

Area sensitivity and edge avoidance: the case of the Three-toed Woodpecker (*Picoides tridactylus*) in a managed forest

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Abstract

Given the extensive progression of industrial forestry in boreal regions that reduces the area of old-growth forests and considerably increases the amount of sharp edges, important declines are to be expected among old-forest specialists area-sensitive or edge-avoiding boreal birds. The Three-toed Woodpecker (*Picoides tridactylus*) is likely to be one of the species most negatively affected by boreal forestry and is possibly sensitive to forest area and edges. In this study, we quantify the area sensitivity and edge-avoidance of the Three-toed Woodpecker by analyzing its pattern of occurrence at 100 playback stations that had from 8 to 100% forest cover within a 300 m radius. Behavioral observations were also conducted to further investigate its response to edges in logged forests using foraging locations in relation to the nearest clear-cut border. Moreover, we document their foraging movement patterns in two contrasting landscapes (continuous versus shredded forests after logging). Although the occurrence of Three-toed Woodpeckers was highly related to the area of suitable habitat around the playback station, this relationship was quasi-linear and no critical threshold was found within the range of forest cover sampled. The amount of edge did not provide additional information on woodpecker occurrence. Individual woodpeckers in shredded forests did not select foraging trees further away from clear-cut edges than available ones. However, based on the results of the movement path analysis, continuous forests might provide better nesting habitat than residual, shredded forests. Indeed, spatial configuration of residual forest seemed to highly constrain foraging movements of this species because of its strong avoidance of open areas. Considering other studies conducted on forest birds, such modified movement patterns could be particularly harmful while both adults must feed their nestlings and behave as central place foragers. Therefore, even if no pattern of area-sensitivity or edge-avoidance were found, harmful consequences of forest shredding following forest logging may still occur for boreal species such as the Three-toed Woodpecker. However, residual forests strips are essential to maintain this species within managed areas, its population density within such residual forests being comparable to the one obtained in continuous forests. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

In temperate forests of eastern North America, numerous studies on the occurrence of breeding birds in fragmented habitats have led to the widespread use of classifications that reflect the influence of landscape structure or habitat fragmentation on patterns of species distribution. Following Whitcomb et al. (1981), species

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were first classified as (1) forest-interior specialists, (2) interior-edge generalists, (3) edge species, or (4) field-edge species. Despite the popularity of this classification, Villard (1998) pointed out that edge avoidance is based on little, often equivocal data. More recently, Freemark and Collins (1992) proposed a classification based on species' responses to the area of forest fragments. In this classification, area-sensitive species are defined as species that occur more frequently or increase in density as fragment size increases. Andrén (1994) showed that such negative area effects are more likely to be observed in landscapes having less than approximately 30% of suitable habitat, although this threshold seems to vary depending on the landscape context (Mönkkönen and Reunamen, 1999).

In contrast to temperate North American deciduous forests, few studies have documented the occurrence of birds in deforested boreal landscapes. Consequently, our knowledge about patterns of area-sensitivity or edge-avoidance among boreal forest birds remains largely unknown. Given the extensive progression of industrial forestry in boreal regions (Bryant et al., 1997) that reduces the area of old-growth forests and considerably increases the amount of sharp edges, important declines are to be expected among boreal birds that could be categorized as area-sensitive or edge-avoiding. Moreover, their foraging movements in residual forests left after logging might be severely altered in response to the increased amount of forest edges (Desrochers and Fortin, 2000).

From a conservation point of view, critical thresholds of remaining habitats for the most area-sensitive species are more important than averaged thresholds more representative of common species (Mönkkönen and Reunamen, 1999). Among all boreal bird species, the Three-toed Woodpecker (*Picoides tridactylus*) is likely to be the species most negatively affected by forestry (Imbeau et al., 2001) and is possibly sensitive to forest area and edges because: (1) it shows a strong affinity to old-growth forests (Virkkala, 1987; Imbeau et al., 1999) which are severely reduced in area and "shredded" (Feinsinger, 1997) by logging, and (2) recent evidence based on its insect prey suggests that it might avoid edge habitats (Fayt, 1999). In this paper, we quantify the area sensitivity of the Three-toed Woodpecker by analyzing its pattern of occurrence according to various amounts of forest cover.

Edge-avoidance was evaluated in logged forests using foraging locations in relation to the nearest clear-cut border. Furthermore, we document their foraging movement patterns in two contrasting landscapes: continuous and shredded forests.

2. Study area and methods

Field work was conducted 120 km north-west of Lac Saint-Jean (48°49'N, 73°08'W), Que., within the Chibougamau-Natashquan forest section of the Canadian boreal forest (Rowe, 1972). This area is described by Saucier et al. (1998) as part of the boreal eastern spruce-mosses forest, belonging to the Ashuapmushuan river ecological region. Forests are mainly composed of black spruce (*Picea mariana*) or black spruce mixed with jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and less often, tamarack (*Larix laricina*). At these northern latitudes, spruce take from 80 to 120 years to reach economic maturity (Gouvernement du Québec, 1998). These forests are highly sought after by the industry, and all public forests south of 50°N in Québec are already allocated for logging to various forest companies by the provincial government (Parent, 1999).

Our study area was divided in two landscape types that differed in their proportion logged. In the northern part of our study area, approximately 3000 ha of continuous old-growth forests were accessible by recently opened logging roads. These forests were scheduled to be logged within 5 years following our study. In this area, dominant spruces were 120–125 years old, had a mean height of 15 m, and the density of snags ≥ 10 cm dbh was 210 stems/ha (Imbeau et al., 1999). Approximately, 10 km south of the unlogged forests, we selected a large block of 10,000 ha of recently logged areas (<20 years) dominated by clear-cuts ranging from 50–250 ha. Forest remnants consisted of 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 constitute old-growth forest shreds (*sensu* Feinsinger, 1997) in recently cut areas that represented less than

15% of the original forest cover (Gingras, 1997). Within the clear-cuts, few snags were left and regenerating trees were ≤ 2 m tall. Therefore, these areas did not offer suitable foraging sites for woodpeckers. Because all clear-cuts were performed before 1991, we assume that enough time had elapsed to avoid a bird crowding effect in the remaining forest shreds (Darveau et al., 1995). Owing to the scale of the study area, landscape types were not replicated, but the vegetation of the whole study area was very homogeneous before logging operations occurred. We therefore assume that results were not confounded by a 10 km north-south gradient over the study area.

2.1. Occurrence of Three-toed Woodpeckers

Field work was carried out during the breeding period, from 20 May to 25 June 1998. We located woodpeckers using playbacks of drummings and calls, which we played twice for 2 min followed by a listening period of 1 min at 100 stations (23 in continuous forests; 77 in shredded forests). Stations were separated by >700 m to limit repeated sampling of same individuals among broadcasts. All of the stations were located inside old-growth spruce dominated forests or forest shreds, and were visited twice between 05:00 and 10:30 in the morning. Territorial birds usually responded by quickly coming to the source of the playback, started to drum and call back to the simulated intruder (see Goggans et al., 1989 for more details on the playback method). Within these forests, the broadcast of drummings and calls could be heard as far as 300 m. Accordingly, we calculated the area of forest and total forest edge (along clear-cuts, bogs, lakes or rivers) in a radius of 300 m around each playback station based on provincial forest inventory maps. Occurrence of Three-toed Woodpeckers were compared between continuous and shredded forests using Fisher's exact test. Relationships between the occurrence of Three-toed Woodpeckers and potential explanatory variables (forest cover and total forest edge within 300 m) were investigated using logistic regression. To evaluate if the relationship between occurrence probability of Three-toed Woodpecker and the area (%) of old-growth forest within stations is perfectly linear, we simulated 1000 occurrence data sets ($n = 100$ each, old-growth forest cover ranging from 1 to 100%) with expected probability as

a linear function of area, corrected for a total frequency of 23. Parameter estimates for the area effect using logistic regressions with real and simulated data sets were compared using a *t*-test (Zar, 1998).

2.2. Movement paths and foraging locations from a clear-cut edge

Once a woodpecker responded to the playbacks, it was observed and followed until it flew out of sight. Each tree used by a bird was flagged with a tape, numbered, and its use (foraging, drumming, or stop only) was noted. This allowed us to backtrack and record precisely the path taken by the bird using a Differential Global Positioning System receiver with an accuracy of ± 5 m (Hurn, 1993). The paths were then analyzed with Fractal 3.14 (Nams, 1999) to measure their tortuosity, as indicated by their fractal dimension (D), at different spatial scales. Fractal dimensions of movement paths can vary from 1.0 (straight line) to 2.0 (random path filling a plane). Fractal D is a scale-dependent measure: it may be greater or lesser when a path is viewed at different spatial scales. Thus, fractal D can be used to understand scale-dependent foraging patterns of animals (Nams, 1999). As opposed to birds found in continuous forests, birds foraging in shredded forests composed mostly of linear strips are constrained in their movements by the spatial configuration of the remaining forested habitats. Therefore, movement paths at a larger scale than the maximum width of these linear strips should be less sinuous than in continuous forests. Such a directionality in their movements will be further accentuated if the birds avoid foraging near forest edges. No more than two non-overlapping paths per bird were recorded. A total of eight paths from seven individuals were obtained in continuous forests whereas a total of 12 paths from nine birds were obtained in shredded forests. As part of another study in the same area, we also followed 11 individually recognizable color-banded birds in the summer of 1997 (five in continuous forests for a total of nine paths, six in shredded forests for a total of 11 paths). The paths of these birds were included in this movement analysis.

For the birds followed in 1998 in shredded forests, we also recorded the distance of each tree used for foraging to the nearest clear-cut border. In each

case, the same measure was also recorded for the nearest available but suitable foraging tree, i.e. a recently dead tree (small branches and twigs still present) with a dbh >15 cm (Imbeau and Desrochers, in press). If woodpeckers avoid suitable foraging trees near a clear-cut edge, we predicted that the mean distance recorded for used trees would be greater than that for unused ones. This prediction was evaluated using a paired *t*-test. A total of 127 tree pairs were recorded for 17 birds (range = 1–27 tree pairs per bird, median = 5). Although all pairs of trees recorded for a given woodpecker individual were used in this test, we ensured by statistical weighting that each individual contributed to only one degree of freedom (see Desrochers, 1992). In this way, we could use all of the information recorded on the trees selected by each woodpecker without pseudo-replicating the data by counting each tree choice by a given individual as independent (Machlis et al., 1985). Furthermore, mean distance of used trees <20 m from a clear-cut border was compared to the distance expected from a random use of trees (10 m) within such bands with a one-sample *t*-test. A threshold of 20 m was chosen because it approximates the width of most permanent forest remnants, i.e. those encompassing streams and small rivers.

3. Results

3.1. Occurrence patterns

Within a 300 m radius of the playback stations, old-growth spruce-dominated stands covered from 65 to 100% of the area in continuous forests (median = 97%), while they ranged from 8 to 57% in shredded forests (median = 22%). Total forest edge and forest area were strongly related to each other in a nonlinear fashion (Fig. 1). Total forest edge varied widely for a given amount of forest cover in shredded forests, but not so in continuous forests.

Three-toed Woodpeckers were detected in 12 of the 27 playback stations located in continuous forests, and within 11 of the 73 stations in shredded forests (Fisher's exact test, $P = 0.003$). This difference can be explained to a large extent by the amount of forest within playback stations. Taken together, forest cover and total forest edge within stations were good

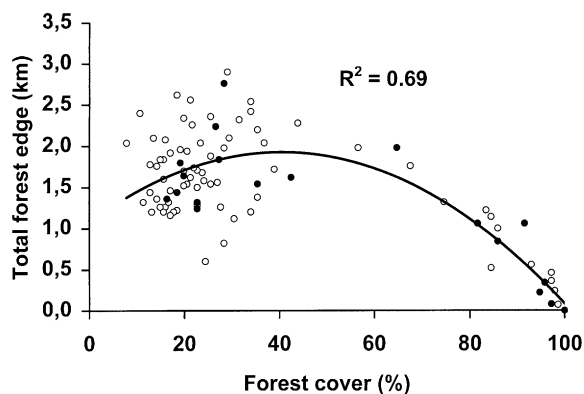


Fig. 1. Association between forest cover and total forest edge calculated within a 300 m radius of each playback station. Solid circles represent presences of Three-toed Woodpecker, open circles absences. A second-order polynomial curve fit was added.

predictors of the occurrence of Three-toed Woodpeckers (LR = 9.79, d.f. = 2, $P = 0.002$; Fig. 2). Nevertheless, the relative importance of the two variables markedly differed when the effect of the other was accounted for. While in the case of forest cover the effect was positive and approached statistical significance (LR = 3.28, d.f. = 1, $P = 0.07$), the effect of total forest edge became negligible (LR = 0.01, d.f. = 1, $P = 0.9$). When the residuals of total forest edge on forest cover are used, forest cover is

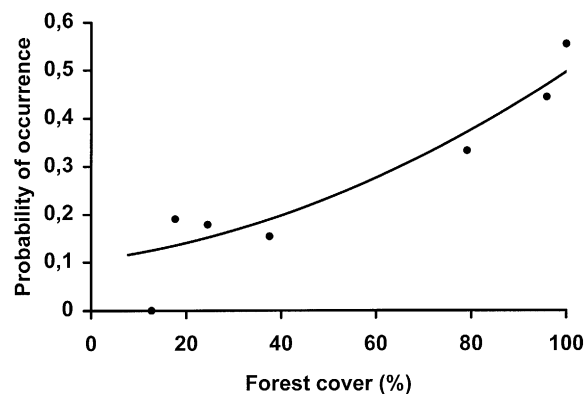


Fig. 2. Occurrence probability of Three-toed Woodpeckers in relation with the percentage of old-growth coniferous forest cover within a 300 m radius of a playback station. Solid circles are observed probability based on the mean of 9–28 playback stations. Using logistic regression, the line represents predicted probability of occurrence in a model containing both forest cover and total forest edge.

highly significant ($LR = 9.8$, $d.f. = 1$, $P = 0.002$) but the residuals of total forest edge do not add more information than what is already included within forest cover ($LR = 0.2$, $d.f. = 1$, $P = 0.6$).

The relationship between the whole range of forest cover and woodpecker probability of occurrence was similar to that expected if density within woodland remained constant throughout the study area. Parameter estimates for the variable old-growth forest area in the logistic regression using real data ($\text{mean} \pm \text{S.E.} = 0.0223 \pm 0.0072$) did not differ from the parameter obtained with 1000 simulated data sets following a strictly linear probability of occurrence ($\text{mean} \pm \text{S.E.} = 0.0281 \pm 0.0003$; $t = 0.80$, n.s.). Indeed, the population density of nesting woodpeckers in shredded forests (2.3 individuals/100 ha of forest remnant) was similar to that obtained in continuous forests (1.7 individuals/100 ha of forest). Because individuals of both sexes responded to the playbacks, this density is therefore of approximately one pair/100 ha of old-growth forest in both landscapes.

3.2. Movement patterns

We were able to follow woodpeckers over paths ranging in total length from 185–2461 m ($\text{mean} = 882$ m) and 76–5076 m ($\text{mean} = 800$ m) in continuous and shredded forests, respectively. Path extent, representing the linear distance between the two most distant points of a path, ranged 89–397 m ($\text{mean} = 227$ m) in continuous forests whereas it ranged 23–1028 m ($\text{mean} = 242$ m) in shredded forests. Fractal dimensions of movements were remarkably similar in both landscape types (Fig. 3): individual paths became increasingly tortuous over distances from <25 to 100 m. However, although few paths (10) were long enough to produce estimates of fractal dimension over 100 m, they differed markedly in the two forest types. Paths in continuous forests remained tortuous, while those in shredded forests became relatively straight with fractal dimension $D < 1.1$ (Mann–Whitney U -test, $P = 0.033$).

3.3. Tree use near forest edges

Foraging trees selected by Three-toed Woodpeckers were 0.2 m nearer forest edges than nearest unused trees ($\text{mean} \pm \text{S.E.} = 14.1 \pm 3.8$ m for used trees;

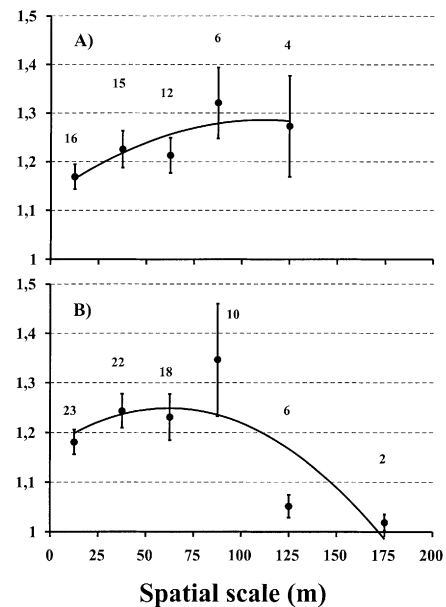


Fig. 3. Relationship between path tortuosity of foraging Three-toed Woodpeckers and spatial scale in continuous forests (A) and in shredded forests left after logging (B). Path tortuosity is lowest (straight line) at fractal dimension $D = 1.0$. Spatial scale is the length of segments sampled randomly from movement paths to calculate fractal D . Numbers above each point represent the number of paths that could be resampled within each classes of 25 m (below 100 m) or 50 m (above 100 m), while vertical bars represent standard errors. Second-order polynomial curves were fitted.

14.3 ± 3.8 m for the nearest unused trees). This difference was not significant (paired t -test, $n = 17$, $t = 0.21$, $P = 0.8$). Locations of foraging trees ranged from 14.1 m outside forest (into clear-cut) to 66.8 m inside forest. When we considered only trees used within the first 20 m, their distribution did not differ from an expected random location ($\text{mean} \pm \text{S.E.} = 8.0 \pm 1.2$ m for used trees; one sample t -test with 10 m as an expected mean, $n = 16$, $t = -1.66$, $P = 0.118$).

4. Discussion

4.1. Area sensitivity and edge avoidance: how strong is the evidence?

In this study, occurrence of Three-toed Woodpecker at a playback station was more than three times greater

in continuous forests than in residual shredded forests after logging. Nevertheless, the density of Three-toed Woodpeckers per 100 ha of old-growth forest did not differ between these two contrasting forest landscapes, as shown by the linear decline in observed occurrence proportional to the remaining area of old-growth forest cover. This result was unexpected because in shredded forests after logging, the mean area of remaining suitable habitat around a playback station (23%) is lower than the critical threshold of 30% described by Andrén (1994). However, the apparent linear relationship between the occurrence of Three-toed Woodpecker and forest cover is only valid for the range sampled, with only one of our 100 stations having less than 10% of forest cover. In the case of the White-backed Woodpecker (*Dendrocopos leucotos*), accelerated population declines occur when the amount of suitable habitat falls below that 10% threshold (Carlson, 2000). Another possible explanation for this quasi-linear relationship with no apparent threshold may come from the fact that forest shreds are not isolated fragments: all residual forests are connected because they are made of linked linear strips. However, even in isolated habitats, a study conducted by Haila et al. (1993) using the spot-mapping method did not find negative area effects and showed that the occurrence of breeding birds in boreal forest fragments in northern Europe follow from abundances in the regional species pool. Haila et al. (1993) argued that the contrast between results of European and North American fragmentation studies may arise from a misuse of point counts in North America. Point counts may be unreliable, because (1) the area they cover depends on the audibility of the vocalizations of the birds, and (2) birds recorded in a point count station include individuals which have most of their singing territories outside the observation area, a possibility that does not exist in small fragments surrounded by alien habitats. Such methodological problems could increase the probability of finding area-sensitive species when a study is based on point count data.

Although the occurrence of Three-toed Woodpeckers was highly related to the area of suitable habitat around the playback station, the amount of edge did not provide additional information on woodpecker occurrence. We also have shown that individual woodpeckers in shredded forests did not select foraging trees

further away from clear-cut edges than available ones, which resulted in similar tortuosity of foraging paths compared to continuous forests at spatial scales inferior to the width of forest shreds. In this case, both occurrence data and individual behavior of woodpeckers concur: no edge-avoidance pattern was found.

4.2. A possible detrimental effect of fragmentation: constrained movement paths

Our study does not support the hypothesis that the Three-toed Woodpecker is an area-sensitive or edge-avoiding species. Consequently, we could conclude that habitat loss is the only concern related to forest management, and that habitat configuration has almost no importance. Although these results could considerably simplify guidelines for forest managers, we believe that it would be irresponsible to reach such a conclusion without data on productivity and survival of individuals. Based on the results of the movement path analysis, we speculate that continuous forests might be better than shredded forests as breeding habitat. Indeed, during that season, both adults behave as central place foragers and must feed their nestlings that stay inside the nesting cavity for a period of 22–26 days (Winkler et al., 1995). According to Bovet and Benhamou (1991), the optimal path sinuosity of a central place forager constitutes a compromise between an over-straight path which result in a lengthy homeward journey and an over-sinuous path which results in too much overlapping between search path loops. Because the movement paths of foraging woodpeckers are constrained at a range that exceed 100 m in shredded forests, it is likely that such a compromise is hard to obtain in those linear habitats. We speculate that these constraints further exacerbate energetic costs related to multiple gap-crossings in deforested habitats (Huhta et al., 1999; Hinsley, 2000). Therefore, even though fragmented boreal forest landscapes do not show the patterns of higher nest predation or nest parasitism near edges (Bayne and Hobson, 1997), harmful consequences of forest shredding following forest logging may still occur for species such as the Three-toed Woodpecker. Finally, we also believe that these results are a good example on the importance of integrating animal behavior studies in wildlife science and management, as pointed out by Martin (1998).

4.3. Management implications

According to current logging rules in the province (Ministère des Ressources Naturelles du Québec, 1996), clear-cut separators can be harvested as soon as the regeneration reach more than a height of 3 m in neighboring areas. Even in riparian strips, some commercial stems may be cut as long as their density does not fall under 500 stems/ha. Moreover, forest industries are not constrained to provide minimum proportions of old-growth forests in their long-term management plans. In managed forests, our results indicated that the number of Three-toed Woodpeckers is directly related to the area of residual old-growth forest shreds retained. In order to maintain this species in managed areas, these shreds should be given a permanent protection status. Even if these linear shreds do not appear to provide an optimal foraging configuration for breeding woodpeckers, they could: (1) constitute a starting point in a form of aggregated structural retention within logged areas (Franklin et al., 1997); (2) ensure a minimum level of suitable habitat for woodpeckers as natural tree death of senescent trees provide a constant recruitment of snags used for foraging, drumming, and nesting (Imbeau and Desrochers, in press); and (3) provide connectivity which might be important for dispersing individuals (Machtans et al., 1996). However, the importance of large-scale regional mature forest cover (Drolet et al., 1999) or distance to nearest large tracts of protected areas (Kouki and Väänänen, 2000) on the occurrence of Three-toed Woodpecker in linear strips should also be investigated.

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