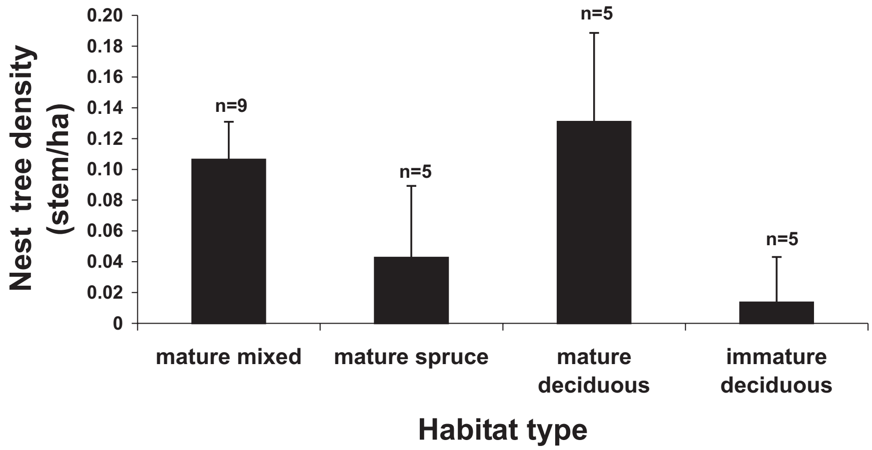
Statistical procedures were run with SPSS for Windows© Version 8.0.0 (SPSS Inc. 1997). All tests were performed at α = 0.05. Standard error is reported unless otherwise noted.

Results

Characterization of habitat types

Canopy height differed significantly among habitat types (range 24–28 m versus 19 m, $F_{[3,184]}$ = 26.2, $P \leq 0.001$, Table 1). Canopy height in mature mixed forest was higher than that in mature deciduous forest (Tukey HSD test, $P \leq 0.01$, Table 1). Canopy height in immature deciduous forest was generally lower than that in all three other habitat types (immature deciduous versus mature mixed, Tukey HSD test, $P \leq 0.001$; immature deciduous versus mature spruce, Tukey HSD test, $P \leq 0.001$; immature deciduous versus mature deciduous, Tukey HSD test, $P \leq 0.001$, Table 1). Tree dbh also differed significantly among habitat types (22–26 cm versus 13.9 cm, $F_{[3,191]}$ = 44.9, $P \leq 0.001$, Table 1). Differences in dbh occurred between mature mixed and mature deciduous stands (Tukey HSD test, $P \leq 0.01$, Table 1), between mature mixed and immature deciduous stands (Tukey HSD test, $P \leq 0.001$, Table 1), and between mature spruce and mature deciduous stands (Tukey HSD test, $P \leq 0.01$, Table 1). Tree dbh in immature deciduous forest was significantly lower than that in mature spruce (Tukey HSD test, $P \leq 0.001$, Table 1) or mature deciduous forest (Tukey HSD test, $P \leq 0.01$, Table 1). Density of large aspens differed significantly

Fig. 2. Mean density of nest trees used by Yellow-bellied Sapsuckers in northwestern Canada. Sample size refers to the number of plots where nests (n = 68) were found.



among habitat types ($F_{[3,192]}$ = 6.0, $P \leq 0.001$, Table 1) and was generally lower in immature deciduous stands than in mature mixed (Tukey HSD test, $P \leq 0.001$), mature spruce (Tukey HSD test, $P \leq 0.01$), and mature deciduous stands (Tukey HSD test, $P \leq 0.05$, Table 1). Percent canopy cover was higher in immature deciduous forest and lower in mature deciduous forest (40%–57% versus 70%, Kruskal–Wallis H = 22.2, df = 3, $P \leq 0.001$, n = 48, Table 1).

Nesting habitat

We found 68 active nests (32 in Fort Liard and 36 in Fort Nelson). All nests were found in trembling aspen. Nest cavity height ranged between 4 and 17 m (mean ± SE: 10.4 ± 0.4, n = 68). Height of nest trees ranged between 9 and 35 m and did not differ from that of random trees (24.8 ± 0.6 m versus 27 ± 0.7 m, $F_{[135,137]}$ = 0.02, P = 0.9). Sapsuckers used nest trees with dbh ranging from 22 to 70 cm. The average nest tree diameter was significantly smaller than the average dbh of random trees (35.1 ± 1.2 cm versus 41 ± 1.6 cm, $F_{[135,137]}$ = 11.6, $P \leq 0.001$). The degree of decay in nest trees also differed significantly from that of random trees (more decay class 2 and 3 among nest trees, likelihood ratio = 8.0, df = 3, P = 0.04, n = 137). Nest trees were generally in a higher state of decline than random trees (54% versus 39%) and had a higher incidence of fungal conks than random trees (81% vs. 42%, likelihood ratio = 22.6, df = 1, $P \leq 0.001$, n = 137). The frequency of trees with inactive nest cavities was significantly higher among nest trees than among random trees (16% versus 5.8%, likelihood ratio = 3.9, df = 1, P = 0.05, n = 137). There was a significant and positive relationship between nest height and nest tree dbh (r = 0.4, $P \leq 0.01$, n = 68).

The use of nest sites by sapsuckers was significantly influenced by vegetation structure. Of the five variables entered in the SLR model, two were significantly related to nest tree use: the presence of fungal conks (logistic regression: LR = 28.1, df = 1, $P \leq 0.001$, n = 137) and dbh (logistic regression: LR = 14.9, df = 1, $P \leq 0.001$, n = 137).

There was a significant difference in the density of nest trees among habitat types (one-way ANOVA: $F_{[3,24]}$ = 5.3, $P \leq 0.01$, Fig. 2). Densities found in the three mature habitat types did not differ significantly. Nest tree density in immature deciduous stands was lower than that found in mature mixed (Tukey HSD test, P = 0.03, Fig. 2) and mature deciduous stands (Tukey HSD test, P = 0.02, Fig. 2).

Foraging habitat

A total of 431 forage trees of six species were used to measure foraging activities of sapsuckers in the Fort Liard study area. Sapsuckers used paper birch for foraging more often than one would expect by chance (66%, χ^2 = 416.13, df = 3, $P \leq 0.001$, n = 431). Green alder was the second most frequently used species (21%), while river alder (9%) and willow (3%) were used less frequently. White spruce and trembling aspen were used only once and twice, respectively. Sapsuckers used a wider range of tree species in mature mixedwood forest, with paper birch being the most frequently used species (76%, χ^2 = 419.1, df = 3, $P \leq$ 0.001, n = 289). Only two species were used in the mature spruce forest: paper birch (38%) and green alder (62%, χ^2 = 5.1, df = 1, $P \leq 0.02$, n = 87). In mature deciduous forest, paper birch was used most frequently (59%, χ^2 = 18.7, df = 3, $P \leq 0.001$, n = 49), but river alder and willow were used at higher proportions than in any other habitat type.

Sapsuckers used small trees for foraging, with paper birch averaging the tallest (8.0 ± 0.8 m, range 1.0–20.0 m, Table 2) and green alder averaging the shortest (2.9 ± 0.1 m, range 2.0–5.0 m). Paper birch, willow, and river alder had similar diameters but were significantly larger than green alder (Kruskal–Wallis H = 209.2, df = 4, $P \leq 0.001$, Table 2). Sapsuckers used small-diameter paper birch trees (9.6 ± 1.3 cm, range 2.0–37.0 cm), with saplings, poles, and trees comprising 0.4%, 34%, and 65%, respectively, of the paper birch trees used. Among all forage trees used by sapsuckers, 82.4% had no apparent defects (355/431), 15.8% had defects, and 1.8% were recently dead. The height at which sapsuckers foraged varied significantly among tree species (H = 111.5, df = 4, $P < 0.0001$, Table 2). Sapsuckers foraged at similar heights in paper birch, willow, and river alder (range 2.1–2.5 m) but foraged at significantly lower heights in green alder (1.4 ± 0.1 m, H = 111.5, df = 4, $P \leq$ 0.001, Table 2).

For all tree species, stems with old sap holes were significantly more frequent (64%) than stems with both recent and old sap hole cavities (32%) and stems with only recent sap

Table 2. Characteristics of foraging substrates used by Yellow-bellied Sapsuckers in northwestern Canada, 2005.

	Paper birch (n = 283)		Willow (n = 13)		Green alder (n = 92)		River alder (n = 40)		
Variable	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	P
Tree height	8.0±0.8	1.0–20.0	4.9±0.5	2.0–7.0	2.9±0.1	2.0–5.0	6.9±0.6	1.5–12.0	<0.001
dbh	9.6±1.3	2.0–37.0	11.0±1.4	5.0–18.0	3.1±0.1	2–4.5	8.4±0.9	4.0–21.0	<0.001
% of stems with defects	19.1		5.4		0.0		30.0		<0.001
Sap well height	2.1±0.2	0.5–7.0	2.5±0.2	1.5–3.5	1.4±0.1	0.2–2.5	2.3±0.2	0.8–4.0	<0.001

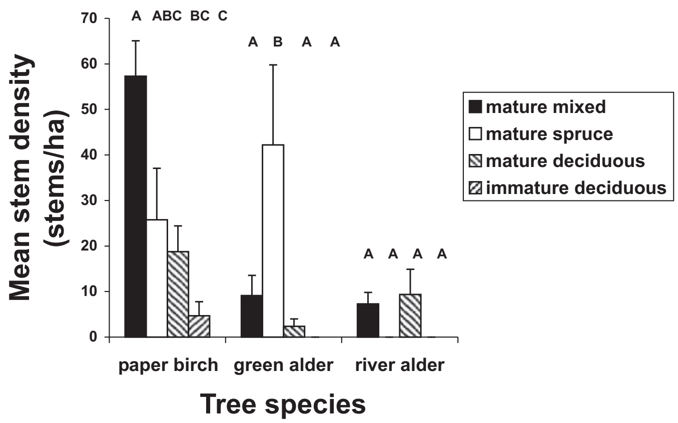
hole cavities (4%, χ^2 = 236.1, df = 2, $P \le 0.001$, n = 415). The frequencies of sap hole types were significantly different for paper birch: a greater proportion of stems had only old sap holes (χ^2 = 159.7, df = 2, $P \le 0.001$, n = 283). Similar patterns were observed for green alder and river alder (χ^2 = 35.8, df = 2, $P \le 0.001$, n = 92 and χ^2 = 36.1, df = 2, $P \le 0.001$, n = 40, respectively). When substrates with only old sap holes were excluded from the analysis, forage substrates with both recent and old sap holes were used more frequently than substrates with only recent sap holes (paper birch: χ^2 = 55.9, df = 1, $P \le 0.001$, n = 98; green alder: χ^2 = 29.5, df = 1, $P \le 0.001$, n = 44; river alder: χ^2 = 2.8, df = 1, P = 0.10, n = 9).

Density of paper birch stems used as foraging substrates differed significantly among habitat types (ANOVA, $F_{[3,44]}$ = 7.5, $P \le 0.001$, n = 48, Fig. 3), with significant differences between mature mixed and mature deciduous stands (Tukey HSD test, P = 0.02) and between mature mixed and immature deciduous stands (Tukey HSD test, P = 0.001). Density of green alder stems used for sap wells also differed significantly among habitat types ($F_{[3,44]}$ = 4.9, $P \le 0.01$, n = 48, Fig. 3), with significant differences between mature mixed and mature spruce forest (Tukey HSD test, $P \le$ 0.01), between mature spruce and mature deciduous forest (Tukey HSD test, P = 0.02), and between mature spruce and immature deciduous forest (Tukey HSD test, $P \le$ 0.01). There were no significant differences in the density of river alder forage stems among habitat types ($F_{[3,44]}$ = 1.9, $P \le 0.14$, n = 48, Fig. 3). In mature mixed forest, the density of paper birch forage stems (57.3 ± 7.7 stems/ha) was significantly higher than the density of green alder (9.1 ± 4.5 stems/ha) and river alder forage stems (7.3 ± 2.5 stems/ha, $F_{[2,69]}$ = 27.9, $P \le 0.0001$, n = 24), but there were no significant differences in forage stem density among tree species in mature deciduous ($F_{[2,21]}$ = 3.1, P = 0.07, n = 8), mature spruce ($F_{[2,21]}$ = 3.1, P = 0.07, n = 8), or immature deciduous stands ($F_{[2,21]}$ = 2.3, P = 0.1, n = 8).

There was a positive and significant correlation between the density of paper birch used for foraging and the density of paper birch available (Pearson correlation, r_p = 0.80, P = 0.002, n = 12).

Comparisons of the percentages of paper birch, green alder, and river alder stems used for feeding activities in the four habitat types are shown in Fig. 4. Overall, the proportion of stems used was greater for paper birch than for green alder and river alder (Fig. 4). Paper birch was used by sapsuckers in all habitat types (Fig. 4), but the highest percent use occurred in mature mixed, mature deciduous, and mature spruce forest (Fig. 4). When all habitat types are considered together, low percentages of green alder and river alder were used by sapsuckers (<2%, Fig. 4). Green alder

Fig. 3. Comparisons of mean densities of stems used as foraging substrates by Yellow-bellied Sapsuckers among four habitat types in northwestern Canada. Mean densities are calculated from twenty-four 350 m long transects in mature mixed forest and along eight transects for mature spruce, mature deciduous, and immature deciduous forest. The same letters above bars indicate nonsignificant differences.



was used in all habitat types but one (i.e., immature deciduous), while river alder was used by sapsuckers only in mature mixed and mature deciduous forest (Fig. 4).

There was no significant correlation between nest density and the mean density of paper birch used for foraging (r_p = 0.42, P = 0.18, n = 12) or between nest density and the density of available paper birch (trees and poles pooled) (r_p = 0.3, P = 0.36, n = 12).

Occurrence of potential nest trees and sapsuckers in forests of various ages

The minimum tree size used for nesting in this study (22 cm) only begins to appear in forests 52 years old (aged by coring the largest trees in the stand) or 68 years old (if only inventory data are relied upon) (Fig. 5). However, sapsuckers are rarely detected in forests younger than 90 years old (aged by either method) (Fig. 6).

Discussion

In this study, we provide the first detailed account of the ecology of nesting and foraging Yellow-bellied Sapsuckers in the mixedwood forest of northwestern Canada. We found that sapsuckers show specific habitat preferences for both nesting and feeding activities, with the highest nesting density found in mature to old deciduous and mixedwood forests. By virtue of their nest-tree selection, sapsuckers would not likely be found nesting in forests younger than about 60 years old, and they were actually rarely detected in forests younger than 90 years old in our study area (Machtans

Fig. 4. Percentage of total stems used for sap-well feeding in four habitat types in the Fort Liard area. Numbers above bars indicate the total number of stems surveyed.

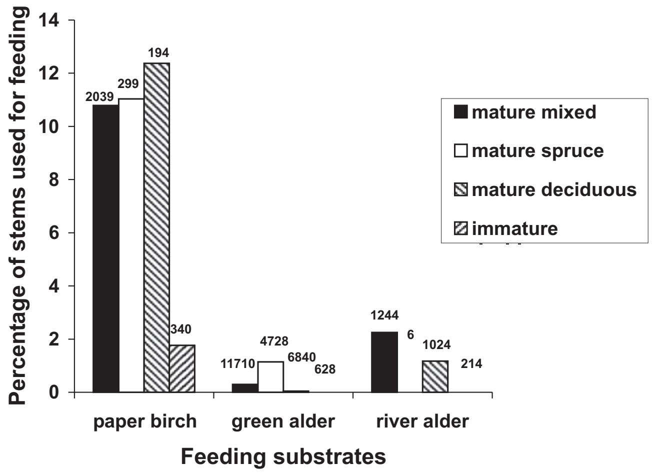


Fig. 5. Median diameter of aspen trees found in forest stands of various ages in the Fort Liard area. Depending on whether stands are aged by coring the largest trees or by using only forest inventory maps, suitably sized nest trees are not present until stands are 52 and 68 years old, respectively.

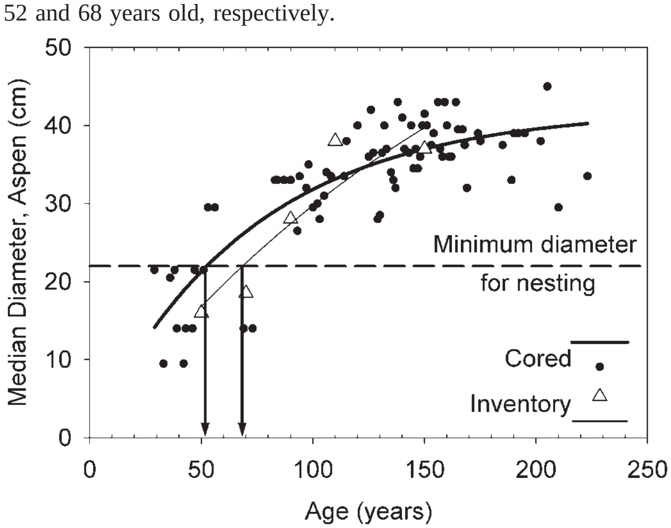
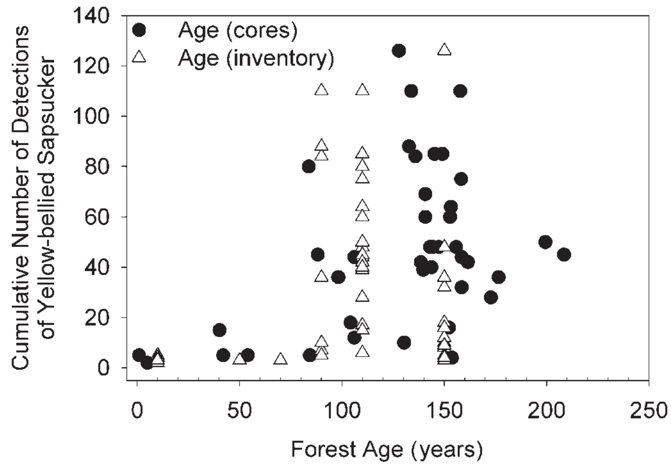


Fig. 6. Cumulative number of point-count detections of Yellow-bellied Sapsuckers over 6 years in forests of various ages in the Fort Liard area (data from Machtans and Latour (2003) and C.S. Machtans). Sapsuckers are rarely detected in forests younger than 90 years old, regardless of whether stand age is determined by coring the largest trees or by relying only on forest inventory maps.



and Latour 2003; C.S. Machtans, unpublished data), creating a conflict with current rotation periods for deciduous and deciduous-dominated forest harvesting.

Nesting habitat

The selection of trembling aspen with heartrot for nesting has been well documented in both eastern (Kilham 1971; Conner et al. 1976; Peck and James 1983; Runde and Capen 1987) and western North America (Harestad and Keisker 1989; Daily 1993; Martin and Eadie 1999). Like our study, studies conducted in the boreal mixedwood forest of northeastern British Columbia showed that Yellow-bellied Sapsuckers nested exclusively in live aspen trees (Murray 1993; Merkens and Booth 1998).

Nest-tree selection can be reasonably predicted by the presence of external fungal conks on the trunk. Eighty percent of all nest trees in our study had external fungal conks (twice as high as the percentage for random trees), similar to results obtained in other studies (Runde and Capen 1987, 84%; Murray 1993, 100%; Merkens and Booth 1998, 98%). In Fort Liard, 91% of the nest cavities found were situated right below or close to conks, supporting previous assertions that the specific conk location is used to assess tree hardness and subsequent excavation difficulty (Anderson and Schipper 1978; Runde and Capen 1987; but see Schepps et al. 1999).

Tree diameter appeared to be the second most important variable affecting nest-tree selection. Sapsuckers nested in trees larger than 22 cm in diameter, similar to nest trees found in northeastern British Columbia (Murray 1993, 28.3 cm; Merkens and Booth 1998, 29.6 cm, minimum 19 cm). This is likely the minimum size of tree large enough for cavities and with heartrot sufficiently advanced to allow easier excavation. Selection of large-diameter trees allows sapsuckers to take advantage of both the presence of a decay column in which to excavate their nest and the hard sapwood layer that can provide maximal protection against predation by mammals (Kilham 1971).

Although sapsuckers used large trees for nesting, they did not select the largest trees available. In fact, sapsuckers nested in trees that were, on average, 15% smaller in diameter than random trees. This contrasts with the findings of Runde and Capen (1987), who suggested that sapsuckers usually nest in the largest stems available. Sapsuckers in our study area may have avoided very large aspen because these trees have thicker sapwood, which increases excavation difficulty. Also, more than half of the random trees did not have fungal conks, so it is possible that the larger trees were not infected by *P. tremulae* and, therefore, had heartwood that was more difficult to excavate.

The presence of old nest cavities on trees (16%) did not appear to be an important variable affecting nest-tree selection. This finding contrasts with other studies that suggest Yellow-bellied Sapsuckers rely on the presence of old nest cavities to assess the quality of nest trees (Runde and Capen 1987; Daily 1993; Murray 1993). Studies conducted in Vermont (Runde and Capen 1987), Colorado (Daily 1993), and northeastern British Columbia (Murray 1993) showed that more than 60% of sapsucker nest trees had old nest cavities. Daily (1993) suggested that sapsuckers cue in on old nest cavities to assess the height of the decay column and to maximize nest height. On the other hand, Eberhardt (1994) showed that sapsuckers reusing old nest cavities had larger clutches than those nesting in new cavities, but that fledgling success in reused nests was less than that in new cavities.

Our study is among the first to estimate the nesting density of Yellow-bellied Sapsuckers across several habitat types in the boreal mixedwood forest (see Walters et al. 2002). Nesting densities in our study area were higher in mature stands (0.10 ± 0.01 nest/ha, n = 20) and lower in immature deciduous stands (0.01 ± 0.01 nest/ha, n = 4). Our estimate for mature stands seems to be among the highest reported in the boreal forest and is similar to the one obtained by Erskine (1977) in mixedwood stands in northeastern British Columbia (0.08 territory/ha, n = 3). In contrast, density estimates obtained for eastern mixedwood boreal forest (i.e., Ontario, Quebec, and New Brunswick) suggest a lower territory density (0.04 territory/ha, n = 2).

Foraging habitat

Paper birch was the main tree used for foraging, similar to findings of other studies (Kilham 1971; Tate 1973; Kessel 1986). Although sapsuckers are known to feed on over a thousand woody plant species across North America, they show a high selectivity toward paper birch because of its sugar concentration and reliable production (Tate 1973). In our study area, only six tree species were used as feeding substrates, with paper birch being the preferred one. The importance of paper birch for sapsuckers in our study area is also demonstrated by the significant, positive relationship between birch used and birch available.

Paper birch was not used evenly by sapsuckers among habitat types. In mature spruce stands, for example, where birch density was half that found in mature mixed stands, sapsuckers used alders more often than paper birch. In coniferous habitat, sapsuckers were probably foraging on green alder as an alternative. However, despite the high abundance of green alder in most forest types surveyed, this species is likely not as suitable as birch as a forage species owing to its smaller diameter, which may prevent sapsuckers from accessing a large amount of sap per stem.

The comparison of sap hole types among forage substrates suggests that sapsuckers were visually assessing the quality of a stem by the presence of old sap wells. Old sap wells could indicate the feeding potential of a particular tree but could also indicate the presence of weakened stems, which produce a higher sugar concentration (Kilham 1964). In fact, sapsuckers usually cluster new sap holes above wounds or old forage cavities to take advantage of the accumulating sap (Kilham 1964; Erdmann and Oberg 1974; Eberhardt 2000).

Habitat use at the forest-stand scale

Yellow-bellied Sapsuckers selected mature and old forest stands for both their nesting and their foraging requirements. The preference for mature and old forest stands found in our study area could be explained by a higher density of suitable nest trees such as large aspen trees with heartwood decay (Merkens and Booth 1998). Fungal infection by *P. tremulae* usually occurs in mature stands (>40 years old) and can account for as much as 60%–70% of stem decay in a stand (Basham 1993; Merkens and Booth 1998). Mature and old stands in our study area also have a high density of paper birch poles, the preferred foraging substrate of sapsuckers during the breeding season. Furthermore, several other studies in the boreal forest have also found that sapsuckers use mature and old stands more frequently than immature stands (see Schieck et al. 1995; Kirk et al. 1996; Merkens and Booth 1998; Hobson et al. 2000). On the other hand, other studies have reported higher sapsucker abundance in extensively cut and regenerating forests (Gibbon 1970; Eberhardt 1994), though it is not clear whether sapsuckers used this habitat strictly for foraging or for nesting habitat as well. Nevertheless, it is clear for our study area that immature forest stands cannot provide suitable habitat for sapsuckers. Subjectively, there appear to be suitable levels of forage substrates available in the younger stands, but suitable nest substrates (minimum dbh 22 cm) are nonexistent.

Yellow-bellied Sapsuckers did select mature forest stands for their nesting and foraging requirements, yet there was no well-defined relationship between nesting density and availability of paper birch stems. Although we cannot rule out the possibility that low sample size affected our results, we believe the weak relationship was mainly due to habitat use patterns in mature spruce and mature deciduous habitats, where densities of foraging substrates used by sapsuckers were relatively low but nesting densities were surprisingly high. When spatial nest distribution is considered for these two habitat types, sapsuckers appear to locate their nests on edges of survey plots (i.e., 89% of nests <50 m from plot edges; C. Savignac and C.S. Machtans, unpublished data). This nest distribution, along with a low density of foraging substrates, seems to indicate that sapsuckers in these two habitats were using these plots mostly for nesting and were likely to defend territories outside survey plots, where foraging habitat was probably more suitable. It is therefore possible that our density estimates were inflated because sapsuckers were taking advantage of suitable nest trees located on edges of apparently ‘‘unsuitable’’ plots but were concentrating their foraging activities mainly outside the survey area.

Management implications

Yellow-bellied Sapsuckers in northwestern Canada have a narrow range of habitat requirements for both nesting and foraging activities. Sapsuckers need large aspen with heartwood rot and a high density of paper birch poles. Suitably sized nest trees do not appear in stands younger than about 60 years old, and sapsuckers are not usually found in stands younger than 90 years old. The nesting and foraging habitat requirements seem to be of equal importance for sapsuckers to occupy an area. A similar pattern was found in Colorado with Red-naped Sapsuckers (*Sphyrapicus nuchalis* Baird, 1858) (Daily et al. 1993), where willow, aspen, *P. tremulae*, and Red-naped Sapsuckers form a keystone species complex. Based on our results, we conclude that Yellow-bellied Sapsuckers, aspen, *P. tremulae*, and paper birch form a keystone species complex in boreal mixedwood forests.

Current forest harvesting practices include short rotation periods (i.e., 60–70 years) (Stelfox 1995) that would dramatically decrease the availability of suitable nest substrates for sapsuckers. Sapsuckers are not using 60–70-year-old forests even though forests of that age can contain trees of the minimize size typically used for nesting. Furthermore, even though suitable nest trees could be left in clear-cuts, it is not clear how these patches would provide suitable long-term sapsucker habitat (Schieck and Hobson 2000). It would therefore be advisable to use a more conservative rotation of at least 90 years and ensure that some older forests always remain on the landscape if forest managers want to maintain long-term populations of this keystone species in the boreal forest.

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