Long-Term Effects of Forestry on Birds of the Eastern Canadian Boreal Forests: a Comparison with Fennoscandia

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Abstract: Logging is considered the most important threat to species in boreal forests. In contrast to eastern Canada, where most boreal forests remain largely untouched, in Fennoscandia it is possible to assess the cumulative, long-term effects of intensive forestry on wildlife. But barvesting of stands is rapidly changing Canadian boreal forests, which represent an important proportion of the world's boreal forests. We show that Fennoscandia and eastern Canada present striking similarities in terms of forest-age structure, natural-disturbance regime, and structure of bird assemblages, and we provide an assessment of the long-term effects of forestry on eastern Canadian birds of the boreal forest. We used life-bistory traits from babitat, nesting site, and geographical range to calculate an index of sensitivity to changes induced by modern forestry for boreal species of each region. Tropical migrants commonly found in eastern Canadian boreal forests have life-bistory traits that are not threat factors in relation to changes caused by modern forestry. Therefore, the general belief that tropical migrants in North America are more sensitive to landscape changes than those in Europe may not hold for species found in the boreal coniferous forests of eastern Canada. Nine Fennoscandian species present high levels of sensitivity, and at least eight eastern Canadian species are of similar concern. In both regions, most of the sensitive species are resident cavity nesters. Given the important similarities between the two regions, the northern expansion of commercial forestry in eastern Canada is likely to result in the significant decline of several resident species, as has occurred in Fennoscandia.

Efectos a Largo Plazo de Actividades Forestales sobre Aves de los Bosques Boreales Canadienses del Este: una Comparación con Fennoscandia

Resumen: La tala es considerada la amenaza más importante para las especies de los bosques boreales. En contraste con el este de Canadá donde los bosques boreales permanecen prácticamente sin tocar, es posible evaluar los efectos acumulativos de largo plazo de la actividad forestal intensiva sobre la vida silvestre en Fennoscandia. Sin embargo, la explotación de madera esta cambiando rápidamente los bosques boreales canadienses, que representan una proporción importante de los bosques boreales del mundo. Mostramos que Fennoscandia y el este de Canadá tienen similitudes notables en términos de la estructura de edades del bosque, el régimen de perturbaciones y la estructura de las comunidades de aves, y aportamos una evaluación de los efectos a largo plazo de las actividades forestales sobre aves de los bosques boreales del este de Canadá. Utilizamos rasgos de la bistoria de vida como bábitat, sitio de anidación y rango geográfico para calcular un índice de sensibilidad a cambios inducidos por actividades forestales modernas en especies boreales del stenen rasgos de bistoria de vida que no son factores de amenaza en relación con cambios causados por la actividad forestal moderna. Por lo tanto, la creencia generalizada de una mayor sensibilidad de los migrantes tropicales a cambios en el paisaje en Norte América en comparación con Europa puede no ser válida

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presentan altos niveles de sensibilidad, mientras que por lo menos ochos especies del este de Canadá son de interés similar. En ambas regiones, la mayoría de las especies sensitivas son residentes y anidan en cavidades. Dadas las importantes similitudes entre las dos regiones, es probable que, como en Fennoscandia, la expansión de las actividades forestales comerciales en el este de Canadá resulte en la declinación significativa de varias especies residentes.

Introduction

Boreal forests represent 26% of the world's total forested area, and 53% of the remaining large, ecologically intact, and relatively undisturbed natural forests are now located in this zone (Bryant et al. 1997). Along with Russia, Canada is a major trustee of this global heritage. As in other boreal regions, this ecosystem is exposed to an increasing demand from commercial logging, which mostly affects old-growth stands (Senate Subcommittee on the Boreal Forest 1999). Although the maintenance of forest biodiversity is a criterion for sustainable forest management in Canada (Canadian Council of Forest Ministers 1997), the long-term cumulative effects of logging in this region are still largely unknown. Even for relatively well-studied Canadian taxa such as forest birds, long-term monitoring has not yet been undertaken on a scale that enables us to assess the status of their populations (e.g., Kirk & Hyslop 1998; Niemi et al. 1998). This is especially true for boreal species because of the limited road system in the northern part of the country (Bradstreet & Dunn 1997; Hussell 1997).

On the other hand, boreal Finnish and Swedish forest landscapes (hereafter called Fennoscandia) have been influenced for centuries by slash-and-burn cultivation and by charcoal, tar, and timber production (Esseen et al. 1992, 1997). The extent of these landscape-scale anthropogenic changes is so pronounced that if conservation measures are not undertaken immediately, these countries will lose many of their last fragments of natural forests (Bryant et al. 1997). Long-term changes in Fennoscandian forest-bird populations are well documented, cover several decades (e.g., Järvinen & Väisänen 1977;



We show that both regions present striking similarities in forest composition, natural-disturbance dynamics, species' life histories, and taxonomic composition of avifauna. Consequently, we suggest that the Fennoscandian experience can be used to predict the effects of landscape changes in eastern Canadian boreal forests. Moreover, we list and rank species likely to be adversely affected by modern forestry based on a classification of threat factors, which were significantly correlated to the magnitude of population changes in Fennoscandian species.

Methods

Study Areas

In Fennoscandia, boreal forests have a latitudinal range from lat. 58°N to lat. 69°N and cover approximately 53 million ha (Fig. 1; Ahti et al. 1968). Tree-species composition is relatively homogeneous, with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) covering about 89% of the forest area (Esseen et al. 1992; Hannelius & Kuusela 1995). Although broad-leaved species such as birches (*Betula pendula* and *B. pubescens*) and European aspen (*Populus tremula*) are also present in old-growth stands, such pioneer species are more preva-



Figure 1. Geographical distribution of boreal forests considered and historical progression of large-scale forest use for saw logs and pulp wood in eastern Canada and Fennoscandia. Data for Fennoscandia from Helander (1949), Oksanen et al. (1995), Angelstam (1997), and P. Angelstam (personal communication). Data for eastern Canada from Rowe (1972), Bryant et al. (1997), Gagnon (1998), and S. Payette (personal communication). lent in early successional stages (Linder et al. 1997). Before the end of the nineteenth century, when fire suppression measures were first introduced, fire controlled the vegetational dynamics of Fennoscandia. Fire-rotation periods were 80–120 years (Zackrisson 1977; Haapanen & Siitonen 1978) or less in areas of intensive slash-andburn cultivation (Lehtonen 1998). It is difficult to estimate the average proportion of old-growth forests (>120 years) under the natural-disturbance regime in Fennoscandia because of extensive human effects spanning several centuries. For instance, Lehtonen (1998) showed that the distance to slash-and-burn cultivation severely affected the age distribution of forests in eastern Finland, whereas in more remote areas in 1913 more than 80% of the stands were older than 150 years.

Boreal forests of eastern Canada present striking similarities with those of Fennoscandia. Extending in a wide band from eastern Alberta to Newfoundland, an area of approximately 205 million ha is largely dominated by only two conifers: black spruce (Picea mariana) and jack pine (Pinus banksiana) (Fig. 1; Rowe 1972; Gagnon 1998). As in Fennoscandia, broad-leaved tree species such as white birch (Betula papyrifera) and quaking aspen (Populus tremuloides) are usually more prevalent in early developmental stages (Carleton & MacLellan 1994). Recent dendrochronological studies show the importance of stand-replacement fires in this part of the boreal forest. Although the period between successive fires varies along latitudinal and longitudinal gradients, it averages 100-130 years (Payette 1992). In Quebec, where most unbroken pure black-spruce forests are located (Gagnon 1998), old-growth stands accounted for approximately 47% of the coniferous-dominated areas in 1994 (Cantin 1996).

The geographical advances of large-scale logging for saw logs and pulp wood followed the same general pattern in both regions, although this took place more than a century earlier in Fennoscandia (Fig. 1; Mönkkönen & Welsh 1994). The southern parts of the boreal forest, close to populated regions, were the first to be harvested. Then logging operations were forced to move progressively northward (Esseen et al. 1992; Boudreau et al. 1997). In Fennoscandia, a general decrease in the area covered by old-growth forests is well documented. In northern Finland (i.e., north of 64°N), as much as 44% of the total forested areas were still old-growth in 1951-1953 (Finnish Forest Research Institute 1997). In comparison, this proportion is roughly the same as that still remaining in Québec's allocated boreal forest in 1994 (44% vs. 47%; Fig. 2a). But logging has converted Finnish forests into a more regulated age structure over the last 40 years (Fig. 2b).

Characteristics of Bird Assemblages

Data for breeding birds at different stages of forest succession were obtained from the literature (Table 1). Only



Figure 2. (a) Age structure of coniferous stands in Québec in 1994 (Cantin 1996) compared with that of forest land in northern Finland during the 1951–1953 National Forest Survey (Finnish Forest Research Institute 1997). In both regions, old-growth forests (>120 years old) account for more than 40% of land area. (b) Over 40 years, as a result of modern forestry, the proportion of mature (80–120 years old) and old-growth forests in northern Finland declined by 15% and 17%, respectively (Finnish Forest Research Institute 1997).

studies conducted in stands dominated by Scots pine or Norway spruce were considered for Fennoscandia. Stands dominated by black spruce or jack pine were considered for Canada. When it was available, we preferred height of vegetation over stand age to define four successional stages: (1) <1.0 m or <5 years, (2) 1.0-4.0 m or 6-25 years, (3) 4.1-10 m or 26-75 years, (4) >10 m or >76years. Each species was categorized into guilds based on migratory status (tropical migrant, short-distance migrant, resident), following Snow and Perrins (1998) or Ehrlich et al. (1988). Proportions of species and of individuals contributed by each guild to the breeding-bird community were calculated for each successional stage. There was a strong correlation between proportions of species and individuals at each stage (all r > 0.65), so we present only the results based on the proportions of species presented. For each region, Kruskall-Wallis tests were used to determine whether the proportion of species among each guild differed among successional stages. Dunnett's T3 tests were used for all post-hoc multiple comparisons.

Table 1.	Details of studies used to com	pare bird assemblages	of Fennoscandian and east	tern Canadian forests do	minated by boreal s	pruce or pine.

Locality and coordinates	Dominant tree species	No. of successional stages				
(lat., long.)		1	2	3	4	Reference
Fennoscandia						
northern Finland (66°N, 29°E)	Norway spruce	1	1	1	1	Helle 1985 <i>a</i>
northern Finland (66°N, 29°E)	Scots pine	1	1	1	1	Helle 1985 <i>a</i>
central Finland (63°N, 28°E)	Norway spruce	1	1	1	1	Mönkkönen 1984
central Finland (63°N, 28°E)	Scots pine	1	1	1	1	Mönkkönen 1984
southern Finland (62°N, 25°E)	Norway spruce	1	1	1	1	Haapanen 1965
southern Finland (62°N, 25°E)	Scots pine	1	1	1	1	Haapanen 1965
sweden (66°N, 21°E)	Norway spruce	0	0	0	1	Edenius & Sjöberg 1997
		6	6	6	7	
Eastern Canada						
Quebec (53°N, 75°W)	black spruce-					
	jack pine	1	1	1	1	Crête et al. 1995
Quebec (49°N, 73°W)	black spruce	1	0	1	2	Imbeau et al. 1999
Quebec (47°N, 71°W)	black spruce	0	2	1	0	Imbeau et al. 1999
Ontario (48°N, 83°W)	black spruce	1	5	0	0	Welsh & Fillman 1980
Ontario (48°N, 79°W)	black spruce	0	0	0	1	Erskine 1971a
Ontario (48°N, 80°W)	jack pine	0	0	0	1	Erskine 1971b
Manitoba (52°N, 101°W)	black spruce	0	0	0	1	Erskine 1972a
Manitoba (52°N, 101°W)	jack pine	0	0	1	0	Erskine 1972b
Saskatchewan (54°N, 107°W)	black spruce	0	0	0	1	Erskine 1973
		3	8	4	7	

Species Ranking Criteria

All forest-associated species or those requiring trees for nesting that possibly breed in the boreal forests of Fennoscandia and eastern Canada were listed according to the best available sources (Fennoscandia: Väisänen et al. 1998; Svensson et al. 1999; eastern Canada: Godfrey 1986; Cadman et al. 1987; Gauthier & Aubry 1996). To evaluate possible long-term effects of current forestry on population trends of these bird species, we tallied all their life-history traits known to be affected by such practices. These traits, involving habitat use and nesting strategy, represented threat factors, and each species was rated from 0 (no threat) to 1 or 2 (most sensitive) for each of the eight traits (Table 2).

Among habitat-related factors, the preferred successional status for a given species is clearly the most important for predicting its response to forest management. Because forest management reduces the availability of

Table 2.	Life-history criteria used to sun	n "threat" factor	s relative to the conve	rsion of natural fores	ts to commercial forests	s by current
forestry p	practices.					

	Threat factors ^a				
Life-bistory variables	0	1	2 old growth or fire specialist		
Habitat related successional status ^b	generalist	mid- to late-			
area requirement ^c snags used for foraging	<3 ha no	>3 and <10 ha ves	>10 ha		
Nesting related					
body size ^d	<13 cm	\geq 13 and $<$ 30 cm	≥30 cm		
excavator" open nest structure requiring large tree	yes no	no yes			
Distribution related species not breeding outside the boreal zone	no	yes			

^a0, no threat; 2, most sensitive.

^bLate-successional species not associated with black spruce or jack pine were not considered. To account for the increase of early successional babitats created by forestry, a total of two babitat-related threat factors were subtracted for species associated with such babitats. ^cOnly species baving already one or two threat factors relative to their successional status were considered.

^dOnly cavity nesters were considered.

old-forest stands, late successional species are likely to be more negatively affected than generalists or early successional species (Askins 2000). Because logging operations often prioritize old-growth or recently burned stands, species restricted to such habitats are especially sensitive (Hejl 1994; Hutto 1995). Furthermore, late successional species with large area requirements are affected negatively by habitat loss or fragmentation (Helle 1985*b*; Rolstad & Wegge 1987; Virkkala 1987, 1991). Finally, to account for the increase in early successional habitats created by forestry, we subtracted two habitatrelated threats to all species known to be associated with such habitats.

Among nesting-related factors, cavity nesters are likely to be negatively affected because industrial forestry attempts to limit natural tree death and decay. Secondary cavity nesters, which depend on abandoned holes or natural cavities, are possibly more affected than primary excavators because they have more limited breeding opportunities (Martin 1993). Furthermore, raptor nesting success is limited in some regions by the availability of nesting sites such as large trees (Newton 1979). Finally, for each species presenting at least one threat factor, we added a breeding distribution restricted to the boreal coniferous zone as a responsibility factor (for rationale see Dunn et al. 1999). Sums of the scores across traits in addition to the responsibility score yielded a total score of threat factors for a given species. Details concerning all species retained are available from the authors.

We evaluated the correlations between habitat-related, nesting-related, and total number of threat factors using recent population trends of Fennoscandian species. Variations in their population size in the last 50 years were based on the 1986-1991 Finnish line transects and were expressed as the percentage of the 1941-1949 population estimates from Väisänen et al. (1998). We used Spearman's rank correlation to account for the arbitrary choices of absolute values given as threat factors. Onetailed p values were retained for these correlations because they were all predicted to be negative. For further analyses, each species for each category of threat factor was categorized into one of four sensitivity levels (-1, 0, 0)1, and 2): -1, benefiting from forestry (-1 threat factors); 0, unaffected by forestry (no threat factors); 1, slightly affected by forestry (1-4 total threat factors and 1-2 habitator nesting-related threat factors); and 2, highly affected by forestry (5 total threat factors and 3 habitat- or nestingrelated threat factors). We compared mean sensitivity levels and their distribution among migratory guilds and regions using Cochran-Mantel-Haenszel tests.

Results

The proportion of residents varied significantly in the course of forest succession in Fennoscandia (Kruskall-

Wallis H = 11.6, df = 3, p < 0.01) and in eastern Canada (H = 9.5, df = 3, p = 0.02), their highest proportion occurring in mature forests in both regions (Fig. 3). Conversely, mature forests presented the lowest proportion of tropical migrants. In Fennoscandia their proportion declined significantly in the course of forest succession (H = 11.6, df = 3, p < 0.01), whereas they peaked in the shrub stage in eastern Canada (H = 15.0, df = 3, p < 0.01). At this stage, short-distance migrants were significantly less abundant in eastern Canada (H = 11.4, df = 3, p = 0.01) but remained stable in Fennoscandia (H = 4.3, df = 3, p = 0.24).



Figure 3. Relative proportion of bird assemblages (mean percentage of all species detected \pm SE) in Fennoscandian and in eastern Canadian boreal sprucepine forests composed of tropical migrants, short-distance migrants, and residents. Each development stage refers to dominant vegetation height or age since last disturbance: I, <1.0 m or <5 years; II, 1.0-4.0 m or 6-25 years; III, 4.1-10 m or 26-75 years; IV, >10 m or >76 years. Studies used are listed in Table 1.

According to our literature review, 119 bird species are forest related or require trees for nesting in the boreal forest of Fennoscandia. A total of 134 species met the same criteria in the eastern Canadian boreal forest. Fennoscandian birds that have declined over the last 50 years had high threat-factor totals ($r_s = -0.22$, df = 88, p = 0.02; Fig. 4a). This relationship was stronger for habitat-related factors ($r_s = -0.26$, df = 88, p < 0.01; Fig. 4b) than for nesting-related factors ($r_s = -0.11$, df = 88, p = 0.16; Fig. 4c). Nevertheless, when we removed nest-box breeding species from the data, we obtained a much stronger correlation between nesting-related threat factors and population changes ($r_s = -0.25$, df = 74, p = 0.02; Fig. 4d). Indeed, population trends of nestbox users increased (average population size in the 1990s was 177% of that in the 1940s, n = 14 species), whereas other cavity nesters decreased slightly (91%, n =10 species). This difference in trends was significant (Mann-Whitney *U* test, z = -2,18; p = 0.03).

Mean threat levels differed among migratory groups (Cochran-Mantel-Haenszel [CMH] test controlling for regions, Q = 48, df = 2, p < 0.01). Residents were more sensitive than short-distance or tropical migrants (Table

3) based on total threat factors, habitat-related factors (CMH test, Q = 45, df = 2, p < 0.01), or nesting-related factors (CMH test, Q = 21, df = 2, p < 0.01). Mean threat levels for each group did not differ significantly between Fennoscandia and eastern Canada (CMH test controlling for migrating strategy; total threat factors: Q = 0.03, df = 1, p = 0.8; habitat-related factors: Q <0.01, df = 1, p > 0.9; nesting-related factors: Q = 0.5, df = 1, p = 0.5). The proportion of species in each of the four threat levels did differ between regions for all factors (CMH general-association test controlling for migrating strategy: Q = 12.4, df = 3, p = 0.006) and for habitat-related factors (Q = 10.7, df = 3, p = 0.014), but not for nesting-related factors (Q = 0.7, df = 2, p = 0.7). The proportion of migrants, especially tropical migrants, that was slightly negatively affected by forestry was greater in Fennoscandia than in eastern Canada (Fig. 5).

In Fennoscandia, nine species presented a high sensitivity level (fewer than four threat factors). Among them, three species do not frequently use nest-boxes, and all have declined by more than 55% in the last 50 years (Table 4). In eastern Canada, eight species present the same sensitivity level, including two Holarctic spe-



Figure 4. Population changes (log transformed) in Fennoscandinavian birds related to (a) all threat factors, (b) habitat-related factors, (c) nest-related factors (all species), and (d) nest-related factors (without nest-box users). Species experiencing population changes higher than 2 are increasing, whereas species experiencing trends lower than 2 are decreasing. Spearman-rank correlation coefficients (r_s) are shown for each scatterplot.

Locality, migratory group	No. of species (%)	$All factors (\overline{\mathbf{x}} \pm SE)$	Habitat-related factors (x ± SE)	Nesting-related factors $(\overline{\mathbf{x}} = SE)$
Fennoscandia				
residents	46 (39)	0.8 ± 0.1	0.5 ± 0.1	0.7 ± 0.1
short-distance migrants	38 (32)	0.2 ± 0.1	-0.1 ± 0.1	0.4 ± 0.1
tropical migrants	35 (29)	0.1 ± 0.1	-0.1 ± 0.1	0.3 ± 0.1
Eastern Canada				
residents	27 (20)	0.9 ± 0.1	0.6 ± 0.2	0.7 ± 0.1
short-distance migrants	53 (40)	0.2 ± 0.1	-0.1 ± 0.1	0.5 ± 0.1
tropical migrants	54 (40)	-0.1 ± 0.1	-0.2 ± 0.1	0.1 ± 0.1

Table 3. Mean sensitivity levels based on the sum of all threat factors, habitat-related threat factors, and nesting-related threat factors for boreal forest-related birds in Fennoscandia and eastern Canada.

cies (Three-toed Woodpecker and Boreal Owl) and two species (Pileated Woodpecker and Boreal Chickadee) that we consider ecological equivalents of high-ranked declining Fennoscandian species (Black Woodpecker and Siberian Tit).

Discussion

In natural conditions, bird-species assemblages of both regions lived in (1) a largely old-growth, coniferous-dominated landscape of *Picea* or *Pinus* tree species; (2) the presence of deciduous trees, usually on recently disturbed areas; and (3) a period of at least 80 years between successive fires. Moreover, because spruce and pine reach economic maturity between 80 and 120 years in both regions (Hannelius & Kuusela 1995; Government of Québec 1998), the future human-shaped forest designed to maintain a sustainable yield of wood products in eastern Canada is likely to be similar to the one presently observed in northern Finland. For example, in Quebec, where the northern advance of Canadian forestry is most pronounced, approximately 13,750,000 ha of old-growth coniferous forest remain in allocated lands (Cantin 1996). If the current rate of harvesting is maintained (300,000 ha/year according to Parent [1999]), one of the last remnants of large, old-growth coniferous forests in this part of eastern Canada will be cut within 45–50 years.

Previous comparisons of Nearctic and Palearctic bird communities and forest succession found pronounced differences in the proportion of tropical migrants in various stages of forest development. In Europe the proportion of migrants generally decreases with increasing vegetation height (Helle & Fuller 1988), whereas the opposite trend is found in eastern and middle North America, where the proportion of migrants is greater in mature forests (Mönkkönen & Helle 1989; Helle & Mönkkönen 1990;



Figure 5. Number of bird species (%) of four sensitivity levels related to changes induced by modern forestry based on the number of threat factors present in their life-bistory traits. Results are shown for each migratory guild and region. Species with <0 threat factors should benefit from forestry; those with >0 should be affected negatively.

Table 4. Bird species in boreal forests of eastern Canada andFennoscandia with more than four threat factors related to changescaused by current forestry.

Species	Total tbreat factors
Eastern Canada	
Three-toed Woodpecker (Picoides tridactylus)	8
Black-backed Woodpecker (Picoides arcticus)	8
Pileated Woodpecker (Dryocopus pileatus)	7
Boreal Owl ^a (Aegolius funereus)	7
Boreal Chickadee (Poecile hudsonica)	5
Brown Creeper (Certhia americana)	5
Barrow's Goldeneve ^a (Bucephala islandica)	5
Bufflehead ^a (Bucephala albeola)	5
Fennoscandia	
Three-toed Woodpecker ^b (<i>Picoides tridactylus</i>)	8
Black Woodpecker ^b (Dryocopus martius)	7
White-backed Woodpecker ^b	
(Dendrocopos leucotos)	6
Siberian Tit ^{<i>a</i>,<i>b</i>} (<i>Poecile cincta</i>)	6
Nuthatch ^{a,c} (Sitta europea)	6
Ural Owl ^{a,c} (Strix uralensis)	6
Tengmalm's Owl ^a (Aegolius funereus)	6
Pygmy Owl ^{a,c} (Glaucidium passerinum)	5
Smew ^{<i>a,c</i>} (Mergus albellus)	5

^{*a}Frequently use artificial nest boxes.*</sup>

^bPopulation declines >55% over the last 50 years.

^cFinnish line-transect data do not provide reliable estimate of population trend.

Helle & Niemi 1996). This general pattern has led to the belief that Nearctic tropical migrants may be more vulnerable to human-induced landscape changes than their Palearctic counterparts (Mönkkönen et al. 1992; Mönkkönen & Welsh 1994). But these reviews pooled studies from both temperate deciduous and boreal coniferous forests that experienced different agents, severity, and frequency of disturbance (Angelstam 1992). By restricting our comparisons to the two northern boreal forests, we found that, in both regions, tropical migrants represented a significantly greater proportion of breeding birds in early- than late-successional stages. This similarity in habitat use occurs even though these species are completely distinct (none are holarctic) and belong to different families in the two regions (Helle & Mönkkönen 1990; Mönkkönen 1992; Böhning-Gaese et al. 1998).

Tropical migrants commonly found in eastern Canadian boreal forests are not categorized as mature forestinterior specialists and are often ranked low in conservation priority by Reed (1992) and Dunn et al. (1999). Moreover, they differ from many other species found in eastern North America because they have life-history traits that are not threat factors in relation to modern forestry. Therefore, the general belief that tropical migrants in North America are more sensitive to landscape changes than those in Europe may not hold for species found in the boreal coniferous forests of eastern Canada.

According to our ranking, in both regions residents were more likely to be negatively affected than shortdistance or tropical migrants (see also Hunter 1992; Mönkkönen & Welsh 1994). Not even one tropical migrant belonged to the group of highly sensitive species that were mostly resident cavity-nesting birds. This ranking correlated well with the population trends of Fennoscandian species, except when nesting-related factors were considered alone. Many European species benefit from large-scale supply of artificial nest boxes, however; in Finland for example, well over 100,000 nest boxes are available for the Goldeneye (Bucephala clangula) alone (Pöysä 1996). Thousands of artificial cavities have also been distributed in Finland for owls, kestrels, and passerines. Therefore, one might not expect as large a decrease among cavity-nesting birds as there would have been without such a large-scale supplement of artificial breeding cavities. Indeed, a significant correlation was obtained between nesting-related threat factors and bird population trends only when species using nest boxes were removed from the data. This result suggests that artificial breeding cavities are important to maintain or increase populations of secondary cavity nesters.

Among 134 eastern Canadian bird species, at least 8 present high levels of sensitivity to changes induced by modern forestry, and four of them are of high Canadian responsibility (Dunn et al. 1999). Unfortunately, most of them are not songbirds, meaning that standard monitoring by point counts is not likely to reveal their future population trends. Furthermore, only three species (Boreal Owl, Barrow's Goldeneye, and Bufflehead) could potentially use artificial nest boxes. Although these species benefit from a supply of artificial breeding cavities, no special effort is currently undertaken in logging areas of eastern Canada. Because Canadian boreal forests are relatively remote, in this case the costs of providing and maintaining artificial cavities might be even higher than the cost of forest-management activities that promote the perpetuation of primary cavity nesters (McKenney & Lindenmayer 1994).

In Fennoscandia, past logging has affected woodpeckers considerably (Angelstam & Mikusinski 1994; Mikusinski & Angelstam 1998), with all high-ranked Fennoscandian species showing decreasing population trends. In the case of the White-backed Woodpecker, declines related to forestry are well documented, and this species is now considered endangered in Sweden and may even disappear as a breeding species in Finland (Aulén & Carlson 1990; Virkkala et al. 1993). In eastern Canada, Threetoed and Black-backed Woodpeckers, mostly restricted to old-growth forests or recent burns (Imbeau et al. 1999), possess a combination of life-history traits that conflicts strongly with present forest-management practices. Although some jurisdictions now include some provision for retaining snags or potential snags as nesting sites within cut blocks, the continuous availability of foraging snags is almost always overlooked. Such species are the most likely to require special conservation action (i.e., a fine-filter approach) to be maintained in managed areas.

Conclusions

Repeating Mistakes

About 50% of the red-listed Fennoscandian species are threatened because of forestry (Berg et al. 1994; Nilsson & Ericson 1997). Compared with other taxa, birdswhich comprise <1% of all species in boreal Fennoscandia-are not a particularly sensitive group. There are 32 threatened bird species in Finland, out of 235 regularly breeding species. Forestry is the main cause of threat for 3 species (9.4% of the threatened species and 1.3% of all breeding birds) and one cause of threat for 6 species (18.8%, 2.6%) (Finnish Environment Institute 2000). Among invertebrates, lichens, and fungi, the number and proportion of threatened species for which forestry is the main cause of endangerment is much higher. For example, there are 202 threatened invertebrates for which forestry is the main cause of endangerment (26.6% out of 759 endangered species and 2.3% out of 8599 surveyed species). For lichens and fungi the respective number is 199 species, which is 53% of 374 threatened species and 4.9% of the surveyed 4027 species (Finnish Environment Institute 2000). Although logging history is considerably more recent in Canada than in Fennoscandia, already 12 out of 17 vulnerable, threatened, or endangered forest-dwelling species of wild flora and fauna are considered susceptible to logging in the boreal shield region (Nadeau et al. 1998). If the patterns we describe apply to a wide array of taxa, large-scale declines can be predicted in the future among many forest-associated species in eastern Canada.

In recent years, a planning system for forest management with a greater emphasis on conservation has been implemented in the Fennoscandian countries (Rülcker et al. 1994; Halman et al. 1996; Angelstam & Petterson 1997). In this new system, termed "ecological forest landscape management," forest stands are not managed in isolation but rather as components of management units measuring at least tens of thousands of hectares. The ultimate goal of this approach is to maintain viable populations of all naturally occurring species in the area, to enhance connectivity among residual patches of oldgrowth forests, and, at the same time, to continue the commercial harvesting of timber in an economically sustainable way.

The challenge for this new management system is to break down the effect of the species-area relationship—in other words, to maintain all species in viable populations even though the area of old forest is further reduced by silvicultural harvesting (Mönkkönen 1999). The main approach of this new management system is to set aside areas permanently or temporarily (e.g., so-called key biotopes, where the probability of the occurrence of endangered species is high) and to enhance dispersal by providing stepping stones and habitat corridors (e.g., riparian strips). Current knowledge implies that for birds these measures are of secondary importance if not accompanied by habitat protection (Andrén 1994; Mönkkönen & Reunanen 1999). In southern Finland, for example, protected areas are key to maintaining old-growth and hole-nesting species (Virkkala et al. 1994a, 1994b). It thus seems clear that corridors or the spatial configuration of remaining habitat cannot compensate for the overall loss of habitat (Harrison & Bruna 1999), particularly at current levels of habitat availability in Fennoscandia, where only <5% of the original old-growth forest area remains. Empirical studies from coniferous-dominated North American forests (McGarigal & McComb 1995; Drolet et al. 1999) have shown that the amount of habitat is of greater importance than its pattern (configuration and connectivity).

Because more than 90% of eastern Canadian boreal forests are publicly owned, the implementation of landscape-scale management guidelines and the design of a network of protected areas should be easier to establish there than in Fennoscandia. But even if individual clearcut sizes are now restricted by the provinces, there are no regulations for the cumulative size of neighboring or nearby cutblocks within landscapes (Senate Subcommittee on the Boreal Forest 1999). In some provinces such as Québec, moreover, only 0.4% of the productive spruce forests are set aside as strictly protected areas (Parent 1999). Probably because of the low number of threatened species presently found in Canadian boreal forests, managers do not see the necessity of coupling landscape management to the protection of a significant amount of the remaining virgin forests. We hope that a comparative study such as ours will encourage recognition that incorporating more conservation actions in Canadian forestry is a necessity even though population levels of most forest-associated species are not yet critical. With the current levels of natural forest areas still remaining in eastern Canada, landscape-level planning similar to that of the ecological forest-landscape management system in Fennoscandia, may turn out to be an effective tool in managing Canadian boreal forests for biodiversity.

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