Effects of Selection Cutting and Landscape-Scale Harvesting on the Reproductive Success of Two Neotropical Migrant Bird Species

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Abstract: We measured the effects of forest harvesting at two spatial scales on the productivity of two Neotropical migrant bird species, the Black-throated Blue Warbler (Dendroica caerulescens) and the Ovenbird (Seiurus aurocapillus). We selected two forest landscapes representing extremes in harvesting intensity for northwestern New Brunswick, Canada. Within each landscape, we selected study plots located either in recent (<5 years) selection-cut stands (30% removal every 20 years) or in stands that were lightly harvested at least 30 years ago. Black-throated Blue Warblers reached higher densities in selection cuts, but their reproductive performance (pairing and fledging success) did not differ significantly between stand types (uncut vs. selection cut) or between landscape types (intensively vs. moderately harvested). In 1998, nonetheless, 61% of the estimated number of fledglings produced in our plots were born in selection cuts. In contrast, this proportion was only 23% for Ovenbirds in 1998 and 1999 combined. Ovenbirds had lower densities, and their reproductive performance was significantly lower in selection cuts than in uncut plots. These results indicate that the effects of selection cutting on demography are species-specific and that Ovenbird persistence in selection cuts may be compromised unless the intensity or frequency of cutting is decreased.

Efectos de Corte por Selección y Cosecha a Escala de Paisaje en el Exito Reproductivo de dos Especies de Aves Migratorias Neotropicales

Resumen: Medimos los efectos de la cosecha forestal a dos escalas espaciales sobre la productividad de dos especies de aves migratorias neotropicales, el chipe azulnegro (Dendroica caerulescens) y el chipe suelero (Seiurus aurocapillus). Seleccionamos dos paisajes forestales que representan a los extremos de las intensidades de cosecha para el noroeste de New Brunswick, Canadá. Dentro de cada paisaje, seleccionamos lotes de estudio localizados en rodales recientemente cortados (< 5 años) con selección de corte (con remoción de un 30% cada 20 años) o en rodales que fueron ligeramente cosechados por lo menos hace 30 años. Los chipes azulnegro alcanzaron sus densidades máximas en áreas con selección de corte, pero su rendimiento reproductivo (establecimiento de parejas y éxito de crías en emplumar) no difirió significativamente entre tipos de rodales (no cortados vs corte de selección) o entre tipos de paisaje (intensivamente vs moderadamente cosechados). A pesar de esto, en 1998, el 61% del número estimado de crías emplumadas producidas en nuestros lotes nacieron en los lotes de corte con selección. En contraste, esta proporción fue de tan solo un 23% para el chipe suelero en 1998 y 1999 combinados. Los chipes sueleros tuvieron densidades más bajas y su rendimiento reproductivo fue significativamente menor en áreas con corte de selección que en los lotes sin corte. Estos resultados indican que los efectos de corte con selección sobre la demografía son especie-específicos y que la persistencia de chipes sueleros en los sitios con corte de selección puede estar comprometida a menos que disminuya la intensidad o la frecuencia de los cortes.

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Introduction

Most studies examining fragmentation effects on avian reproduction have been conducted in agricultural landscapes (Paton 1994; Tewksbury et al. 1998). Results from these studies may not be relevant to landscapes fragmented by forestry (Hansen & Urban 1992; Thompson 1993) because this activity tends to produce landscapes characterized by (1) more complex mosaics of interconnected stands of varying age, structure, and composition; (2) softer edges; and (3) lower abundances of nest predators. Furthermore, brood parasitism by the Brown-headed Cowbird (Molothrus ater) is rarely an important factor in landscapes fragmented by forestry because the species often is absent there (King et al. 1996; Sabine et al. 1996; Hagan et al. 1997; M.-A. V., unpublished data).

In New Brunswick, landscape structure is being altered by silvicultural treatments. Gradually, relatively unbroken mature forests are being replaced by mosaics of recent clearcuts, spruce plantations, selection cuts, and scattered uncut stands. Provincial regulations prohibit clearcutting of healthy, shade-tolerant deciduous stands. Although selection cutting would be expected to be less damaging to these forest ecosystems, its effects on biodiversity have received little attention (Thompson et al. 1995). Several studies have shown that selection cutting causes a turnover in avian species composition (Medin & Booth 1989; Hutto et al. 1992; Annand & Thompson 1997; Norton & Hannon 1997). We wanted to determine whether this silvicultural practice affects not only avian abundance but also demographic parameters, because conservation planning should be based on the maintenance of viable populations. To our knowledge, only Ziehmer (1993) has examined the effects of selection cutting on avian demographic parameters. That study showed that pairing success in the Red-eyed Vireo (Vireo olivaceus) was lower in selectively harvested plots than in control plots. His sample sizes, however, were rather small (n = 5 territorial males in selection cuts and n = 15 in control plots).

Indicators of reproductive success such as pairing success (Villard et al. 1993; Hagan et al. 1996) and the observation of family groups (Poneluzi et al. 1993; Buford & Capen 1999) often have been used to estimate reproductive performance. Direct monitoring of nests is required to determine (1) causes of nest failure, (2) number of nesting attempts, (3) clutch and brood sizes, and (4) parasitism rates. We conducted intensive nest searches in two contrasting landscapes: intensively harvested and moderately harvested. In each landscape type, we selected one study plot located in a stand that had been lightly harvested at least 30 years ago and one or two plots in recent selection cuts. This design allowed us to examine harvesting effects on bird reproductive success simultaneously at the local and landscape scales.

For each bird species, we tested three alternative predictions: (1) reproductive success will be lower in selection cuts than in uncut stands, irrespective of landscape characteristics; (2) reproductive success will be lower in the intensively harvested than in the moderately harvested landscape, independent of local stand conditions; and (3) reproductive success will be lowest in selection cuts within the intensively harvested landscape.

Methods

Study Area

Our study is part of an ongoing research project examining the effects of harvesting intensity on faunal diversity and persistence within two landscapes. These landscapes (49 km²) are located 10 km apart within 25 km of Riley Brook (lat 47°11′N, long 67°13′W) in northwestern New Brunswick, Canada (Fig. 1). Each landscape represents an extreme in the regional gradient of harvesting intensity and will hereafter be referred to as either moderately or intensively harvested. According to forest inventory maps, mature forest cover was approximately 45% in the intensively harvested landscape and over 70% in the moderately harvested landscape. The remainder of each landscape was represented by spruce plantations, selection cuts, clearcuts, naturally regenerating stands, or roads. The dominant deciduous species in both landscapes were sugar maple (Acer saccharum), American beech (Fagus grandifolia), and yellow birch (Betula alleghaniensis). The dominant coniferous species, which are mainly restricted to ravines, were balsam fir (Abies balsamea), black spruce (Picea mariana), and white cedar (Thuja occidentalis). The shrub layer consists mainly of seedlings or saplings of canopy trees, and its density varies according to the silvicultural treatment applied.

In each landscape type, we selected 500 X 500 m (25 ha) grids, one in a stand in which no selection cutting had taken place for at least 30 years and one or two in recent (<5 years) selection cuts (Fig. 1). In 1997 we surveyed the uncut plots. In 1998 we added one selection-cut plot to each landscape. The selection-cut plot within the intensively harvested landscape is hereafter referred to as selection-cut 1. In 1999 we surveyed all four plots but added another selection-cut plot in the intensively harvested landscape, hereafter called selection-cut 2. In the intensively harvested landscape, the uncut plot was surrounded on three sides by 10-year-old black spruce plantations. The selection-cut plots were embedded in larger selection cuts (>200 ha), and each had narrow dirt roads crossing their corners (Fig. 1). In the moderately harvested landscape, both study plots were surrounded by uncut deciduous forest, except for an 8-ha plantation adjacent to the uncut plot. A dirt road approxi-
Intensively harvested landscape

Moderately harvested landscape

7 km
mately 5 m wide bisected the selection-cut plot (Fig. 1). The selection cuts we studied were harvested in 1993 (moderately harvested landscape) and 1994 (intensively harvested landscape). We chose these selection cuts based on their availability (only one selection cut of adequate size was present in the moderately harvested landscape) and on the structural and compositional similarity of their vegetation, as indicated by forest inventory maps and ground-truthing.

The term selection cutting describes logging practices that vary greatly among regions in their frequency and in the proportion of total basal area harvested (Thompson et al. 1995). In our study area, selection cutting of deciduous stands is performed mainly by individual loggers with chainsaws, who remove approximately 30% of the basal area on a 20-year cycle (G. Couturier, personal communication).

Indicators of Habitat Quality

We selected two species for study, the Black-throated Blue Warbler (Dendroica caerulescens) and the Ovenbird (Seiurus aurocapillus). Black-throated Blue Warblers are generally abundant in relatively undisturbed forests (Holmes 1994) and select patches with a high density of shrubs for nesting (Steele 1992, 1993). Ovenbirds are associated with closed-canopy forests with a sparse shrub layer (Van Horn & Donovan 1994). We selected these species because they (1) may be sensitive to habitat fragmentation (Porneluzi et al. 1993; Villard et al. 1993; Donovan et al. 1995; Villard et al. 1995; Hagan et al. 1996), (2) are expected to respond negatively or positively to selection cuts because this harvesting method favors the development of a dense shrub layer, (3) are relatively common in the study area, and (4) nest in places that are fairly easy to find. We studied Black-throated Blue Warblers in 1997 and 1998 and Ovenbirds from 1997 to 1999.

We measured several indicators of habitat quality in each study plot for each target species: density of territorial males, pairing success, and fledging success per territory. Between the last week of May and the first week of July, we visited each plot eight times between 0500 and 1000 hours on mornings when bird detection was not impeded by wind or rain. Using a standard spot-mapping protocol (Bibby et al. 1992), we mapped all songbird territories in each study plot. Because red squirrels (Tamiasciurus hudsonicus) and eastern chipmunks (Tamias striatus) are important nest predators (Boag et al. 1984; Reitsma et al. 1990), we also noted the position of all individuals of these species that were seen or heard. After the first three spot-mapping visits, we drew the approximate position of territories of both target species, which helped us concentrate our nest-searching efforts in specific portions of each study plot.

We determined densities of territorial males by counting the number of territories located entirely within the plots and by adding estimated fractions of territories (to the nearest 0.25) partially overlapping the plots. We used the mean number of detections per visit as an index of red squirrel and chipmunk density.

On average we conducted 6.4-7.2 visits per territory per year. For both species, we attempted to follow each territorial male for a total of at least 60 minutes of direct visual contact ("track time;" Probst & Hayes 1987). We then plotted against track time the cumulative percentage of males classified as paired or unpaired. These curves reached a plateau after 45 minutes and 30 minutes for Black-throated Blue Warbler and Ovenbird, respectively (Fig. 2). Thus, we were confident that males followed for longer periods were indeed unpaired if we failed to detect a female. Because Ovenbirds are sexually monomorphic, a nonsinging individual seen interacting with a singing male was considered its mate. A family group was considered as belonging to the territory monitored if the young could not fly more than 1 m, indicating they had fledged recently. More mobile family groups were not considered in the analyses.

Nest Monitoring

We searched intensively for the nests of all Black-throated Blue Warbler and Ovenbird pairs detected in each plot and within a 50-m band around the plot. We found most nests by locating and following females interacting with singing males, but a few were found incidentally. When marking the location of nests, we were careful not to disturb vegetation. Nest location was indicated with flagging tape placed no closer than 3 m from Black-throated Blue Warbler nests. Because Ovenbird nests are particularly inconspicuous, we also placed two small flags in shrubs on either side of their nests.

We visited nests every 3 days to record their status, either number of eggs or young or cause of failure. We were careful not to leave trails that could lead predators to nests. Nests were considered successful if nestlings lived to at least 8 days of age. when fledging is known to occur (Darveau 1995; Drapeau & Darveau 1995), unless there was evidence of predation (e.g., nest damaged or destroyed). In most cases, nests were visited every day after nestlings reached 7 days of age and nest success could be confirmed by the observation of fledglings near the nest. To facilitate identification of family groups, nestlings were banded when approximately 6 days old.
when possible. Using hoop nets, we also captured and banded as many adults as possible (Nolan 1961). If the first nesting attempt was unsuccessful or if nestlings fledged early in the season, we continued to monitor the territory for possible renesting or double brooding. Renesting was observed in a few cases, but no case of double brooding was observed for either species.

Vegetation Sampling

To compare vegetation structure and composition among the study plots, we sampled the vegetation at nine points distributed over the entire 25-ha plot. At each point, we sampled three 20 × 10 m areas: one was centered on the point itself, and the other two were placed randomly at any of three possible locations (75 m north, southeast, or southwest). These peripheral areas were oriented so that their shorter sides were perpendicular to the 75-m radii.

The shape of the selection cut within the moderately harvested landscape did not allow us to sample nine points; we could fit only six points 250 m apart within the plot. In each sampling area, we recorded the species and diameter of all trees (diameter at breast height [dbh] ≤ 8 cm), measured canopy height with a clinometer, and determined percent canopy cover with an ocular tube. We took 20 readings along the 20-m lateral lines of the areas and calculated canopy cover as the percentage of readings where canopy foliage could be seen at the crosshair of the ocular tube. We recorded the number of stumps and identified the species (whenever possible), degree of decomposition (1, recent; 5, completely rotten), and diameter of coarse woody debris intersecting the lateral lines of the areas. Finally, we recorded the height and species of each shrub within a smaller quadrat (10 × 2 m) nested within each area. These variables were chosen because we believe they reflect structural differences between uncut plots and selection cuts and are important components of Ovenbird habitat (Holmes 1994; Van Horn & Donovan 1994).

Data Analyses

For data collected in 1997, we used G tests to compare indicators of reproductive success for both target species between landscapes. For Black-throated Blue Warbler data collected in 1998, we used loglinear models to determine the relationships between each indicator, local habitat characteristics (selection-cut vs. uncut plot), and landscape type. The contingency classes were 1, landscape type (moderately vs. intensively harvested); 2, stand type (uncut vs. selection cut); and 3, either pairing success (paired vs. unpaired territorial males) or fledging success (territories with vs. without family groups). For the Ovenbird, we also included the year (1998, 1999) as a variable. For each species, these variables were first entered in a model including the main effects and their interactions (two- and three-way). The terms with the least significant effect (lowest likelihood-ratio chi-square value) were removed from the model until all the remaining variables had a significant ($p < 0.05$) effect.

For each plot, we calculated daily nest mortality (Mayfield 1975) for each species by dividing the number of unsuccessful nests by the total number of exposure days (julian date when success or failure occurred minus date when the nest containing eggs or nestlings was found or the first egg was laid) (Mayfield 1975). This method allows the calculation of the rate of loss associated with several factors, including predation, abandonment, and starvation (Tables 1 & 3), during the time that the nests are followed. Using daily nest mortality values, we then compared an estimator ($T$) of nesting success between the two landscapes, between uncut and selection cut plots for each bird species, and to a chi-square distribution (Johnson 1990). This method is considered the most
powerful for comparing two groups of nests (D. H.
Johnson, personal communication). Because the num-
ber of Ovenbird nests was low in selection cuts (n = 2
in 1998 and n = 2 in 1999), we only compared Oven-
bird nesting success between uncut plots for each year
separately.

For each successful nest, we considered the number
of fledglings to be equal to the number of nestlings pre-
sent on the last visit before fledging occurred. Because
brood sizes on the last visit to successful nests did not
differ significantly among sites and years ($\chi^2$ tests,
$p > 0.05$), we used the mean brood size for all sites and
years combined in calculations. Family groups observed in
territories where a nest had not been found were assumed
to comprise a number of fledglings equal to the mean
brood size. These data were then used to estimate the
total number of fledglings produced in each plot, per
species, per year. We also estimated mean annual pro-
ductivity of each species (i.e., the mean number of fledg-
lings produced per territory) for each plot. We com-
pared mean annual productivity to a source-sink threshold
representing the minimum number of fledglings that
have to be produced per territory to maintain a viable
population. If the mean annual productivity for a given
plot was higher than the calculated source-sink thresh-
old, the plot was considered a demographic source. The
source-sink threshold was calculated according to the
following equation (Trine 1998):

$$\text{source-sink threshold} = \frac{2 \times \text{adult mortality}}{1 - \text{juvenile mortality}}.$$ (1)

To estimate adult mortality, we used average return
rates reported in the literature (reviewed by Holmes
1994; Van Horn & Donovan 1994). For Black-throated
Blue Warblers, average return rates for adult males and
females ranged from 39% to 62% and 36% to 42%, re-
spectively. Average return rates of adult Ovenbirds were
54–55% (Van Horn & Donovan 1994), corresponding to
a maximum mortality of 46%. It is unlikely that these return
rates correspond to actual survival rates because adult
birds have been shown to disperse from their pre-
vious territory following an unsuccessful breeding at-
tempt (Haas 1998 and references therein). For this rea-
son, we used a range of 30–40% adult mortality for both
target species.

There is a paucity of data on juvenile survival rates be-
cause of the low return rate of banded individuals. Some
authors, however, have calculated or hypothesized for
migratory bird species that return rates represent ap-
proximately 31–50% of adult survival rates (Temple &
Cary 1988; Roth & Johnson 1993). This range of values
has been used by several authors in models of popula-
tion dynamics (Temple & Cary 1988; Howe et al. 1991;
Thompson 1993; Donovan et al. 1995; Trine 1998).
Thus, we estimated juvenile mortality rate to be 70%
in both species. According to these estimations of adult
and juvenile mortality, between 2.0 and 2.7 fledglings
need to be produced per territory in each plot to main-
tain a viable population.

Finally, to compare vegetation characteristics among
the five plots, we used discriminant function analysis.
When necessary we used transformations to normalize
the data, following Legendre and Legendre (1984).

**Results**

Females were detected relatively quickly ($\bar{x} = 5.3$
minutes for Ovenbirds and $\bar{x} = 5.9$ minutes for Black-
throated Blue Warblers) when present on a male’s terri-
ory. For Black-throated Blue Warblers and Ovenbirds,
respectively, 81% and 74% of males were considered
paired after only 10 minutes of track time (Fig. 2). Over
the 3 years of the study, 13 Black-throated Blue Warblers
(14%) and 15 Ovenbirds (10%) could not be classified as
either paired or unpaired because of insufficient track
time (<45 minutes for Black-throated Blue Warblers and
<30 minutes for Ovenbirds) and were therefore ex-
cluded from the analyses.

We found 50 Black-throated Blue Warbler nests (17 in
1997 and 33 in 1998) and 52 Ovenbird nests (13 in
nests were found during nest building, but they were
abandoned before egg laying and were excluded from
the analyses. Of the nests where at least one egg was
laid, nest failure reached 40.0% in 1997, 25.5% in 1998,
and 60.0% in 1999. Predation was the main cause of nest
failure, accounting for 66.7%, 83.3%, and 100% of all
nest failures in 1997, 1998, and 1999, respectively. None
of the nests we found was parasitized by the Brown-
headed Cowbird during the 3 years of the study. In fact,
no adult cowbird was detected in or around the study
plots in any of the 3 years (M.-A. V., unpublished data; S.
Rhaumé, personal communication).

**Black-Throated Blue Warbler**

 Territory densities of the Black-Throated Blue Warbler
varied substantially among sites and years but were gen-
erally higher within selection cuts than in uncut plots
(Fig. 3). In 1997, pairing success, hatching success, and
fledging success per territory were lower in the inten-
sively harvested landscape ($G$ tests, $p \geq 0.15$), whereas
daily nest mortality was lower in the moderately har-
vested landscape ($T = 1.41, \text{df} = 1, p = 0.23$). None of
these differences, however, was statistically significant.

In 1998, pairing success was relatively high in both
landscapes, but it was significantly lower in the inten-
sively harvested landscape (Table 1). The fact that 3 of
18 males did not find a mate in the selection-cut plot
within the intensively harvested landscape accounted
for this difference. In 1998, hatching and nesting suc-
Figure 3. Densities (territories/10 ha), pairing success, and fledging success of Black-throated Blue Warblers and Ovenbirds in plots within moderately harvested (MH) and intensively harvested (IH) landscapes. Only the uncut plots (UC) were monitored in 1997. In 1998 we added plots within selection cuts (SC and SC 1) in each landscape to monitor both species, and in 1999 we added another selection-cut plot (SC 2) but monitored only Ovenbirds in all the plots. Number of territories monitored is shown above bars.

Table 1. Productivity of Black-throated Blue Warblers in moderately harvested (MH) and intensively harvested (IH) landscapes in 1997a and 1998b in northwestern New Brunswick, Canada.

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<tbody>
<tr>
<td>Total nests found</td>
<td>10</td>
<td>10</td>
<td>7</td>
<td>4</td>
<td>10</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fledging success per nest (%)</td>
<td>70.0</td>
<td>60.0</td>
<td>42.9</td>
<td>75.0</td>
<td>90.0</td>
<td>88.9</td>
<td></td>
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<tr>
<td>Depredated nests (%)</td>
<td>30.0</td>
<td>30.0</td>
<td>14.3</td>
<td>25.0</td>
<td>10.0</td>
<td>11.1</td>
<td></td>
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<tr>
<td>Daily nest mortality</td>
<td>0.022</td>
<td>0.032</td>
<td>0.051</td>
<td>0.022</td>
<td>0.008</td>
<td>0.009</td>
<td>0.33d (0.57)</td>
<td>2.64d (0.10)</td>
</tr>
<tr>
<td>Total number of fledglings produced in the plote</td>
<td>30.96</td>
<td>24.08</td>
<td>17.20</td>
<td>24.08</td>
<td>41.28</td>
<td>34.40</td>
<td></td>
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<tr>
<td>Mean annual productivityf</td>
<td>2.21</td>
<td>1.72</td>
<td>1.72</td>
<td>2.68</td>
<td>2.29</td>
<td>1.91</td>
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</table>

a Only uncut plots (UC) were monitored.
b We added one plot within selection cuts (SC) in each landscape.
c With Williams’ correction (Williams 1976).
d Following Johnson (1990).
e Number of successful territories multiplied by the mean number of fledglings they produced.
f Number of fledglings produced in each plot divided by the number of territories within that plot.
Table 2. Ovenbird productivity in moderately harvested (MH) and intensively harvested (IH) landscapes in 1997, 1998, and 1999 in northwestern New Brunswick, Canada.

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<tbody>
<tr>
<td>Total nests found</td>
<td>4</td>
<td>3</td>
<td>10</td>
<td>9</td>
<td>9</td>
<td>13</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Fledging success per nest (%)</td>
<td>75.0</td>
<td>66.7</td>
<td>20.0</td>
<td>55.6</td>
<td>55.6</td>
<td>53.8</td>
<td>100</td>
<td>50.0</td>
<td>—</td>
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<tr>
<td>Depredated nests (%)</td>
<td>0</td>
<td>0</td>
<td>80.0</td>
<td>44.4</td>
<td>44.4</td>
<td>46.2</td>
<td>0</td>
<td>50.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Daily nest mortality</td>
<td>0.016</td>
<td>0.023</td>
<td>0.134</td>
<td>0.034</td>
<td>0.032</td>
<td>0.042</td>
<td>0</td>
<td>0.023</td>
<td>—</td>
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<tr>
<td>Total number of fledglings produced in the plot</td>
<td>24.54</td>
<td>20.47</td>
<td>8.18</td>
<td>36.81</td>
<td>40.90</td>
<td>28.63</td>
<td>24.54</td>
<td>4.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Mean annual productivity</td>
<td>1.89</td>
<td>1.14</td>
<td>0.58</td>
<td>1.84</td>
<td>1.86</td>
<td>1.51</td>
<td>2.23</td>
<td>0.68</td>
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aOnly uncut plots (UC) were monitored.
bWe added one plot within selection cuts (SC) in each landscape.
cA selection-cut plot was added in the intensively harvested landscape.
dNumber of successful territories multiplied by the mean number of fledglings they produced.
eNumber of fledglings produced in each plot, divided by the number of territories within that plot.

Ovenbird

Territory densities of the Ovenbird varied substantially among sites and years, but, with the exception of one site in a single year (selection cut in the moderately harvested landscape in 1998), densities were consistently lower in selection cuts than in uncut plots (Fig. 3). In 1997, pairing success and the proportion of territories producing nestlings and fledglings did not differ significantly between the two landscapes (G test, p = 0.15). In 1998 and 1999, loglinear models indicated that pairing success differed significantly between stand types but was independent of landscape type (Table 2). Fledging success per territory was also related to stand type: it was lower in selection cuts (Table 2).

For all years combined, daily nest mortality did not differ significantly between landscapes in the uncut plots (T = 1.68, df = 1, p = 0.19). In 1998 and 1999, 77% of the estimated number of young that fledged in all our study plots (126) were born in uncut stands. Fledging success per territory decreased steadily from 1997 to 1999 in the uncut plot within the moderately harvested landscape, and it remained stable in the uncut plot in the intensively harvested landscape over the same period. The declining trend in the former plot was not statistically significant (G test, p = 0.20). Between 1998 and 1999, fledging success also decreased noticeably, although not significantly, in the selection cut within the moderately harvested landscape (G test, p = 0.14). In summary, the first prediction, of negative effects of local harvesting only, was supported for the Ovenbird.

Vegetation Analysis

We used discriminant function analysis to examine vegetational differences among the five plots. The first two standardized canonical discriminant functions accounted for 88.9% of the variation. The first discriminant func-

Table 3. Results of loglinear models best explaining pairing and fledging success of the Black-throated Blue Warbler and the Ovenbird in northwestern New Brunswick, Canada.

<table>
<thead>
<tr>
<th>Species</th>
<th>Demographic parameter</th>
<th>Significant variables</th>
<th>Pearson chi-squarea (df, p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-throated Blue Warbler</td>
<td>pairing success</td>
<td>none</td>
<td>8.30 (6, 0.22)</td>
</tr>
<tr>
<td></td>
<td>fledging success</td>
<td>none</td>
<td>2.96 (5, 0.71)</td>
</tr>
<tr>
<td>Ovenbird</td>
<td>pairing success</td>
<td>pairing success, stand typeb × pairing success</td>
<td>17.91 (13, 0.16)</td>
</tr>
<tr>
<td></td>
<td>fledging success</td>
<td>fledging success, stand type</td>
<td>15.83 (13, 0.26)</td>
</tr>
</tbody>
</table>

aSignificant Pearson chi-square values indicate the model does not fit observed frequencies.
bUncut forest versus selection-cut forest.
Table 4. Standardized loadings of vegetation variables on the first two canonical discriminant functions (DF1, DF2) for five forest plots in northwestern New Brunswick, Canada.

<table>
<thead>
<tr>
<th>Variable</th>
<th>DF1</th>
<th>DF2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy height</td>
<td>0.24</td>
<td>0.41</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>-0.13</td>
<td>-0.04</td>
</tr>
<tr>
<td>Number of stumps</td>
<td>-0.38</td>
<td>-0.23</td>
</tr>
<tr>
<td>Number of fallen trees with a decomposition index of 1-3*</td>
<td>-0.52</td>
<td>-0.36</td>
</tr>
<tr>
<td>Number of fallen trees with a decomposition index of 4-5*</td>
<td>-0.28</td>
<td>-0.21</td>
</tr>
<tr>
<td>Number of treetops</td>
<td>0.12</td>
<td>0.04</td>
</tr>
<tr>
<td>Shrub density, shrubs 0.5-2 m high</td>
<td>-0.08</td>
<td>0.66</td>
</tr>
<tr>
<td>Shrub density, shrubs &gt;2 m high</td>
<td>0.89</td>
<td>-0.64</td>
</tr>
<tr>
<td>Total basal area of all trees</td>
<td>0.17</td>
<td>-0.22</td>
</tr>
</tbody>
</table>

*See Hunter (1990) for description of decomposition index.

tion (DF1) mainly represented an increase in the density of shrubs >2 m high, whereas DF2 mainly reflected an increase in the density of shrubs 0.5–2 m high (Table 4). There was a surprising degree of overlap between the two plots from the moderately harvested landscape (Fig. 4), which probably reflects the structural features associated with treefalls along a stream that crossed the plot.

We also used discriminant function analyses to perform pairwise comparisons of plot vegetation. Vegetation characteristics did not differ significantly between the two uncut plots (Wilk’s λ = 0.42, F = 1.73, df = 9, 53, p = 0.15) and the selection cut within the moderately harvested landscape and selection-cut 1 (Wilk’s λ = 0.79, F = 1.32, df = 8, 40, p = 0.26). Although we were careful to choose plots within selection cuts with apparently similar structure, vegetation characteristics in selection-cut 2 differed significantly from those of the other selection cuts (Wilk’s λ = 0.51, F = 7.05, df = 9, 66, p < 0.001). Selection cut 2 was characterized by a higher canopy (F = 4.62, df = 2, p = 0.013), a lower basal area of trees (F = 5.77, df = 2, p = 0.005), a greater density of shrubs <2 m high (χ² = 14.25, df = 2, p < 0.001), and a greater number of fallen trees (χ² = 16.14, df = 2, p < 0.001).

Discussion

The Black-throated Blue Warbler and the Ovenbird exhibited nearly opposite responses to recent selection cutting. Black-throated Blue Warblers generally responded positively, both in terms of density and reproductive success, although in the latter case differences were not significant. Ovenbird densities and reproductive performance were markedly lower in selection cuts, except in the moderately harvested landscape in 1998.

Neither local- nor landscape-scale harvesting had a significant effect on the reproductive performance of Black-throated Blue Warblers. High-quality Black-throated Blue Warbler habitat is characterized by a dense understory (Holmes et al. 1996). Shrub density was high in selection cuts, yet reproductive success was not significantly higher. When we compared the overall production of fledglings, however, it was 1.4-1.7 times higher in selection cuts. Nevertheless, if we assume 30% adult mortality, the mean annual productivity of Black-throated Blue Warblers barely reached sustainable levels in all of the plots studied, in spite of the absence of cowbird parasitism.

In New Hampshire, productivity of Black-throated Blue Warblers was closely related to double brooding (Holmes et al. 1992, 1996). In our study area, there was no evidence that early nesters produced a second brood. In 2 years, no female was observed initiating a second clutch after successfully completing a first brood, although renesting was frequent. Furthermore, two fe-
males that fledged their broods early were observed still caring for banded young from their first brood in mid-July. Graves (1997) suggested that approximately 95–100 frost-free days are required in a breeding season for multiple brooding to occur. Based on 12 years of data ranging from 1951 to 1980, the average number of frost-free days was 73 days per year at a meteorological station located within 40 km of the study area (G. Morin, personal communication). Moreover, Black-throated Blue Warblers arrived 1 week later than was reported in New Hampshire (Holmes et al. 1992; Bourque 1999), which further reduced the amount of time available to initiate a second brood. This might explain the lower productivity we found compared to that reported in New Hampshire (4.3 young per female, Holmes et al. 1992), even though daily nest survival rates were similar (0.979, Holmes et al. 1992; 0.981, this study). The absence of double brooding might make New Brunswick populations more vulnerable to habitat alterations.

Even though selection cuts apparently had no adverse effects on Black-throated Blue Warblers, successional changes might make these stands less hospitable in the years preceding subsequent cuts. For example, females showed a preference for American beech saplings for nesting in selection cuts (Bourque 1999). Beech seedlings and roots or stump sprouts can reach 1.5–4.0 m in height after 20 years (Burns & Honkala 1990), thus reducing their suitability as nesting substrates. Black-throated Blue Warbler densities might thus gradually return to the levels found in uncut stands.

Ovenbird densities were lower in selection cuts in both landscape types. The only exception was the plot located in the moderately harvested landscape in 1998. Other researchers studying the effects of selection cuts on bird community composition found that Ovenbirds were less abundant in managed stands than in control plots (Annand & Thompson 1997; Norton & Hannon 1997; Rodewald & Smith 1998; Robinson & Robinson 1999). Throughout their range, Ovenbirds feed almost exclusively on the ground and are associated with mature forests with an open understory (Van Horn & Honkala 1990; Annand & Robinson 1994). Although patches of open understory were small and dispersed in selection cuts, this is where the core of Ovenbird territories tended to be located. Patches of dense shrubs might represent suboptimal foraging and nesting microhabitat, perhaps because a dense understory reduces the quantity, quality, or accessibility of the leaf litter. Burke and Nol (1998) found that both leaf litter depth and biomass of litter invertebrates were significantly higher within Ovenbird territories than at random locations.

Ovenbird reproductive success was also significantly lower in selection cuts. In fact, according to our indicators of reproductive performance, it seems unlikely that the selection cuts located in the intensively harvested landscape could maintain viable populations of Ovenbirds. Over the duration of the study, only three males (33.3%) in these plots were considered paired, and none produced fledglings. The mean annual productivity of Ovenbirds reached its highest level in the selection cut located in the moderately harvested landscape in 1998. Even when this plot is included, however, selection cuts produced only 23% of the estimated number of young that fledged in all our study plots in 1998 and 1999. The fact that density is not necessarily positively correlated with reproductive success (Van Horne 1983) does not mean that it is not still an important factor to consider when measuring habitat quality.

In summary, the higher productivity of the Black-throated Blue Warbler in selection cuts is attributable to the greater density of territories rather than to greater reproductive performance. Ovenbird reproductive success was not significantly affected by harvesting intensity at the landscape scale. Nevertheless, territory density, pairing success, and fledging success per territory were lower in selection cuts than in uncut plots, resulting in a low production of fledglings in selection cuts in all but one of the combinations of site and year.

**Conservation Implications**

The ultimate cause of the reported declines in many Neotropical migratory birds is still debated. The observation of a correlation between local reproductive success and recruitment the following year (Nolan 1978; Virolainen 1984; Holmes et al. 1992; Sherry & Holmes 1992) led Sherry and Holmes (1995) to suggest that habitat alteration on the breeding grounds cannot be ruled out as a cause of decline in populations. From this perspective, it follows that large-scale forest management could have major implications for the conservation of Neotropical migratory birds.

Several studies suggest that forest fragmentation as a result of timber harvesting and silviculture might have less deleterious effects on breeding birds than fragmentation by agriculture (King et al. 1996; Sabine et al. 1996; Schmiegelow et al. 1997). In managed forest landscapes in Maine, however, ovenbirds had a lower pairing success in forest fragments than in extensive tracts shortly after harvesting (Hagan et al. 1996). We also predicted that productivity of the target species would be lower in the intensively harvested landscape, but harvesting intensity at the landscape scale did not have a statistically significant effect on our indicators of reproductive success for either target species. Moreover, daily nest mortality did not differ significantly between the two landscapes for either species. It has been suggested that the negative effects of landscape fragmentation on the abundance and distribution of birds and mammals might occur only when less than approximately 30% of suitable habitat remains (Andrén 1994). Within the intensively harvested landscape, mature forests still covered ap-

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proximately 45% of the landscape (excluding selection cuts). Thus, negative landscape effects might not have been severe enough to be detectable, which suggests that current levels of harvesting at the landscape scale in northwestern New Brunswick are not detrimental to the persistence of the Black-throated Blue Warbler and Ovenbird.

Selection cutting is generally preferred over clearcutting by the general public, even though it appears to be nearly as detrimental to species such as the Ovenbird. Because selection cutting is becoming more prevalent in landscapes fragmented by forestry, closed-canopy deciduous stands might become increasingly scarce. In fact, the uncut plot located within the intensively harvested landscape was the only remaining mature, closed-canopy deciduous stand that was large enough to accommodate a 500 x 500 m plot. Therefore, we might witness the gradual disappearance of these stands if active measures are not taken to ensure their availability in the future.

Using land-survey records, evidence from pristine landscapes, and ancient charcoal deposits, Lorimer and Frelich (1994) showed that northern deciduous forests are generally characterized by fine-scale gap dynamics rather than by frequent large-scale natural disturbance. The extent and frequency of selection cutting in northwestern New Brunswick deciduous stands probably greatly exceeds historical disturbance levels. If we are to make these habitats more suitable to Ovenbirds and other species or taxa responding similarly to selection cutting, conservation measures should be taken to at least slow the current pace of harvesting in this and other regions.

For both species, assuming 40% adult mortality and 70% juvenile mortality meant that 2.7 young were required to maintain stable populations. None of the plots produced enough young of either target species to reach this level of sustainability. We need more information on adult and especially juvenile mortality to verify the accuracy of our source-sink thresholds.

To determine whether the trends we observed in this study can be generalized, we need to monitor reproductive success in selection cuts over the long term. Another conservation issue that needs to be addressed is the time required for a selection cut to become suitable habitat for Ovenbird reproduction. In the meantime, large tracts of mature, closed-canopy deciduous forest should be maintained in management units at all times. In selection cuts, the proportion of basal area removed should be reduced, or cutting cycles should be extended so that some blocks become at least temporarily suitable for Ovenbird foraging and nesting.

Acknowledgments

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