

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Anthropogenic edges: Their influence on the American three-toed woodpecker (*Picoides dorsalis*) foraging behaviour in managed boreal forests of Quebec

Caroline Gagné^a, Louis Imbeau^{b,*}, Pierre Drapeau^a

^a *Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Québec, Canada H3C 3P8*

^b *Département des sciences appliquées, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec, Canada J9X 5E4*

Received 21 December 2006; received in revised form 18 June 2007; accepted 19 June 2007

Abstract

We studied edge effects on the American three-toed woodpecker (*Picoides dorsalis*) foraging behaviour in 18 remnant forest edges of black spruce and feather moss forests managed with a dispersed checkerboard pattern of clear-cuts. Our objectives were to assess (1) the characteristics of foraging substrates used by woodpeckers, (2) whether birds foraged according to the availability of high-quality foraging substrates found at varying distances from edges and (3) to characterize the movement patterns of foraging individuals near clear-cut boundaries. Behavioural observations of individuals allowed us to characterize all trees used for foraging according to their DBH, decay state, bark cover, tree species and top condition. We also georeferenced those trees, which allowed us to determine their distance from the edge and the orientation of the bird movements with regards to the edge. We sampled snags and downed woody debris along 80 m line transects that were oriented perpendicularly to the edge. Our results show that woodpeckers foraged in a relatively high proportion of live trees (35%). For live trees, woodpeckers used trees of larger diameter and black spruce was underused with regards to its availability. Among snags, woodpeckers preferred snags with a larger diameter, a lower decay class and a higher bark cover than nearest available snags. The density of high-quality foraging substrates (large recently dead trees) increased near the edge and decreased as we got farther into the forest interior. When comparing the distribution of used foraging snags with the one of available high-quality foraging substrates, our results show that these two distributions are significantly different. High-quality substrates located at 40 m or less from an edge were used less frequently than their availability. Hence, we can conclude that foraging woodpeckers can use snags near edges but are less prone to use these foraging trees even though they become more available than in the interior of remnant stands of managed forests. Nevertheless, bird movements were oriented parallel to the edge as far as 80 m away from the clear-cut boundary. Considering the under-utilisation of high-quality substrates near edges, we suggest that foraging substrate availability cannot explain the results obtained; the hypothesis that edges are acting as movement conduits likely explain woodpecker movement patterns we observed. Finally, the retention of larger tracks of mature and overmature forests would reduce the amount of edge habitat and provide better foraging conditions for American three-toed woodpecker in extensively managed landscapes.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Edge effect; American three-toed woodpecker; Dispersed clear-cuts; Boundary; Forest fragmentation; Snags; Foraging behaviour

1. Introduction

Fragmentation induced by forest harvesting generates sharp edges that are very dissimilar from natural boundaries found in unmanaged landscapes, in terms of vegetation composition and structure, length and distribution in the landscape (Matlack and

Litvaitis, 1999). Forest-dwelling birds can nonetheless use these sharp edges that can vary in width with regards to habitat type, for different purposes. For instance, some of them use linear forest remnants, which are constituted of edge habitat given their narrow width (Mascarúa-López, 2005; Mascarúa-López et al., 2006), as movement corridors to enhance dispersal of individuals and to avoid crossing open habitats (Machtans et al., 1996; Brooker et al., 1999; Sieving et al., 2000). Indeed, clear-cuts can effectively be perceived by birds as hostile areas even though they are vagile organisms. For instance, Machtans et al. (1996)

* Corresponding author. Tel.: +1 819 762 0971x2033; fax: +1 819 797 4727.
E-mail address: Louis.Imbeau@uqat.ca (L. Imbeau).

showed that in the boreal mixed-wood forest region of Alberta, forest bird species movements were more frequent within corridors adjacent to clear-cuts as compared to cut blocks themselves. In a forested landscape fragmented by agriculture, Desrochers and Fortin (2000) also showed that chickadee flocks tended to move parallel to boundaries up to 100 m away within forest remnants, suggesting that these boundaries were acting as movement conduit for chickadees. According to these recent studies, the presence of edges can therefore influence bird behaviour even at a relatively great distance from them.

On the other hand, some species might be more sensitive to edges and, thus, avoid such habitats (Kuitunen and Mäkinen, 1993; Villard, 1998; Huhta et al., 1999). The American three-toed woodpecker (*Picoides dorsalis*), considered a late-successional species (Conseil canadien des ministres des forêts, 1997; Imbeau et al., 1999, 2001) is thought to be one of these sensitive species. Fayt (1999) showed that in Finland, its close counterpart, the European three-toed woodpecker (*Picoides tridactylus*), foraged mainly on bark beetles found on spruce stems associated with forest interior conditions. According to this study, individuals may show a lower foraging effectiveness in fragmented mature forests as the proportion of forest interior habitat diminishes (Fayt, 1999). Nonetheless, we still lack knowledge as to what minimal distance the interior forest conditions take place and what is the magnitude of this possible edge effect. The presence of clear-cut edges may then negatively affect foraging behaviour of some boreal woodpeckers. Surprisingly, in North American boreal forests, Imbeau and Desrochers (2002a,b) failed to show that its North American counterpart, the American three-toed woodpecker, was negatively affected by human-induced edges within remnant forests of linear configuration (riparian and buffer strips) within aggregated clear-cuts in Quebec, Canada. In this case, the greater availability of dead trees near clear-cut edges along such strips (Mascarúa-López, 2005; Mascarúa-López et al., 2006) may compensate for the loss of mature and old-growth forests

since American three-toed woodpeckers are closely associated with standing dead wood (snags) for nesting and foraging (Leonard, 2001). Edges induced by forest harvesting are effectively prone to show a high rate of windthrow caused by the increased velocity of wind after clearing (Franklin and Forman, 1987; Esseen, 1993; Darveau et al., 1995; Ruel et al., 2001). Furthermore, because of its life history traits, this species might be adapted to forest fragmentation that occurs within the range of variability of the natural disturbance regime. In the black spruce forests of Quebec, the level of fragmentation caused by the extensive areas of adjoining clear-cuts may nevertheless be outside this range of natural variation (Leduc et al., 2000; Bergeron et al., 2002).

Consequently, if we aim to manage the boreal forest while preserving its biodiversity, it is imperative to understand how forest-dwelling species respond to such changes in their environment. Hence, the main goal of our study was to document how the American three-toed woodpecker foraging behaviour is affected by the presence of human-induced edges. More specifically, our objectives were to assess (1) the characteristics of foraging substrates used by woodpeckers, (2) whether the distance from boundaries affects the distribution of foraging substrates used by woodpeckers and particularly high-quality foraging trees, (3) whether birds foraged according to the availability of high-quality foraging substrates found at varying distances from edges and (4) whether bird foraging movements were oriented parallel to edges and if so, whether the proximity of edges induced a higher rate of parallel movements compared with movements conducted at a greater distance from edges.

2. Study area

The study area was located within the black spruce and feather moss bioclimatic zone (Robitaille and Saucier, 1998) of the north-western Québec region (49°43' to 49°53'N and 75°44' to 76°26'W; Fig. 1) and covers an area of 918 km². Since our

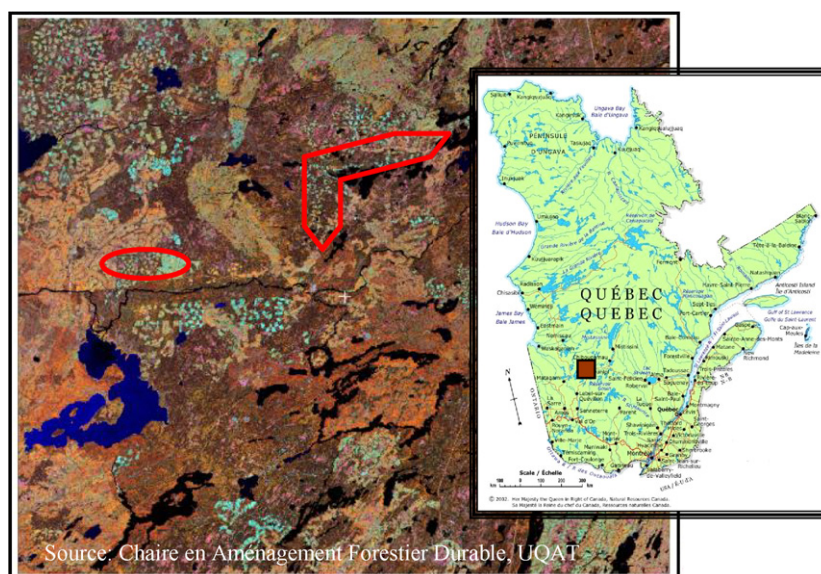


Fig. 1. Satellite photo showing the study area in the Nord-du-Québec region, Québec, Canada. Behavioural observations of American Three-toed woodpeckers were conducted within areas circumscribed by red lines.

study area is located on public lands, logging activities have substantially modified its landscape structure over the last two decades; the dispersed clear-cuts areas and the well-developed road networks have spread throughout these natural forest landscapes, leaving only relatively small blocks of remnant virgin forests that are 85–100 ha in size (MRNQ, 2003). Cut blocks adjacent to our sampling sites were harvested from 1995 to 2002, and now constitute regenerating forests between 3 and 10 years old. Remnant patches are composed of mature and old growth forests (>90 years old) in which black spruce (*Picea mariana*) is the dominant tree species with sparsely distributed jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), larch (*Larix laricina*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). The topography is flat with some scattered low elevation hills. The proglacial Ojibway lake has left glaciolacustrine deposits on the land while depressions are covered by clay deposits (Vincent and Hardy, 1977). The mean temperature ranges from -2.5 to 0.0 °C and the mean annual precipitation ranges from 800 to 900 mm (Robitaille and Saucier, 1998).

3. Methods

3.1. Behavioural observations of foraging American three-toed woodpecker

Behavioural observations were carried out in 2005 during the month of May. We broadcasted the drumming and calls of American three-toed woodpecker within the remnant forests at 40 m from the nearest clear-cut edge to attract individuals. Territorial birds usually responded by quickly coming to the source of the playback, started to drum and call back to the simulated intruder. When the playback was stopped, in usually less than a few minutes, responding woodpeckers resumed their foraging activities, as no intruders could be found. We chose a 40 m distance from the nearest clear-cut edge to give the bird the option of moving deeper into the forest or closer to the edge after the playback was stopped. When a responding individual resumed its foraging activities, we followed him until he flew out of sight, blazing all used trees. On foraged trees, we recorded the diameter at breast height (DBH), the deterioration state (Table 1) following Imbeau and Desrochers (2002a), the top condition (intact/broken), the bark cover [(1) 100% present, (2) $\geq 95\%$ present, (3) between ≥ 75 and $< 95\%$ present, (4) between ≥ 50 and $< 75\%$ present, (5) between ≥ 25 and $< 50\%$ present, (6) between ≥ 5 and $< 25\%$ present, (7) between ≥ 1 and $< 5\%$ present and (8) 0% present] and the tree species. We recorded the same variables for the nearest available stems and for the nearest available stems in the same state (live/dead) as the stems used for foraging. Nearest trees were chosen according to their base-to-base distance from the foraged trees. Foraging trees were also georeferenced with a GPS Trimble GeoExplorer XM Pocket PC which had a precision of ± 1 m; this procedure allowed us to compute the distance from the clear-cut edge of trees used for foraging with the Arc GIS 9.0 computer program. We also computed the angle formed between each movement made by individuals and the edge, a

Table 1

Characteristics of live trees, snags and downed logs according to their deterioration class, Nord-du-Québec, Québec, Canada, 2004–2005

| Deterioration class | Tree characteristics |
|--------------------------|--|
| Live trees | |
| 1 | Alive and healthy, $\geq 95\%$ foliage, no signs of deterioration |
| 2 | Declining, remaining foliage between $\geq 20\%$ and $< 95\%$, senescent tree |
| 3 | Dying, $< 20\%$ foliage remaining |
| Snags | |
| 4 | Recently dead, hard wood, firm bark cover, dead foliage and small twigs still remaining |
| 5 | Hard wood, firm bark cover, 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 |
| 8 | Stump, height < 2 m |
| Downed logs ^a | |
| 4 | Recently fallen, hard wood, firm bark cover and small twigs still remaining |
| 5 | Hard wood, no dead foliage, no small twigs, bark cover still remaining but more easily removable |
| 6 | Wood still hard but less than the previous classes, loose bark cover, can be partially covered by mosses |

^a Downed logs were classified using the same classes as for snags, but for analysis, all dead trees were considered whether as (1) standing stems or (2) downed stems.

movement representing the linear distance between two foraging trees (Desrochers and Fortin, 2000).

3.2. Dead wood availability

We sampled snags and downed logs within 28 forest remnant edges of dispersed clear-cuts. The sampling was conducted along three 10 m broad transects per edge; transects were initiated at the clear-cut boundaries and extended 80 m deep into the forest patches to capture the entire expected edge effect gradient. DBH, deterioration state, top condition, bark cover and tree species were recorded for all stems; these stems were then classified in four categories according to their distance from the clear-cut edge: 0–20, 20–40, 40–60 and 60–80 m. We also noted the presence of foraging signs such as flaked bark and foraging holes (signs made mostly by the American Three-toed Woodpecker in our study area, and to a lesser extent by Black-backed woodpecker) to quantify whether past foraging activities of woodpeckers were similar to those occurring currently in terms of the distance from the edge.

4. Statistical analyses

To evaluate the effect of explanatory variables characterizing each tree on its potential use as a foraging substrate, we used logistic regression for matched case-control pairs, following the same methodology as Imbeau and Desrochers (2002a). 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). Based on previous knowledge (Imbeau and Desrochers, 2002a), our predictions were that (1) woodpeckers should forage more frequently on snags, (2) birds should choose the largest snags and the less deteriorated ones and (3) among live trees, only large ones should be preferred. This first step was, however, necessary to identify high-quality foraging substrates that were specifically selected within our study area. In all analyses, each individual bird was considered a statistically independent unit to avoid pseudo-replication (Desrochers, 1992), except in two cases: (1) in the analysis aiming to assess whether foraging birds preferred standing over fallen snags, since the sample size would have been too small ($n = 42$ stems, 11 woodpeckers) and (2) in the analysis of live trees with the explanatory variable tree species. For these two analyses, we considered the sample size as being equal to the number of used stems instead of weighting cases according to the number of individual birds.

We then used an analysis of variance with polynomial contrasts on the stem density (number of stems/ha) of all snags and downed logs to obtain a global portrait of dead wood distribution at varying distances from edges. The same analysis was conducted to assess whether the distribution of high-quality foraging substrates, as defined by the previous case-control logistic regression models, was influenced by the distance from the edge. If the edge distance had an effect on the availability of such stems, polynomial contrasts were used to determine more precisely the nature of this relationship. In some cases, the normality distribution and the variance homogeneity assumptions of the ANOVA were not met; consequently, we used the square-root, the fourth-root and the log transformations to meet these assumptions. We then calculated, for the 18 edges where behavioural observations were conducted, the proportion of recently dead large trees used by foraging woodpeckers by distance class (number of recently dead large trees used in a particular distance category/total number of recently dead large trees used in all distance categories). We performed a chi-square test to assess whether birds foraged on high-quality foraging substrates according to their availability with regards to distance from the edge. In this analysis, used foraging substrates were expected to follow the same distribution as the one obtained for available ones. The same test was done to compare distributions of high-quality foraging substrates with snags having foraging signs.

Our prediction concerning dead wood availability was that there should be more snags and downed woody debris near the edge and that the density should decrease as we moved into the forest. We expected that the spatial distribution of high-quality foraging substrates for American three-toed woodpeckers would follow the same pattern. Given their edge sensibility, woodpeckers foraging response could show two contrasting patterns: (1) birds showing no edge avoidance should forage on high-quality foraging substrates according to their availability or (2) birds showing edge avoidance should forage more often on trees located further from the edge and overuse these trees according to their availability.

To assess whether the boundary affects the orientation of woodpecker movements between foraging trees and at what distance such an effect takes place, we followed the methodology developed by Desrochers and Fortin (2000) and we calculated the expected proportion of movements with an angle $\leq 20^\circ$ relative to the boundary. This threshold proportion of expected movements (22% within this $\leq 20^\circ$ range) represents our null hypothesis that edges have no effect on movement orientation. Indeed, if the observed proportion of movements parallel to the edge ($\leq 20^\circ$) is close to this threshold, movements have no specific orientation; they are randomly oriented. However, if the observed proportion of movements $\leq 20^\circ$ relative to the edge is clearly superior to this threshold, this implies that movements are oriented parallel to the edge. With regards to this assumption, a correlation analysis was conducted to determine whether the proportion of parallel movements was higher near the edge than farther away from it using 20 m classes up to 100 m from edges. The 80–100 m distance category contained 26 movement observations that ranged from 80 to 185 m from the edge. We grouped them because their sample size was insufficient to generate distinct classes away from edges. Only 9 movements were located in the 80–100 m distance category, while 17 were situated farther than 100 m from the edge. Our prediction was that the proximity of the edge should increase the proportion of woodpecker movements with angle less or equal to 20° relative to the edge.

5. Results

5.1. Characteristics of trees used for foraging

Twenty-five different individuals were followed (12 males, 11 females, two for which sex could not be determined) to collect foraging observations on a total of 145 foraging substrates. Since foraging substrate selection is not known to differ by sex for this species (Imbeau and Desrochers, 2002a), data for all individuals were pooled in the following analyses, thus increasing our sample size. In our study sites, 65% of trees used by birds were dead (snags and logs) whereas live trees represented 35% of foraging substrates. However, when comparing used stems with the nearest unused ones, we notice that dead trees were overused with respect to their availability, but the difference was not significant (case-control logistic regression, $n = 145$ stems, weighted according to $n = 25$ woodpeckers; $\chi^2 = 1.865$, $p = 0.172$). Among dead trees used by foraging woodpeckers, 92.5% were snags whereas 7.5% were logs; when comparing used dead trees with the nearest available dead trees, snags were significantly overused with regards to their availability (case-control logistic regression, $n = 42$ stems; $\chi^2 = 5.062$, $p = 0.024$; Table 2). Individual case-control logistic regression models show that foraging woodpeckers used snags with a greater DBH (on average 17% larger), with a lower deterioration class and with a higher bark cover than neighbouring snags (Table 2). For live trees, woodpeckers used trees of larger diameter (on average 15% larger) than neighbouring trees and

Table 2

Characteristics of snags used for foraging by American three-toed woodpeckers and nearest available snags, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Québec, Canada, 2004–2005

| Characteristics | Used snags | | Nearest available snags | | Logistic regression | |
|--|---------------|--------------|-------------------------|--------------|---------------------|--------------|
| | Mean (median) | S.E. (range) | Mean (median) | S.E. (range) | χ^2 | p^a |
| Diameter at breast height ^b | 17.79 | 0.57 | 14.78 | 0.64 | 7.27 | 0.007 |
| Deterioration class ^b | (4.00) | (4.00–8.00) | (5.00) | (4.00–8.00) | 8.81 | 0.003 |
| Top condition (% broken) ^b | 22.99 | 4.54 | 19.54 | 4.28 | 0.66 | 0.416 |
| Bark cover ^b | (1.00) | (1.00–6.00) | (2.00) | (1.00–7.00) | 4.11 | 0.043 |
| Tree species (%) ^b | | | | | 0.02 | 0.886 |
| Black spruce | 88.51 | 3.44 | 86.21 | 3.72 | – | – |
| Jack pine | 6.90 | 2.73 | 5.75 | 2.51 | – | – |
| Trembling aspen | 2.30 | 1.62 | 1.15 | 1.15 | – | – |
| White birch | 2.30 | 1.62 | 3.45 | 1.97 | – | – |
| Others | 0.00 | 0.00 | 3.45 | 1.97 | – | – |
| Snag position (% fallen) ^c | 7.45 | 2.72 | 12.77 | 3.46 | 5.06 | 0.024 |

^a Results in bold are significant at the 0.05 level.

^b Results are based on $n = 24$ woodpeckers, for a total of 87 pairs of snags.

^c Results are based on $n = 11$ woodpeckers, for a total of 42 pairs of dead trees (snags and logs).

black spruce trees were underused with respect to their availability (Table 3).

5.2. Edge effect on dead wood availability

The density of recently dead trees (class 4) was significantly higher near the clear-cut edge but there was no significant difference for intermediate (class 5), old (class 6) and very old (class 7) snags (Table 4). The density of stumps (class 8) also decreased as we moved away from the edge (Table 4). For downed woody debris, the effect of distance was significant for recently fallen snags (class 9) and intermediate logs (class 10), which were more abundant near the edge than within the forest (Table 4).

When looking at stems DBH, the edge distance affected the distribution of snags larger or equal to 15 cm (Table 4); their density decreased as we moved away from the edge. For large (DBH ≥ 15 cm) recently dead trees, there was a significant

trend towards a higher density near the clear-cut edges of our study sites (Table 4).

5.3. Edge effect on trees used by foraging woodpeckers

Overall, 22% of the foraging trees were located within the forest interior habitat, i.e., over 80 m from edges, whereas 60% and 18% were within edges and in cut blocks, respectively. Large recently dead trees used by foraging birds are equally distributed within the edge, whereas available large recently dead trees are more abundant near the boundary. The chi-square test revealed that the distribution of used foraging substrates did not fit with the distribution of available foraging substrates with regards to distance from the edge ($\chi^2 = 11.833$, $p = 0.008$). Within the first 40 m from the edge, foraging substrates are underused compared to their availability and they are overused in the 40–60 and 60–80 m distance categories (Fig. 2). The distribution of snags with foraging signs was also significantly different from the

Table 3

Characteristics of live trees used for foraging by American three-toed woodpeckers and nearest available live trees, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Québec, Canada, 2004–2005

| Characteristics | Used live trees | | Nearest available live trees | | Logistic regression | |
|--|-----------------|--------------|------------------------------|--------------|---------------------|--------------|
| | Mean (median) | S.E. (range) | Mean (median) | S.E. (range) | χ^2 | p^a |
| Diameter at breast height ^b | 13.62 | 0.67 | 11.55 | 0.74 | 3.93 | 0.048 |
| Deterioration class ^a | (3.00) | (1–3) | (3.00) | (1–3) | 0.05 | 0.832 |
| Top condition (% broken) ^b | 4.00 | 2.80 | 2.00 | 2.00 | 0.35 | 0.555 |
| Bark cover ^b | (1.00) | (1.00–3.00) | (1.00) | (1.00–3.00) | 0.65 | 0.422 |
| Tree species (%) ^c | | | | | 3.96 | 0.047 |
| Black spruce | 68.00 | 6.66 | 80.00 | 5.71 | – | – |
| Trembling aspen | 2.00 | 2.00 | 0.00 | 0.00 | – | – |
| White birch | 4.00 | 2.80 | 0.00 | 0.00 | – | – |
| Balsam fir | 26.00 | 6.27 | 20.00 | 5.71 | – | – |

^a Results in bold are significant at the 0.05 level.

^b Results are based on $n = 51$ pairs of live trees; data are weighted for $n = 20$ woodpeckers.

^c Results are based on $n = 51$ pairs of live trees; data are not weighted.

Table 4
Mean density of snags and downed logs according to their deterioration and DBH classes and the distance to forest boundaries, in remnant forests of dispersed clear-cuts of the Nord-du-Québec region, Québec, Canada, 2004–2005

| | Distance from boundary (m) | | | | | | | | Linear contrast | <i>p</i> ^a |
|---------------------|----------------------------|--------|-------|--------|-------|--------|-------|--------|--------------------|-----------------------|
| | 0–20 | | 20–40 | | 40–60 | | 60–80 | | | |
| Deterioration class | | | | | | | | | | |
| Snags | | | | | | | | | | |
| 4 | 130.4 | (16.2) | 97.0 | (9.7) | 85.0 | (10.7) | 97.6 | (15.1) | –0.22 ^b | 0.039 |
| 5 | 98.2 | (13.8) | 116.1 | (17.0) | 87.0 | (13.1) | 87.0 | (9.8) | –0.55 ^c | 0.448 |
| 6 | 56.6 | (11.0) | 47.1 | (8.5) | 40.5 | (7.0) | 58.9 | (11.5) | 0.04 ^c | 0.955 |
| 7 | 72.6 | (10.4) | 69.6 | (9.4) | 74.9 | (10.4) | 56.6 | (7.7) | –0.45 ^c | 0.463 |
| 8 | 122.6 | (15.0) | 129.1 | (16.5) | 112.6 | (12.5) | 84.0 | (10.6) | –1.46 ^c | 0.026 |
| Downed logs | | | | | | | | | | |
| 4 | 28.0 | (6.3) | 17.4 | (5.0) | 9.6 | (2.6) | 9.6 | (2.6) | –0.87 | 0.007 |
| 5 | 80.4 | (12.2) | 53.1 | (10.5) | 48.8 | (8.9) | 54.8 | (8.5) | –1.43 ^c | 0.030 |
| 6 | 61.2 | (7.4) | 59.5 | (10.6) | 48.2 | (8.2) | 50.7 | (6.0) | –9.59 | 0.248 |
| DBH class | | | | | | | | | | |
| 5–9.5 cm | 146.5 | (18.8) | 183.9 | (26.8) | 169.6 | (22.9) | 151.8 | (17.0) | 0.38 | 0.986 |
| 10–14.5 cm | 161.9 | (19.6) | 129.8 | (12.9) | 118.4 | (13.0) | 131.6 | (16.2) | –22.86 | 0.147 |
| 15–19.5 cm | 109.6 | (14.8) | 92.8 | (11.9) | 77.9 | (9.4) | 66.1 | (9.2) | –1.83 ^c | 0.004 |
| ≥20 cm | 62.5 | (12.9) | 52.4 | (10.8) | 33.9 | (7.0) | 34.6 | (6.2) | –1.61 ^c | 0.032 |
| Foraging trees | | | | | | | | | | |
| Class 4, DBH ≥15 cm | 52.9 | (9.2) | 41.1 | (5.4) | 30.4 | (5.8) | 29.2 | (4.9) | –1.54 ^b | 0.009 |

Means are followed by their standard errors. Results are based on *n* = 28 edges.

^a Results in bold are significant at the 0.05 level.

^b ANOVA has been conducted with the fourth root of the density.

^c ANOVA has been conducted with the square root of the density.

distribution of large recently dead trees with regards to distance from the edge ($\chi^2 = 12.564$, *p* = 0.006; Fig. 3).

5.4. Woodpecker movements along the edge

Across all distances, our observations were above the random movements' breakpoint of 22.2% indicating that birds moved often parallel to the edge (Fig. 4). Moreover, as woodpeckers got closer to the edge, regardless of the side (cut block side or interior forest side), a higher proportion of their movements was parallel to the edge. This trend was, however, not significant at the 0.05 level (Spearman correlation, $\rho = -0.700$, *p* = 0.094; Fig. 4).

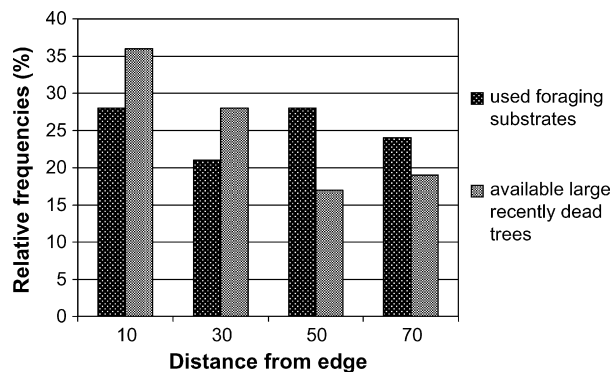


Fig. 2. Relative frequencies of large recently dead trees used by foraging woodpeckers and of available large recently dead trees with regards to distance from the edge. Distance classes are represented as follows: 10 (0–20 m), 30 (20–40 m), 50 (40–60 m) and 70 (60–80 m). Results are based on *n* = 25 woodpeckers within 18 edges.

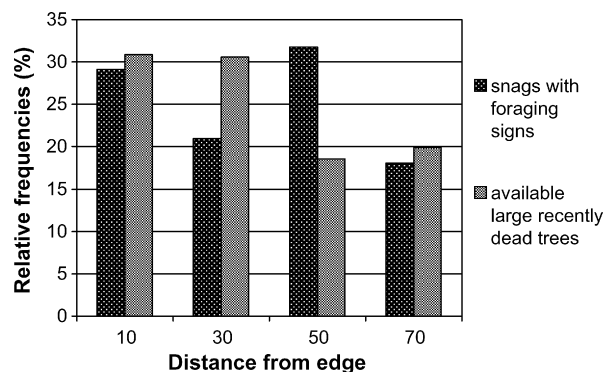


Fig. 3. Relative frequencies of snags showing foraging signs and of available large recently dead trees with regards to distance from the edge. Distance classes are represented as follows: 10 (0–20 m), 30 (20–40 m), 50 (40–60 m) and 70 (60–80 m). Results are based on *n* = 17 edges.

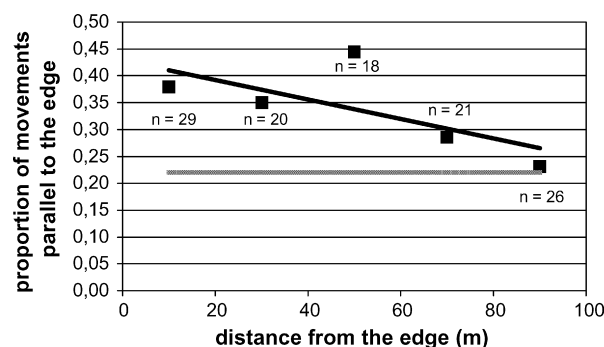


Fig. 4. Observed proportion of movements parallel relative to the boundary (black dots) and expected percentage of movements with angle less than or equal to 20° relative to the edge (dashed line), Nord-du-Québec, Québec, Canada, 2004–2005. The tendency curve (black line) was added *a posteriori*.

6. Discussion

6.1. Characteristics of trees used by foraging woodpeckers

Our first prediction that birds should forage more frequently on snags than on live trees was partly supported. Overall, the American tree-toed woodpecker foraged twice as much on dead trees than on live trees. However, when looking more closely at the used versus available trees and snags, the difference between dead and live foraging trees was not statistically significant with regards to the availability of the nearest available tree. The proportion of live trees used by foraging woodpeckers was indeed relatively high (35%), indicating that during the spring season, this species may rely not only on snags but also on live trees to satisfy its energetic requirements. Indeed, many of the foraged live trees on which woodpeckers sap licked were balsam firs located within the forest patches or within cut blocks. This foraging behaviour has been documented in some parts of Europe (Glutz von Blotzheim and Bauer, 1980) but in North America, this behaviour has seldom been reported (Short, 1974, 1982; Villard, 1994, but see Imbeau and Desrochers, 2002a). Among the 25 individuals followed, at least three individuals used the sap licking technique. We, however, noticed that American three-toed woodpeckers sap licked from the spring time until early June and that birds stopped afterwards. In early Spring, the sap of trees is the most abundant and nutritious (D. Gagnon, personal communication) and birds may take advantage of this temporary food supply. Among live trees, we expected birds to forage more on large stems; our results effectively showed that larger live trees were preferred over smaller ones. On the other hand, black spruce did not seem to be the preferred tree species. In fact, woodpeckers foraged less on black spruce than what was predicted by its availability.

Our second prediction that foraging birds should choose the largest and the less deteriorated snags was supported by our results. Imbeau and Desrochers (2002a) obtained similar results; in their study, the mean DBH of snags used by foraging woodpeckers was 19.2 cm. Goggans et al. (1989) also showed that American three-toed woodpeckers foraged mainly on trees with a DBH greater than 17.5 cm. In the study of Imbeau and Desrochers (2002a), recently dead trees were also preferred over older snags, which is consistent with our results. Analyses showed that among dead trees, birds foraged most often on standing snags compared with downed logs, these results being consistent with those of Murphy and Lehnhausen (1998) and Imbeau and Desrochers (2002a).

6.2. Edge effect on dead wood availability

Several studies have documented tree mortality within human-induced edges (Franklin and Forman, 1987; Esseen, 1993; Darveau et al., 1995; Mascarúa-López, 2005). In the study of Mascarúa-López (2005), it is shown that the log density is higher in the first 10 m from the clear-cut edge but, conversely, there is no edge effect on snags, whatever their deterioration state. Our results show the same patterns whereas recently fallen snag density is higher near the edge and

decreases linearly as we move away from it. However, we were able to detect a positive edge effect on stumps (<2 m high) and on recently dead trees, in both cases the densities being higher near the edge and decreasing linearly with distance from the edge. Following harvesting, increases in wind speed can induce a higher rate of broken stems and blowdown at clear-cut edges (Esseen, 1993). In his study, Esseen (1993) indeed showed that following a clear-cut, the most common type of wind-induced mortality was uprooting (67%), stem breakage (24%) and trees that died standing (9%). In our study, recently fallen snags probably fell down after the opening of the adjacent area. Their bark was still present and basically intact, and the logs were not yet covered by mosses; in this area of the boreal forest, it is generally believed that downed logs are indeed rapidly buried beneath a thick layer of mosses once they have reached the ground (Imbeau and Desrochers, 2002a). On the other hand, older woody debris probably fell down before clearings and they were evenly distributed within forest edges. Recently dead trees were recruited, however, after harvesting. It is well documented that the microclimate at edges is quite different from conditions found within forest interiors; the solar radiation being more intense, the daily temperatures higher and the degree of humidity lower (McCollin, 1998; Matlack and Litvaitis, 1999). Elevated soil temperatures and changes in plant water use efficiency are in fact well-established consequences of the increased exposure near the edge (Chen et al., 1993; Kapos et al., 1993). On the other hand, downed logs, while falling, can also have injured nearby trees, hence allowing fungi to penetrate them and bring about death. Esseen (1993) also found a positive relationship between the mortality of trees and their diameter – tree mortality being higher for large stems. Our results are consistent with this study since larger recently dead trees seem to be slightly more abundant near edges than all recently dead trees pooled together.

6.3. Do foraging woodpeckers avoid edge habitat?

Our prediction concerning edge avoidance by the American three-toed woodpecker was partly supported by the data. Foraging trees were evenly distributed from the edge to the forest interior whereas high-quality foraging substrates, ca. large recently dead trees, were, however, more abundant near the boundary. Hence, even though birds did not avoid feeding near edges, they did not forage on those trees in proportion to their availability. Our results not only reflect the current response of birds to edges, but the same response is obtained for past foraging signs indicating some level of consistency in the foraging patterns of this species over time since timber harvesting. This result also suggests that our playback method did not affect woodpecker response to openings. Our results thus indicate that foraging American three-toed woodpeckers can use snags near edges but are less prone to use these foraging trees even though they become more available than elsewhere in remnant stands of managed forests. Although Imbeau and Desrochers (2002b) previously reported no pattern of edge avoidance by foraging American three-toed woodpeckers, their study sites were located in linear residual strips (usually less

than 60 m in width according to provincial forest regulations) of shredded forests within agglomerated clear-cuts. Our study, within larger forest residual patches, partly corroborate their results but show that interior forest conditions (further away than 40 m along edges) may provide better foraging conditions than along edges, when available.

Our study provided information on the distribution of foraging substrates along edges, but we did not quantify prey availability in such substrates. Therefore, we cannot link prey distribution with woodpecker substrate selection with regards to edge location. Nevertheless, given that large recently dead trees were more abundant near edges, we could hypothesize that woodpeckers foraging would be more efficient because large stems generally support higher larvae densities (Nappi et al., 2003). However, Fayt (2004) showed that the bark beetle species richness as well as the overall abundance of spruce bark beetles responded negatively to edge vicinity in remnant forest patches surrounded by harvested surroundings. This could partly explain why foraging woodpeckers did not preferentially use edge habitats in our study, even when foraging substrates were more abundant; this higher availability of substrates being offset by a presumed lower abundance of insect preys and a lower species richness in these substrates. On the other hand, it has been shown that European three-toed woodpeckers diet is variable with respect to the period of the year, and was mainly composed of bark beetles (*Scolytidae*) from autumn to spring time (Fayt, 1999). A comparison of woodpecker's diet and foraging movements at different times of the year would be required to determine if foraging along edges may be affected by seasonal variation in prey preferences.

The higher proportion of foraging movements oriented parallel to the clear-cut edge near the edge indicates that individuals move less freely in all directions near edges than within interior forest conditions. This suggests that when American three-toed woodpeckers forage near and at edges, they avoid moving far into harvested timber open habitats, which are likely to be more risky environments with regards to predation risk. On the other hand, woodpecker parallel movements relative to the edge also occurred at a greater distance from the edge, where available foraging substrates were less abundant. Hence, this result suggests that the "movement conduit" hypothesis, rather than the availability of foraging substrates, is more likely to explain the observed pattern of movements along edges. In their study Desrochers and Fortin (2000) showed that chickadee flocks tended to move parallel to boundaries more frequently when moving near edges; our results follow the same pattern even though the relationship is not significant (although $p < 0.1$). This can partly be explained by the fact that woodpeckers can use foraging substrates within clear-cuts, when such substrates are available and suitable. They are indeed not as constrained within the clear-cut edge as it is the case for chickadees, for which there were no foraging substrates available within agricultural fields. In the Desrochers and Fortin's (2000) study, edges also influenced the orientation of movements as far as 125 m within the forest. Our results point in the same direction since woodpecker movements were oriented parallel to the edge at least until 80 m from the boundary.

Haila (1983) found that European three-toed woodpecker can have a relatively large territory. In its study, the smallest island colonized by woodpeckers was 99 ha (Haila, 1983), but in highly fragmented habitats, we can expect their territory to reach threefold this size (Mykrä et al., 2000). One single territory can then encompass numerous artificial edges in a managed landscape of dispersed clear-cuts since remnant blocks must have 85–100 ha in size (MRNQ, 2003). Thus, individuals may perceive the landscape in a fine-grained manner. Costs in terms of time, energy and exposure to predators can then be incurred when individual movements occur between several habitat patches (Hinsley, 2000). However, before extensive forestry spread over pristine boreal forests, habitat fragmentation was naturally generated by wildfires and windthrows (Bergeron, 1991; Johnson, 1992; Payette, 1992; Angelstam, 1997; Gauthier et al., 2001; Bergeron et al., 2004). The American three-toed woodpecker evolved under these natural conditions and may be well adapted to cross large open habitats when searching for food resources. Hence, this species may be quite tolerant to habitat loss and fragmentation generated by forest harvesting. However, burned areas may represent a less hostile environment than cutover areas since islets of live trees, partially burned and dead trees are spread throughout those areas (Leduc et al., 2000; Haeussler and Kneeshaw, 2003), providing suitable foraging substrates for American three-toed woodpeckers and other species.

7. Management implications

Since foraging American three-toed woodpeckers are less prone to forage near clear-cut edges, the extent of boundaries at the landscape level may have an impact on this species' behaviour. In fact, landscapes showing a large amount of edge habitat combined with a low proportion of forest interior conditions, such as linear forest remnants of aggregated clear-cuts, may become less suitable habitats for foraging individuals. Those linear strips indeed support a lower abundance of American three-toed woodpecker (and of several other primary cavity excavator birds) than larger forest remnants of a dispersed clear-cuts pattern (Gagné, 2006). The dispersed clear-cutting pattern nevertheless generates a large amount of edges, particularly when the proportion of remaining habitat turns around 50% (Franklin and Forman, 1987). Hence, the retention of larger tracks of mature and overmature forest would reduce the length of edges and, conversely, enhance the amount of forest interior habitat. This in turn could provide better foraging conditions for American three-toed woodpeckers and, perhaps, other forest-dwelling species that are known to benefit from inside forest conditions in our study area (e.g. Boudreault et al., 2002 (Bryophyte and lichen communities); Drapeau et al., 2003 (bird communities)).

Acknowledgements

Special thanks to Marie-Claude Fontaine and Jean-Rémi Julien for their field work assistance. This project was funded by the FQRNT – Fonds Forestier, the Networks of Centres of

Excellence – Sustainable forest management network, the NSERC-UQAT-UQAM industrial chair in sustainable forest management and an NSERC Discovery grant to P. Drapeau. Finally, we thank André Desrochers and Daniel Gagnon for their comments on an earlier version of this manuscript.

References

- Angelstam, P., 1997. Landscape analysis as a tool for the scientific management of biodiversity. *Ecol. Bull.* 46, 140–170.
- Bergeron, Y., 1991. The influence of island and mainland lakeshore landscapes on the boreal forest fire regimes. *Ecology* 72, 1980–1992.
- Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., Lefort, P., 2004. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. *Ambio* 33 (6), 356–360.
- Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fennica* 36 (1), 81–95.
- Boudreault, C., Bergeron, Y., Gauthier, S., Drapeau, P., 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Can. J. Forest Res.* 32, 1080–1093.
- Brooker, L., Brooker, M., Cale, P., 1999. Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use and dispersal mortality. *Conservation Ecol.* 3 (1), 4. Available from the Internet: <http://www.consecol.org/vol3/iss1/art4/>.
- Chen, J., Franklin, J., Spies, T., 1993. Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agric. Forest Meteorol.* 63, 219–237.
- Conseil canadien des ministres des forêts, 1997. Critères et indicateurs de l'aménagement durable des forêts du Canada. Ressources naturelles Canada. Service canadien des forêts, Ottawa.
- Darveau, M., Beauchesne, P., Bélanger, L., Huot, J., Larue, P., 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *J. Wildl. Manag.* 59 (1), 67–78.
- Desrochers, A., 1992. Age and foraging success in European Blackbirds: variation between and within individuals. *Anim. Behav.* 43, 885–894.
- Desrochers, A., Fortin, M.-J., 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos* 91, 376–384.
- Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S., Savard, J.-P., 2003. Les communautés d'oiseaux des vieilles forêts de la pessière à mousses de la ceinture d'argile: Problèmes et solutions face à l'aménagement forestier. *Forestry Chronicle* 79, 531–540.
- Esseen, P.-A., 1993. Tree mortality patterns after experimental fragmentation of an old-growth forest. *Biol. Conservation* 68 (1), 19–28.
- Fayt, P., 1999. Available insect prey in bark patches selected by the three-toed woodpecker *Picoides tridactylus* prior to reproduction. *Ornis Fennica* 76, 135–140.
- Fayt, P., 2004. Old-growth boreal forests, three-toed woodpeckers and saproxylic beetles – the importance of landscape management history on local consumer-resource dynamics. *Ecol. Bull.* 51, 249–258.
- Franklin, J.F., Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecol.* 1 (1), 5–18.
- Gagné, C., 2006. La répartition spatiale des coupes forestières et ses effets sur la distribution et le comportement alimentaire des oiseaux excavateurs en forêt boréale. M.Sc. Thesis, Université du Québec à Montréal, 101 pp.
- Gauthier, S., Leduc, A., Harvey, B., Bergeron, Y., Drapeau, P., 2001. Les perturbations naturelles et la diversité écosystémique. *Naturaliste Canadien* 125, 10–17.
- Glutz von Blotzheim, U., Bauer, K., 1980. *Handbuch der Vögel Mitteleuropas*, vol. 9. Akademische Verlagsgesellschaft, Wiesbaden, Germany.
- Goggans, R., Dixon, R.D., Seminara, C.L., 1989. Habitat use by three-toed and black-backed woodpeckers, Deschutes National Forest, Oregon. Oregon Department of Fish and Wildlife, Nongame Wildlife Program, Deschutes National Forest, Technical Report 87-3-02.
- Haessler, S., Kneeshaw, D., 2003. Comparing forest management to natural processes. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), *Towards Sustainable Management of the Boreal Forest*. NRC Research Press, Ottawa, Ontario, Canada, pp. 307–368.
- Haila, Y., 1983. Colonization of islands in a north-boreal Finnish lake by land birds. *Annales Zoologici Fennici* 20, 179–197.
- Hinsley, S.A., 2000. The costs of multiple patch use by birds. *Landscape Ecol.* 15, 765–775.
- Huhta, E., Jokimäki, J., Rahko, P., 1999. Breeding success of pied flycatchers in artificial forest edges: the effect of a suboptimally shaped foraging area. *Auk* 116 (2), 528–535.
- Imbeau, L., Desrochers, A., 2002a. Foraging ecology and use of drumming trees by three-toed woodpeckers. *J. Wildl. Manag.* 66 (1), 222–231.
- Imbeau, L., Desrochers, A., 2002b. Area sensitivity and edge avoidance: the case of the Three-toed woodpecker (*Picoides tridactylus*) in a managed forest. *Forest Ecol. Manag.* 164, 249–256.
- Imbeau, L., Mönkkönen, M., Desrochers, A., 2001. Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. *Conservation Biol.* 15 (4), 1151–1162.
- Imbeau, L., Savard, J.-P.L., Gagnon, R., 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Can. J. Zool.* 77, 1850–1860.
- Johnson, E.A., 1992. *Fire and Vegetation Dynamics—Studies From the North American Boreal Forest*. Cambridge University Press, Cambridge.
- Kapos, V., Gamade, G., Matsui, E., Victoria, R.L., 1993. $\delta^{13}\text{C}$ as an indicator of edge effects in tropical rainforest reserves. *J. Ecol.* 81, 425–432.
- Kuitunen, M., Mäkinen, M., 1993. An experiment on nest site choice of the Common Treecreeper in fragmented boreal forest. *Ornis Fennica* 70, 163–167.
- Leduc, A., Bergeron, Y., Drapeau, P., Harvey, B., Gauthier, S., 2000. Le régime naturel des incendies forestiers : un guide pour l'aménagement durable de la forêt boréale. L'Aubelle. Novembre-Décembre, in press.
- Leonard Jr., D.L., 2001. Three-toed woodpecker (*Picoides dorsalis*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*. Cornell Laboratory of Ornithology, Ithaca, USA, pp. 1–24.
- Machtans, C.S., Villard, M.-A., Hannon, S.J., 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biol.* 10, 1366–1379.
- Mascarúa-López, L., 2005. Structure et effets de lisières des habitats linéaires résiduels en pessière à mousses aménagée du nord du Québec. Thesis, Université du Québec à Montréal, M.Sc., 68 pp.
- Mascarúa-López, L., Harper, K., Drapeau, P., 2006. Edge influence on forest structure in large forest remnants, cutblock separators and riparian buffers in managed black spruce forests. *Ecoscience* 13 (2), 226–233.
- Matlack, G.R., Litvaitis, J.A., 1999. Forest edges. In: Hunter, Jr., M.L. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, pp. 210–233.
- McCollin, D., 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* 21, 247–260.
- Ministère des Ressources Naturelles du Québec (MRNQ), 2003. Règlement sur les normes d'intervention dans les forêts du domaine de l'État. Éditeur officiel du Québec, Québec.
- Murphy, E.C., Lehnhausen, W.A., 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *J. Wildl. Manag.* 62 (4), 1359–1372.
- Mykrä, S., Kurki, S., Nikula, A., 2000. The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland. *Annales Zoologici Fennici* 37, 79–91.
- Nappi, A., Drapeau, P., Giroux, J.-F., Savard, J.-P.L., 2003. Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in a recently burned eastern boreal forest. *Auk* 120 (2), 505–511.
- Payette, S., 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), *A systems Analysis of the Boreal Forest*. Cambridge University Press, Cambridge, pp. 144–169.
- Robitaille, A., Saucier, J.-P., 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec. Gouvernement du Québec, Canada.
- Ruel, J.-C., Pin, D., Cooper, K., 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. *Forest Ecol. Manag.* 143, 105–113.

- Short, L.L., 1974. Habits and interactions of North American three-toed woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). *Am. Museum Novitates* 2547, 1–42.
- Short, L.L., 1982. *Woodpeckers of the World*. Delaware Museum of Natural History, Greenville, USA.
- Sieving, K.E., Willson, M.F., De Santo, T.L., 2000. Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biol.* 14 (4), 1120–1132.
- Villard, M.-A., 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* 115 (3), 801–805.
- Villard, P., 1994. Foraging behavior of Black-backed and Three-toed woodpeckers during spring and summer in a Canadian boreal forest. *Can. J. Zool.* 72, 1957–1959.
- Vincent, J.L., Hardy, L., 1977. L'évolution et l'extinction des grands lacs glaciaires Barlow et Ojibway en territoire québécois. *Géographie Physique et Quaternaire* 31, 357–372.