Foraging Ecology and Use of Drumming Trees by Three-Toed Woodpeckers

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FORAGING ECOLOGY AND USE OF DRUMMING TREES BY THREE-TOED WOODPECKERS

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Abstract: Among boreal forest bird species, the three-toed woodpecker (*Picoides tridactylus*) is closely associated with old-growth forests (>120 years), and possibly the most negatively affected by long-term changes induced by commercial forestry in eastern Canada. Part of this conflict is related to the woodpecker's use of standing dead trees as nesting sites. Moreover, this woodpecker's foraging behavior and its choice of feeding and drumming substrates may increase its vulnerability in managed forests. We describe foraging behavior of three-toed woodpeckers, and characterize foraging and drumming trees used by this species in Québec's black spruce (*Picea mariana*) forests. During summer (May–Jul) and mid-winter (Jan–Feb), birds of both sexes used a highly specialized feeding technique consistent with searching for bark beetles (Coleoptera: Scolytidae). Snags were highly preferred over live trees as foraging substrates. Snags used for foraging had a greater diameter at breast height (dbh) and were less deteriorated than paired nearest available snags. When live trees were selected for foraging, they also had a greater dbh but were more deteriorated than nearest available live trees. Thus, only a limited number of trees had all characteristics preferred by foraging woodpeckers, probably as a result of the ecology of its phloem-boring prey. Snags also were highly preferred over live trees as drumming substrates. Drumming snags differed from paired nearest available snags by having a broken top, less bark cover, and a lower deterioration class, which probably provided better acoustic towers for territorial birds. Given the extensive use of snags with different characteristics for foraging and drumming by three-toed woodpeckers, models estimating snag requirements for this species based only on nesting requirements are probably of limited use to maintain populations in managed areas. Wildlife habitat management objectives that specifically require the maintenance and renewal of snags in early decaying stages found in old-growth forests are essential to the conservation of this woodpecker species in managed forests.

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Key words: black spruce, drumming, foraging behavior, *Picoides tridactylus*, Québec, snags, three-toed woodpecker.

In North America, boreal forests are the last relatively undisturbed forest ecosystem. However, each year, the southern edge of these undisturbed areas is increasingly logged in response to an increasing demand for wood fiber (Bryant et al. 1997). Currently, more than 60% of logging operations in Canada occur in virgin old-growth forests (Senate Subcommittee on the Boreal Forest 1999). In the province of Québec alone, ≥300,000 ha of mature coniferous forests are cut annually (Parent 1999). Although harvested areas regenerate naturally or by means of plantations, optimal short logging rotations (<100 years) will prevent future managed forests from developing characteristics associated with old-growth stands (>120 years), including abundant large dead and decaying trees.

The three-toed woodpecker is a year-round resident and 1 of the species most closely associated with old-growth spruce stands (Virkkala 1987, Imbeau et al. 1999). This strong association can be explained by several life history characteristics. As a primary cavity-nesting bird, this woodpecker requires trees with a dbh ≥17.5 cm to excavate its nesting and roosting cavities (Goggans et al. 1989). But more importantly, even if this species can drill holes to sap-lick on live trees (Villard 1994), most of its foraging activities occur on snags (Hogstad 1978, Steeger and Dulisse 1997). This potential dependence on snags is likely to be linked to the woodpeckers' diet, which is composed mainly of phloem-boring bark beetles (Pechacek and Krištín 1993, Steeger and Dulisse 1997, Murphy and Lehnhausen 1998, Fayt 1999). However, current knowledge of the characteristics of foraging substrates (e.g., stage of decay, dbh) used by three-toed woodpeckers is still too fragmentary to be used effectively in snag management models or habitat management plans (Goggans et al. 1989, Bull et al. 1997). Furthermore, specific require-

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ments for drumming substrates are completely overlooked in the existing scientific literature, despite their potential importance for intraspecific relationships, such as conspecific attraction (Reed and Dobson 1993, Lima and Zollner 1996). Before developing efficient conservation strategies to maintain the three-toed woodpecker in managed forests, a much deeper understanding of the ecology of this poorly known species is required.

To assess whether snag retention prescriptions must go beyond the aim of maintaining a supply of potential nesting trees, and be designed to ensure a continuous supply of foraging and drumming trees, we focused on 3 main goals: (1) to describe the three-toed woodpecker's foraging behavior, (2) to characterize its foraging and drumming substrates, and (3) to determine whether foraging requirements vary between sexes and seasons.

STUDY AREA

We conducted this study 120 km northwest of Lac Saint-Jean (48°49′N, 73°08′W), Québec, Canada, which is described by Rowe (1972) as the Chibougamau–Natashquan forest section of the Canadian boreal forest. Described by Saucier et al. (1998) as part of the boreal eastern spruce–mosses forests, this area belongs to the Ashuapmushuan River ecological region. Forests are composed mainly of black spruce or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and occasionally tamarack (*Larix laricina*). Spruces usually take from 80 to 120 years to reach economic maturity (Gouvernement du Québec 1998). These forests are highly sought, and all public forests south of 50°N in Québec are allocated for cutting to various forest companies by the provincial government (Parent 1999).

Our study area was composed of 2 forest types that differed in their level of modifications by logging. In the northern part of our study area, approximately 3,000 ha of continuous old-growth forests were accessible by logging roads and scheduled to be logged within 5 years following our study. In this area, spruces were 120–125 years, and the density of snags ≥10 cm dbh was 210 stems/ha (Imbeau et al. 1999). Approximately 10 km south of the unlogged forest, we selected a 10,000-ha block of recently logged areas (<20 years) dominated by clearcuts ranging from 50–250 ha. Forest remnants persist in linear clear-cut separators (60–100 m wide) and in riparian strips (20 m wide) in accord with the rules defined by the provincial government (Ministère des Ressources Naturelles du Québec 1996). Together, this network of forested clear-cut separators and riparian strips constitutes old-growth forest shreds (sensu Feinsinger 1997) in recently cut areas that represent less than 15% of the original forest cover (Gingras 1997).

METHODS

Location of Woodpeckers and Measurement of Foraging Behavior

Fieldwork was carried out during 3 different field seasons: 2 summers (1997: 22 May–30 Jul; 1998: 20 May–25 Jun) and 1 winter (1998: 6 Jan–4 Feb). During preliminary fieldwork in summer 1996, 2 pairs of woodpeckers found in continuous forests were captured at their nests with a hoop net and marked with color rings. In summer 1997, these 2 pairs were still present within the same area: 1 of them was nesting in the same hole and the other was using a new one approximately 500 m from the previous nest. In addition, we located 4 new pairs (1 in continuous forests, 3 in shredded forests after logging) and, using a hoop net, also banded them at their nests. We then concentrated our observations (98%) during 1997 on these 12 individually recognizable birds. Although 4 of them could be sighted again in 1998, we did not add further observations on these marked birds in order to concentrate our efforts on as many different individuals as possible. We located woodpeckers by using playbacks of drumming and calls, which were broadcasted from 0500 to 1100 at stations separated by ≥1 km to reduce the risk of observing the same unmarked individual more than once during a given field season. To avoid pseudoreplication, each bird was considered a statistically independent unit in the analyses. Unmarked woodpeckers observed in 2 nearby playback stations often could be easily differentiated from each other if they were of different sexes or if they presented a clearly distinctive pattern of white markings on their backs. Since other woodpeckers were observed at locations separated by ≥2 km, we assumed that unmarked birds observed within a given field season were different individuals. Reported home ranges of individual three-toed woodpeckers were 50–300 ha in summer (partially logged forests; Goggans et al. 1989) and approximately 80 ha in winter (continuous forests; Hogstad 1970). All playback stations were selected using provincial forest inventory maps for their road accessibility and locations within old-growth black spruce-dominated forests or forest shreds.

Once a bird was found, it was observed until it flew out of sight. Every 30 sec, we recorded the following variables on audiotape: foraging height, substrate diameter at foraging height, foraging technique, and foraging site (trunk or branches). We recorded foraging height in 6 numerical classes: 0 (ground level or fallen tree), 1 (<2 m), 3.5 (≥2 and <5 m), 7.5 (≥5 and <10 m), 12.5 (≥10 and <15 m), and 17.5 (≥15 and <20 m). As most mature spruces reach a height of approximately 15 m in this area (Imbeau et al. 1999) and usually do not exceed 20 m, such classes were easily estimated in the field. Substrate diameter at foraging height was recorded into 5-cm classes, using the bird as a benchmark. Three foraging techniques were differentiated according to possible feeding strategies (Villard 1994, Murphy and Lehnhausen 1998): (1) bark scaling accompanied by surface pecking (for feeding mainly on bark beetles and first instar wood boring larvae), (2) excavating into sapwood (used to pick later instars of wood boring larvae), and (3) sap licking. This latter technique is easily recognized by the rings of small holes that are excavated around live trees for feeding on the emerging sap (Villard 1994).

Using only individuals that could be followed for more than 10 min, a total of 38 hr 26 min of observation was recorded on 53 birds over 3 field seasons (43.5 ± 5.5 min per individual; mean ± SE): 20 hr 48 min on 31 individuals in summer (12 hr 29 min in continuous forests; 8 hr 19 min in shredded forests) and 17 hr 38 min on 22 individuals in winter (we had road access to continuous forest only in that season).

Characterization of Trees Selected for Foraging and Drumming

While 1 observer recorded the foraging observations, a second observer flagged each tree used by the focal woodpecker after it had moved to another tree. After losing sight of a bird, we recorded species, dbh, tree condition (standing or fallen), bark cover (in classes of 10%), top condition (broken or intact), and deterioration class of each used tree. Following Bergeron et al. (1997), our classification recognized 8 deterioration classes (Fig. 1): (1) alive and healthy, ≥95% foliage, no signs of deterioration; (2) declining, remaining foliage between ≥20% and <95%, senescent tree; (3) dying, <20% foliage remaining; (4) recently dead, hard wood, firm bark cover, 0% green foliage, and small twigs still remaining; (5) hard wood, no dead foliage, no small twigs; (6) hard wood, loose bark cover, broken top, height still more than 50% of what is observed on trees with same dbh; (7) soft, decomposed wood, broken top with height less than 50% of what is observed on trees with same dbh; and (8) stump, height <2 m. To evaluate the potential preference for snags, each used tree was paired with the nearest tree available to the woodpecker (as determined on a base-to-base distance), and its state (live or dead) was recorded. Furthermore, all characteristics of used trees were also noted for the nearest available tree in the same state (if the used tree was a snag, it was paired with the nearest available snag; if the used tree was alive, it was paired with the nearest available live tree). This pairing allowed us to compare pairs of live and dead trees separately.

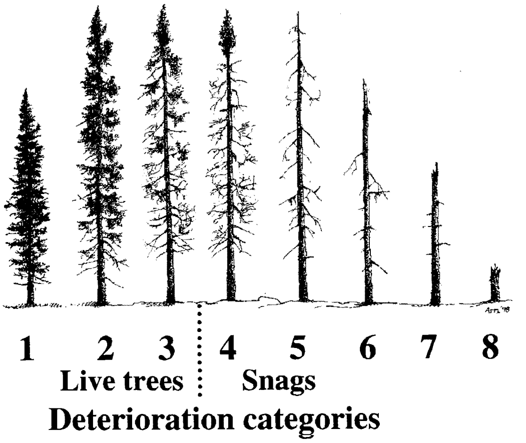

Fig. 1. Visual aspect of tree deterioration categories as they appeared on black spruce, northwestern Lac Saint-Jean, Québec, Canada, 1997–1998.

Based on observations made during preliminary fieldwork in 1996, we noted that used trees always had a dbh ≥5 cm. Therefore, we considered a tree available only if its dbh was at least this size. Indeed, all the trees used by three-toed woodpeckers for foraging and drumming that we recorded (with 1 exception) were at least this size ($n = 785$). However, since fallen trees were never used as drumming substrates, only standing trees were considered available for drumming. Moreover, in 1996, we noted that fallen trees were rapidly covered by mosses (mostly by a thick layer of *Pleurozium schreberi*) and that these were not used by foraging woodpeckers. Therefore, only recently fallen trees whose bark was still devoid of mosses were considered available for foraging.

Statistical Analysis

We used a 2-way analysis of variance (ANOVA) to quantify the effects of sex, season, and their interaction on foraging height and substrate diameter at foraging height, using only birds for which we had a minimum observation time of 10 min. Distribution normality was assessed using a Kolmogorov-Smirnov test; variance homogeneity was assessed using Levene's test (both assumptions were met). To ensure that any seasonal effect is not confounded by the fact that birds foraging in shredded forests after logging were observed only in summer, *t*-tests were used to test a possible landscape context effect before pooling all summer data.

To evaluate the effect of explanatory variables characterizing each tree on its potential use as a foraging or drumming substrate, we used stepwise logistic regression (SLR) for matched case-control pairs with backward elimination of least significant variables (Hosmer and Lemeshow 1989). The likelihood-ratio χ^2 criterion was used to construct each model in which entry and removal thresholds of variables were set at $\alpha = 0.05$ and $\alpha = 0.10$, respectively. To test for the potential effect of state of the tree alone (live vs. dead), a first analysis was done on pairs based on the nearest available trees. Other characteristics were evaluated for pairs based on trees of same state (used live trees vs. nearest available live trees, used snags vs. nearest available snags).

Unlike most ecological studies in which logistic regression is used, the binary response variable in our study was fixed by stratification (case-control sampling). Trees in the matched pairs were measured on each predictor variable of interest (state, species, dbh, tree condition, bark cover, top condition, and deterioration class), and the difference between the values of the case and control were calculated. Then, although the roles of the explanatory and response variables are reversed in the study, their association can still be analyzed through standard logistic regression (Agresti 1996). Because sex, forest type, and season remain constant within pairs, such effects were evaluated as interaction terms with other explanatory variables retained in our regression models. Because fallen trees are not available in the winter and birds in shredded forests could not be investigated in that season, the effect of tree condition and landscape type were tested in models containing summer data only. All pairs of trees recorded for a given individual were used in our logistic regression analyses. However, by statistical weighting, each individual contributed only 1 degree of freedom in each model, regardless of the number of trees it was observed using (Desrochers 1992). In this way, we could include all of the information recorded on the trees selected by each woodpecker without pseudoreplicating the data by counting each tree choice by a given individual as independent (Machlis et al. 1985).

RESULTS

Foraging Behavior

Substrate diameter at foraging height was on average 33–43% larger for males than for females ($F = 67.6$, df = 1, $P \leq 0.001$; Table 1), but females foraged 27–46% higher up in trees compared to males ($F = 25.5$, df = 1, $P \leq 0.001$; Table 1). No seasonal effects were found ($P > 0.070$). In both sea-

Table 1. Substrate diameter at foraging height, foraging height, foraging technique, and foraging position of three-toed woodpeckers in black spruce forests located in northwestern Lac Saint-Jean, Québec, Canada, 1997–1998.

						Foraging behavior (% of time)							
		Substrate diameter at foraging height (cm)		Foraging height (m)		Pecking or scaling		Excavating		Sap licking		Foraging location (% on trunk)	
Season	*n*	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Summer													
Male	18	13.5	0.5	4.8	0.4	97.9	0.8	0.7	0.4	1.4	0.8	99.3	0.7
Female	13	9.0	0.6	6.6	0.8	99.1	0.6	0.3	0.2	0.6	0.6	97.6	1.8
Winter													
Male	13	14.9	0.6	4.5	0.4	99.9	0.1	0.1	0.1	0.0	0.0	99.9	0.1
Female	9	8.5	0.9	8.4	0.6	100.0	0.0	0.0	0.0	0.0	0.0	91.6	6.3

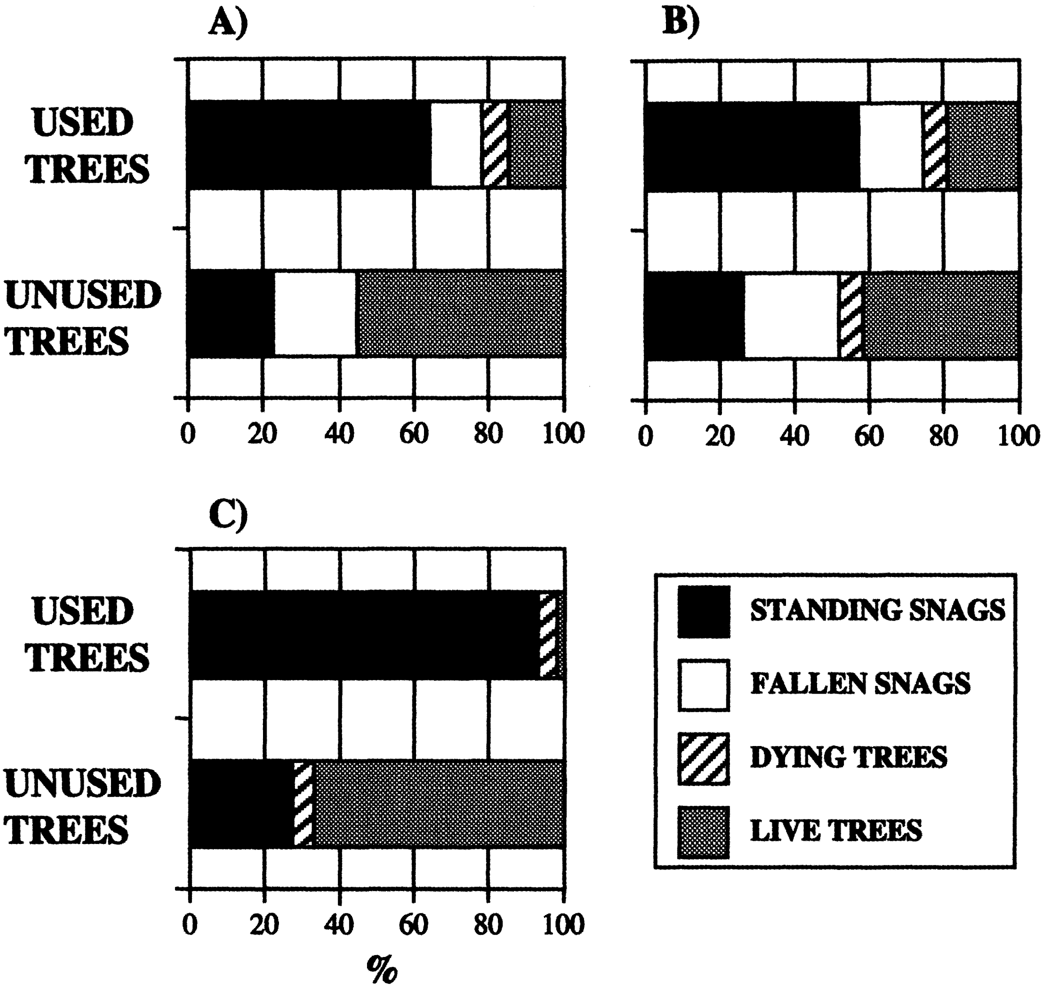

Fig. 2. Relative importance of snags, dying, and live trees as foraging substrates for three-toed woodpeckers in northwestern Lac Saint-Jean, Québec, Canada, 1998. (A) summer, shredded forests (*n* = 19); (B) summer continuous forests (*n* = 22); (C) winter, continuous forests (*n* = 29).

sons, woodpeckers of both sexes foraged mainly (>97%) by pecking or scaling the bark of trees and concentrated (>92%) their foraging activities on trunks (Table 1).

Relative Importance of Snags and Live Trees for Foraging

Three-toed woodpeckers foraged primarily (78–93%) on standing or fallen snags independent of forest type and season (Fig. 2; sample sizes given in Table 2). Compared with the nearest tree available, use of snags was disproportionately higher ($\chi^2 = 72.5$, df = 1, $P \leq 0.001$, $n = 70$ birds) and consistent between sexes ($\chi^2 = 0.1$, df = 1, $P = 0.792$). Although woodpeckers concentrated their foraging on snags in both seasons, this selectivity was more pronounced in winter (interaction with season: $\chi^2 = 4.4$, df = 1, $P = 0.037$). In summer ($n = 41$ birds), the preference for snags was similar between forest types ($\chi^2 = 0.1$, df = 1, $P = 0.667$).

Characteristics of Trees Used for Foraging

Using data obtained in both seasons ($n = 68$ birds; Table 3), foraging three-toed woodpeckers selected snags with a greater dbh ($\chi^2 = 20.6$, df = 1, $P \leq 0.001$), which were on average 26% larger, and a lower deterioration class ($\chi^2 = 4.7$, df = 1, $P = 0.031$) than available snags. Such characteristics were consistent between sexes ($\chi^2 = 1.9$, df = 3, $P = 0.602$) and seasons ($\chi^2 = 0.8$, df = 3, $P = 0.852$).

Table 2. Number of foraging and drumming trees characterized (number of pairs of used vs. nearest available tree) and number of different three-toed woodpeckers followed in black spruce forests located in northwestern Lac Saint-Jean, Québec, Canada, 1997–1998.

		Summer				Winter	
		Continuous forests		Shredded forests		Continuous forests	
Use	Sex	*n* of tree pairs	*n* of woodpeckers	*n* of tree pairs	*n* of woodpeckers	*n* of tree pairs	*n* of woodpeckers
Foraging							
Nearest tree[a]	Males	90	14	76	10	176	18
	Females	48	8	55	9	77	11
Snags[a]	Males	76	13	55	10	147	18
	Females	36	7	35	9	73	11
Live trees	Males	29	7	37	10	28	6
	Females	23	10	26	9	5	2
Drumming							
Nearest tree	Males	44[b]	11	56[b]	13	6	5
	Females	24	8	28[b]	8	5	2
Snags	Males	42	11	53	13	6	5
	Females	21	8	23	7	5	2
Live trees	Males	1	1	2	1	0	0
	Females	3	3	4	3	0	0

[a] For the pairs based on nearest tree and nearest snag, data recorded for foraging trees in the summer of 1997 were omitted as distances to fallen snags were not evaluated from the base of a used tree to the base of the nearest available one. As a consequence, the total number of pairs (nearest tree) is not the sum of paired snags and live trees.

[b] The sum of pairs based on nearest tree is not the sum of paired snags and living trees because of 3 lost data.

However, based on summer data (1997 and 1998, $n = 39$ birds; Table 2), our analysis also revealed that standing snags were preferred over fallen ones as foraging substrates ($\chi^2 = 14.1$, df = 1, $P \leq 0.001$). This preference was consistent between forest types ($\chi^2 = 0.4$, df = 3, $P = 0.946$).

Live trees selected ($n = 44$ birds; Table 4) had a greater deterioration class ($\chi^2 = 8.9$, df = 1, $P = 0.003$), being more often at a dying stage than available ones, and had on average a 24% greater dbh ($\chi^2 = 6.7$, df = 1, $P = 0.009$) than available live trees. Such characteristics were consistent between sexes ($\chi^2 = 1.5$, df = 3, $P = 0.685$) and seasons ($\chi^2 = 1.1$, df = 3, $P = 0.779$). Moreover, when only summer data were considered (1997 and 1998, $n = 36$ birds; Table 2), no differences were observed between forest types ($\chi^2 = 4.2$, df = 3, $P = 0.242$).

Characteristics of Trees Selected for Drumming

Three-toed woodpeckers used mainly snags as drumming substrate (95% of drumming trees selected, $n = 47$ birds; Table 2). Compared with the nearest tree available, snag use was disproportionately higher ($\chi^2 = 27.1$, df = 1, $P \leq 0.001$, $n = 47$ birds). This preference for snags was consistent between sexes ($\chi^2 = 0.5$, df = 1, $P = 0.489$) and forest types ($\chi^2 < 0.1$, df = 1, $P = 0.893$).

Compared with the nearest standing snag not used by woodpeckers, only tree species was not retained in our final model, once we accounted

Table 3. Characteristics of snags used for foraging by three-toed woodpeckers compared to the nearest available snags[a], in black spruce forests located in northwestern Lac Saint-Jean, Québec, Canada, 1998.

	Used snags		Nearest available snags	
Characteristics	$\bar{x}$ (median)	SE (range)	$\bar{x}$ (median)	SE (range)
Deterioration class	(4.0)	(4.0–6.5)	(4.5)	(4.0–7.5)
Bark cover	(9.0)	(9.0–9.0)	(9.0)	(3.5–9.0)
Diameter at breast height	19.2	0.5	14.3	0.5
Tree species (%):				
Black spruce	92.1	2.4	82.3	3.3
Jack pine	6.3	2.3	5.2	2.2
Balsam fir	0.3	0.2	3.1	1.1
White birch	0.7	0.4	5.3	1.8
Others	0.6	0.5	4.1	1.8
Top condition (% broken)	11.2	2.2	24.0	3.7
Snag position (% fallen)[b]	22.5	4.7	68.8	5.9

[a] Results are based on $n = 68$ woodpeckers, for which 1–27 snags were characterized (median = 5, total = 422).

[b] Results based on summer data only.

Table 4. Characteristics of live trees used for foraging by three-toed woodpeckers compared to the nearest available live trees[a], in black spruce forests located in northwestern Lac Saint-Jean, Québec, Canada, 1997–1998.

	Used live trees		Nearest available live trees	
Characteristics	$\bar{x}$ (median)	SE (range)	$\bar{x}$ (median)	SE (range)
Deterioration class	(2.0)	(1.0–3.0)	(2.0)	(1.0–3.0)
Bark cover	(9.0)	(8.0–9.0)	(9.0)	(9.0–9.0)
Diameter at breast height	20.4	0.6	15.6	0.7
Tree species (%):				
Black spruce	87.3	4.2	82.3	4.5
Jack pine	5.2	2.7	3.1	2.3
Balsam fir	0.0	0.0	9.5	3.3
White birch	6.9	3.2	3.3	1.7
Others	2.2	2.0	1.8	1.2
Top condition (% dead or broken)	15.6	0.7	9.0	3.9

[a] Results are based on n = 44 woodpeckers, for which 1–20 pairs of live trees were characterized (median = 2, total = 148).

for other variables (Table 5). Characteristics differentiating drumming snags from available ones were an average 35% larger dbh ($\chi^2 = 28.2$, df = 1, $P \leq 0.001$), a 40% lower bark cover ($\chi^2 = 9.6$, df = 1, $P = 0.002$), a broken top ($\chi^2 = 9.2$, df = 1, $P = 0.002$), and a lower deterioration class, once we accounted for other variables ($\chi^2 = 6.2$, df = 1, $P = 0.013$). Such preferences were consistent between sexes ($\chi^2 = 2.7$, df = 4, $P = 0.602$) and forest types ($\chi^2 = 1.7$, df = 4, $P = 0.795$). Only 11 snags were characterized in the winter months when woodpeckers are less territorial, so we did not test for a potential seasonal effect.

Table 5. Characteristics of snags used for drumming by three-toed woodpeckers compared to the nearest available snags[a], in black spruce forests located in northwestern Lac Saint-Jean, Québec, Canada, 1997–1998.

	Used snags		Nearest available snags	
Characteristics	$\bar{x}$ (median)	SE (range)	$\bar{x}$ (median)	SE (range)
Deterioration class	(6.0)	(4.0–7.0)	(5.0)	(4.0–8.0)
Bark cover	(6.0)	(0.0–9.0)	(9.0)	(0.0–9.0)
Diameter at breast height	22.0	0.6	14.3	0.5
Tree species (%):				
Black spruce	42.0	6.4	82.3	3.3
Jack pine	37.1	6.5	5.2	2.2
Balsam fir	4.1	2.4	3.1	1.1
White birch	0.4	0.4	5.3	1.8
Others	16.3	4.9	4.1	1.8
Top condition (% dead or broken)	86.5	3.6	24.0	3.7

[a] Results are based on n = 47 woodpeckers, for which 1–18 pairs of snags were characterized (median = 2, total = 150).

DISCUSSION

Foraging Ecology of Three-toed Woodpeckers

In European boreal forests, where most behavioral studies have been conducted on three-toed woodpeckers, a sexual divergence in their foraging behavior is well recognized. Hogstad (1976, 1978, 1991) showed that males forage lower than females, mainly on trunks, and prefer larger trees. Females forage higher and have a greater niche breadth, using relatively small trees and branches. Our results on foraging height and diameter of the substrate at foraging height are consistent with such findings. This sexual differentiation could arise from dimorphism in bill size (Hogstad 1978), or through a social dominance of males over females (Hogstad 1991).

According to Murphy and Lehnhausen (1998), the three-toed woodpecker should be considered a beetle specialist, particularly on scolytids, which are phloem-boring insects that occur only in the inner bark and cambium of attacked trees (Coulson and Witter 1984). In contrast to other sympatric species, such as the black-backed woodpecker (*P. arcticus*), Murphy and Lehnhausen (1998) showed that three-toed woodpeckers rarely forage by excavating into the sapwood to feed on wood-boring larvae. Our results clearly support their conclusions because more than 97% of our foraging observations were consistent with a feeding strategy for bark beetles (i.e., pecking and scaling the bark of trees). This specialization, as determined through foraging behavior or from gizzard-content analyses, seems widespread throughout its North American (Villard 1994, Steeger and Dulisse 1997) and European ranges (Hogstad 1970, 1991; Pechacek and Krištín 1993; Fayt 1999). Nevertheless, the extent to which this woodpecker relies on sap licking seems to vary according to region. Sap licking seems frequent in some parts of Europe (Glutz von Blotzheim and Bauer 1980), whereas in North America, Short (1974, 1982) reported that three-toed woodpeckers did not sap lick apart from taking sap from sapsucker (*Sphyrapicus* spp.) wells. In northern Manitoba, Villard (1994) reported sap-licking behavior for only 1 individual, and concluded that in the Nearctic, three-toed woodpeckers have not fully developed this behavior, perhaps because this niche already is occupied by sapsuckers. In our study, all sap wells were drilled in live black spruces and, as observed in Europe, used trees became covered with rings of sap holes from the base of the trunk to the crown. Birds often used trees that had been previously drilled. Therefore, our observations suggest that European and American three-toed woodpeckers do not differ in this behavior as much as Villard (1994) suggested, a conclusion based on a smaller number of individuals (only 7 hr 25 min of observation on 15 individuals).

Foraging and Drumming Trees Preferred by Three-toed Woodpeckers

In old-growth spruce forests, where small-scale gap dynamics are prevalent, primary bark beetles, which are able to kill healthy trees, are scarce (Martikainen et al. 1999). This contrasts with the abundant secondary scolytids that preferentially attack weak, dying, or recently dead trees. Within a few years, these trees decay to a point at which they become unsuitable for such insects (Coulson and Witter 1984, Speight and Wainhouse 1989). Foraging trees used by three-toed woodpeckers should reflect a similar pattern. Accordingly, we found that woodpeckers mainly selected foraging trees with a larger dbh on the basis of their deterioration class. Among snags, which were preferred over live trees for foraging, recently dead trees were used more often than more deteriorated ones. Among live trees, more deteriorated, dying trees were preferred over healthy ones. Such results were consistent between forest types, sexes, and seasons. Therefore, our study not only emphasizes the importance of snags for foraging three-toed woodpeckers, which has also been reported elsewhere (Hogstad 1977, Villard 1994), but also that in mature forests only a limited number of snags are suitable for bark beetle attacks and thus appropriate foraging substrates for three-toed woodpeckers. Demonstrating the importance of recently dead or dying trees—as opposed to all types of snags—for foraging three-toed woodpeckers, illustrates the importance of natural disturbance dynamics as a key factor ensuring woodpecker persistence in managed forests. This relationship with recently dead snags also explains the restricted distribution of this woodpecker species to old-growth stands at a time when multiscale gaps and fire are actively prevented in managed stands.

This limited number of suitable foraging trees is further exacerbated during winter, when fallen snags are buried under snow. Such trees, which often result from storms which blow over, snap, or partially uproot trees, provide bark beetles with abundant breeding substrate (Speight and Wainhouse 1989). Although standing snags were clearly preferred over fallen ones as foraging substrates in the summer months, our data show that during this period, as much as 22.5% of all snags selected had fallen. Although the three-toed woodpecker is not recognized as an ant specialist (Pechacek and Krištín 1993) and may lack the chemical derivatives required for protection against formic acid ingested with adult ants (Stradi et al. 1998), on several occasions individuals were seen feeding on ant larvae in colonies of *Myrmica alaskensis* exposed after flaking the bark of fallen snags. Such observations show the greater availability of food resources in the summer, when sap licking is possible and fallen snags are available as foraging substrates.

In addition to being the preferred substrate for foraging, snags also were preferred over live trees for drumming. Although we did not compare the acoustic properties of used and available snags, woodpeckers probably choose trees that could produce loud sounds required for long-distance acoustic transmission (Eberhardt 1997). In our study area, drumming trees differed from foraging snags and other available snags by having a broken top, less bark cover, and a lower deterioration class. Therefore, even if the importance of the drumming behavior to attract conspecifics is not precisely known in the case of the three-toed woodpecker, good drumming trees may still represent critical habitat components for this species.

MANAGEMENT IMPLICATIONS

Retention of standing dead stems during harvesting operations is often suggested as a management option aimed at maintaining habitat for cavity-nesting birds (e.g., Conner 1978, Mannan et al. 1980, Dickson et al. 1983). Hunter (1990) summarized various models estimating minimum snag requirements for different woodpecker species, which are based only on their use of snags as nesting trees. Such models implicitly assume that snags required for nesting are an important limiting factor to woodpecker populations. Because in many cases knowledge of woodpecker biology is too limited to be used in such models, Hunter (1990) reported that many forest and wildlife managers suggest that leaving 5–10 snags per ha should be adequate. Based on a similar model, Watt and Caceres (1999) recently suggested that in black spruce forests of northeastern Ontario, leaving approximately 1 snag with a dbh >30 cm per ha may be sufficient to maintain 60% of the maximum density of three-toed woodpeckers. However, they noted that this model was untested and did not account for snags used during foraging. Considering the extensive and stage-specific use of snags by foraging three-toed woodpeckers that we observed, we believe that such models are highly unlikely to be successful in predicting long-term habitat needs of this species. Indeed, leaving already existing snags on clearcuts will not provide suitable foraging sites for more than a few years, assuming that the woodpeckers use dispersed snags left out in the open in such disturbed areas. Providing old-growth forest structure using partial or selective cutting (Bergeron et al. 1999) probably would also be ineffective, as these logging techniques do not ensure snag continuity over a long time. Although actively killing trees by girdling or notching might be an effective way to provide foraging substrates for woodpeckers (Aulén 1991), we also believe that such a method should be regarded only as a last resort considering the probable high labor costs involved.

Our study emphasizes the potential importance of remaining old-growth forests for maintaining viable populations of three-toed woodpeckers as they probably require a continual recruitment of recently dead snags as foraging substrates. Among the variety of snags found in such old-growth forests, they can find snags with the characteristics required for drumming and nesting. However, companies that harvest forest products on Québec public lands are not constrained to maintain specific amounts of old-growth stands to meet wildlife habitat objectives. Such objectives clearly should be established to provide more suitable habitat for three-toed woodpeckers (see also Goggans et al. 1989) and other species dependent on decaying wood found in old-growth spruce forests. However, the minimal area of these habitats required is still open to speculation as knowledge of the home range size of individual three-toed woodpeckers for time periods >6 months and its overlap within pair members are critical information presently lacking throughout its range. Home range sizes during winter months, when fallen trees are buried under snow, are potentially greater than in summer months, when snag preference is less pronounced. Such information, as well as the potential use of three-toed woodpecker as a possible umbrella species to define minimum area of old-growth boreal spruce forests that should be left in managed areas (Nearctic and Palearctic regions alike), should be investigated.

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