DO BLACK-THROATED GREEN WARBLERS PREFER CONIFERS? MESO- AND MICROHABITAT USE IN A MIXEDWOOD FOREST[1]

ISABELLE ROBICHAUD AND MARC-ANDRÉ VILLARD[2]

Département de biologie, Université de Moncton, Moncton NB, E1A 3E9 Canada,
e-mail: villarm@umoncton.ca

Abstract. Throughout most of its range, the Black-throated Green Warbler (*Dendroica virens*) is generally associated with coniferous forests, but it also breeds in mixedwood and deciduous stands. To measure the relative use of deciduous and coniferous trees in pristine boreal mixedwood stands of northern Alberta, we examined the influence of conifer distribution on territory placement at the mesohabitat scale (25-ha study plots) and substrate use for singing and foraging at the microhabitat scale (within individual territories). Black-throated Green Warblers clustered their territories where conifers reached their highest density, and tended to avoid areas where conifers were rare or absent. At the microhabitat scale, logistic regression models indicate that tree species and diameter at breast height were significant predictors of tree use; Black-throated Green Warblers mainly used large white spruce (*Picea glauca*) trees as songposts and foraging substrates. For foraging, trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), the two most abundant tree species in our plots, were less frequently used than white spruce, whereas paper birch (*Betula papyrifera*) was used according to its availability. These results indicate that Black-throated Green Warblers were relatively stereotyped in their substrate use, in spite of the availability of both deciduous and coniferous trees. However, the treefall gaps and dense deciduous shrub layer typical of old boreal mixedwood stands might be important at the fledgling stage. Thus, the conversion of mixedwood forests into pure deciduous stands and conifer plantations could have negative impacts on this and other ecologically-similar species in the boreal forest.

Key words: Black-throated Green Warbler, boreal mixedwood forest, Dendroica virens, foraging ecology, microhabitat, songposts.

INTRODUCTION

The Black-throated Green Warbler (*Dendroica virens*) has a large breeding range encompassing a wide variety of forest types across North America. According to Morse (1993), it is generally associated with coniferous forests, but it also breeds in mixedwood or even deciduous forests in parts of its range. Among 16 wood warbler species studied by Collins et al. (1982) in Minnesota, the Black-throated Green Warbler was classified into a group of species occurring primarily in mature undisturbed forests containing coniferous vegetation. In the northern hardwood forests of Hubbard Brook, New Hampshire, this species had a nonsignificant tendency to be associated with the sparse coniferous trees present (Sherry and Holmes 1985). The Black-throated Green Warbler is frequently associated with tree species forming a multi-layered foliage profile (Holmes and Robinson 1981). However, when Collins (1983) compared habitat use

around song perches in five study areas scattered across the breeding range of the species, consistent structural features among the different habitat types sampled were difficult to identify.

The Black-throated Green Warbler is, thus, a wide-ranging habitat generalist exhibiting substantial geographical variation in its habitat use and, more specifically, in its requirement for conifers. In a controlled experiment with captive Black-throated Green Warblers, Parrish (1995b) gave individuals a choice between coniferous and deciduous perching and foraging substrates. Birds from coniferous forests preferentially used coniferous substrates, whereas individuals from a hardwood-dominated forest showed a preference for deciduous substrates, even though both substrate types were available in their forests of origin. Habitat selection thus differs among populations of Black-throated Green Warblers as a function of the forest type they inhabit.

To our knowledge, no one has investigated the detailed micro- or mesohabitat use of Black-throated Green Warblers in mixedwood forests. Collins (1983) measured microhabitat characteristics around song perches in some mixedwood

stands, but did not provide data on the characteristics of the song perches themselves. Parrish's (1995b) experimental study was conducted with birds that held territories in relatively pure deciduous or coniferous stands. Do birds breeding in stands containing substantial proportions of both deciduous and coniferous trees tend to use both substrates to the same extent? Given the extensive variability in habitat use exhibited by the Black-throated Green Warbler across its breeding range, some plasticity in substrate use would be expected, at least in some portions of its range.

In this study, we examined (1) the influence of spatial distribution of conifers on Black-throated Green Warbler territory location, and (2) variables predicting individual tree use for singing and foraging in the boreal mixedwood forest of northern Alberta. This forest biome is characterized by stands dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), with scattered conifers. In mature and old boreal mixedwood stands, conifers are represented mostly by irregularly-spaced mature white spruce (*Picea glauca*) trees (Rowe 1972). We examined habitat use over two spatial scales because previous studies (Sedgwick and Knopf 1992, Steele 1992) have shown that species' response to habitat characteristics may differ with the spatial scale considered.

Because the two song types of the Black-throated Green Warbler have been shown to play different roles in this species' breeding biology (Morse 1967, 1970), and different selection pressures could translate into different choices of substrates for both song types, we examined separately the substrates used to perform each song type by this species. We also compared the characteristics of trees used for foraging by males and females, because differences have been shown in the use of foraging substrates by males and females (Holmes 1986) as well as in foraging heights (Morse 1968, Holmes 1986).

METHODS

STUDY AREA

This study was conducted in the summer of 1995 near Calling Lake, Alberta, Canada (55°15′N, 113°19′W). We selected two plots of 500 × 500 m (25 ha) each, within old boreal mixedwood stands (115 and 135 years old, according to forest inventories). These stands have

never been harvested, nor have they received any silvicultural treatment. Fire has historically been the major natural disturbance in the region (Rowe and Scotter 1973, Eberhart and Woodard 1987, Stelfox 1995). One of the plots (hereafter called South Plot) was part of a 40 km² block of unbroken forest. The other plot (North Plot) was selected in a continuous tract of forest 11.9 km to the north. In both plots, trembling aspen and balsam poplar dominated the canopy, whereas white spruce and paper birch (*Betula papyrifera*) were present at much lower densities. On average, canopy height was 28 m in both plots. The shrub layer was relatively dense, and dominated by alders (*Alnus crispa, A. tenuifolia*), willows (*Salix* spp.), and prickly rose (*Rosa acicularis*).

MESOHABITAT USE

We use the term mesohabitat to refer to our 25-ha plots. This scale is intermediate between the microhabitat (leaf to habitat patch) and macrohabitat (patch to geographic region) scales (Block and Brennan 1993). Upon the arrival of territorial males, we conducted total mapping, which consists in mapping all locations occupied by a focal individual while following it (Verner 1985). This allowed us to know the approximate location of territories early in the breeding season. We then used a standard spot mapping protocol (Bibby et al. 1992) to refine our knowledge of territory boundaries, and trees used during behavioral observations (see microhabitat use below) also were located on plot maps. By superimposing these three sources of information, we could accurately determine the location of each territory (Fig. 1).

To determine whether territory location was related to conifer distribution, we mapped conifer density in each plot. We counted the number of conifer trees (mainly white spruce) in each quadrant of an 11.3-m radius circle at every 50-m point in each plot. Only trees with a diameter at breast height (dbh) ≥ 10 cm were considered, because this corresponds to the diameter of the smallest trees used by our focal birds. Inside each plot, we sampled 121 points for a total of 4.0 ha, or 16% of plot area. We then mapped conifer densities by assuming that densities recorded in each quadrant (0.01 ha) were representative of the corresponding 25 × 25 m square (Fig. 1). The area of each plot in
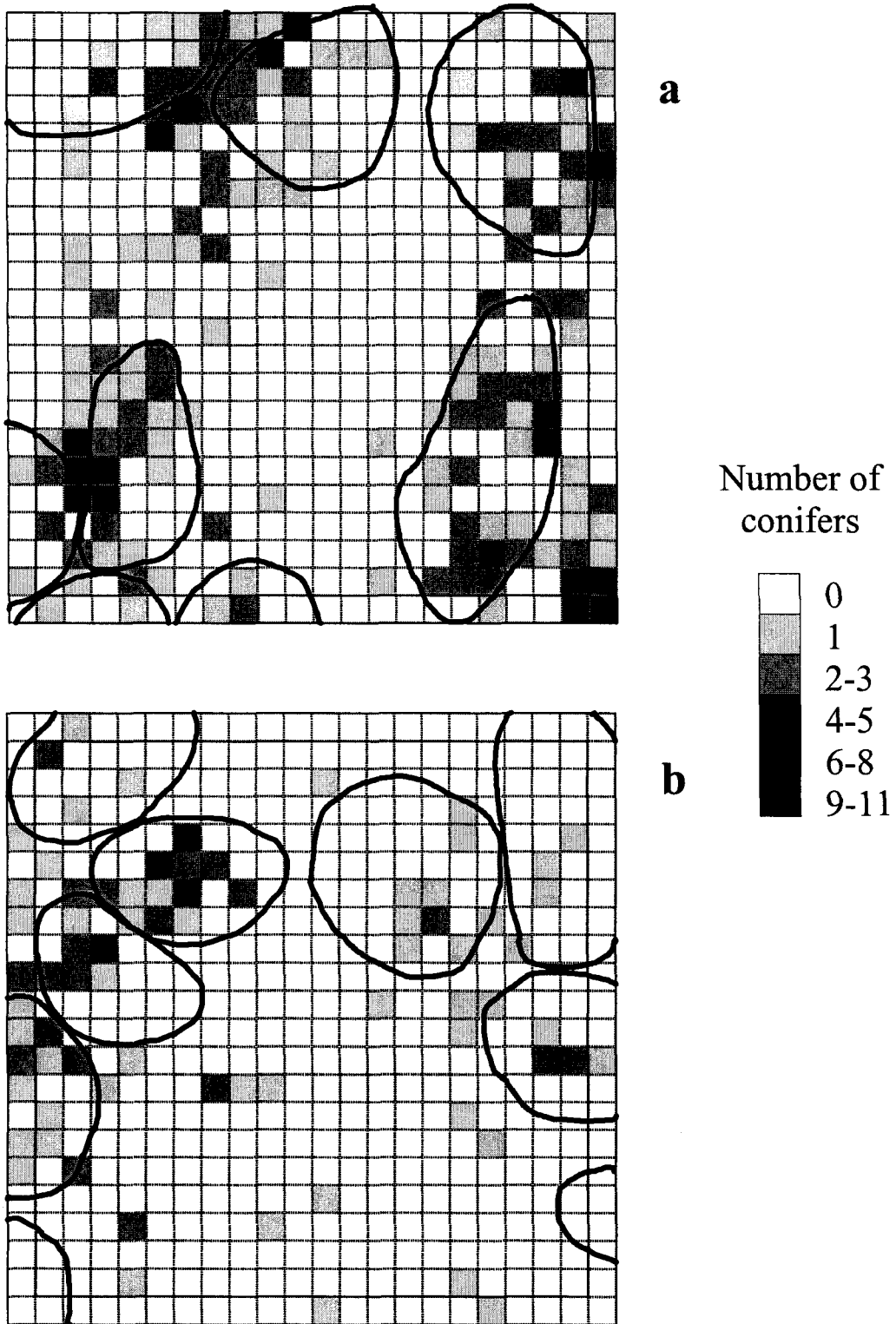
FIGURE 1.   Distribution of conifer trees (>10 cm dbh) and location of Black-throated Green Warbler territories in (a) North Plot and (b) South Plot. Each cell is 25 × 25 m in size. Darker cells contain a greater number of conifers.

Figure 1 is slightly greater than 25 ha because conifers also were sampled at perimeter points.

MICROHABITAT USE

We use the term microhabitat to refer to habitat components within the territories. We conducted behavioral observations on focal adult birds from the time they arrived on the plots in mid-May to the time when young started to fledge and territory boundaries became indistinct (early July). All trees observed to be used by focal birds were marked with flagging tape, and we indicated on each flag the behavior observed, and the date of observation. In total, 16.7 hr of direct observation were conducted on 17 breeding males whose territory overlapped partially or totally our plots, and 8 females were observed for a total of 2.4 hr. The large difference in observation time between the sexes is due to the relatively secretive behavior of females compared to males. Most individual males could be identified by their location and distinctive characteristics of their songs.

To evenly distribute sampling effort, we always alternated observation days between the two plots so that possible site differences could not be attributed to slightly different phenologies between the two plots. As many bird territories as possible were visited each day. Birds usually were observed for relatively long periods of time (>2 min) on each tree; trees used "in transit" for a few seconds were not included in the analyses. Each tree was included only once in the analyses even though it might have been used for two or more different behaviors, or at different dates. To further test for independence among trees used by individual birds, we included the territory within which each tree was located in our analyses to determine whether tree selection differed among individuals.

We recorded the following behaviors: (1) singing type A or (2) B song, and (3) foraging. Song type A (Nice and Nice 1932, Morse 1967, 1970) also is known as the unaccented ending song (Ficken and Ficken 1962, Morse 1989b), and the type B song also is referred to as the accented ending song. Type B songs predominate earlier in the breeding season, when most males are still unpaired, whereas type A songs are mainly used after males are paired (Morse 1970, 1993). We only considered an individual as foraging when we observed it catching, carrying, and/or eating a prey. We also noted the

sex of focal individuals. In total, we compiled information on 106 used trees in the North Plot and 89 used trees in the South Plot. Trees used for other behaviors, such as preening or calling, or as nesting substrates ($n = 6$), were not included in our analyses due to insufficient sample sizes. Used trees were revisited after the breeding season to record species and map their location. We measured the height of used trees with a clinometer and the dbh of used and unused trees with a diameter tape. We used the point-centered quarter method (Mueller-Dombois and Ellenberg 1974), with used trees as central points, to collect data (species, height, and dbh) on the nearest tree (dbh $\geq$ 10 cm) in each quadrant that had not been used for the same behavior during observation periods.

STATISTICAL ANALYSES

To determine whether males tended to defend territories in areas with greater conifer densities than elsewhere in each of our two plots, we compared conifer densities in the grid cells falling within territories and over the 484 cells in each plot (Fig. 1). For each cell, we calculated a "conifer score" by multiplying each fraction of cell falling inside a territory by the average number of conifer trees within the semi-quantitative class we recorded for this cell. We used Mann-Whitney U-tests because the distributions were heavily skewed towards conifer scores of zero and 1 and could not be normalized.

To determine which variables influenced tree use by Black-throated Green Warblers, we built logistic regression models. The binary dependent variable, tree use, was coded as 1 = used, 0 = not used. The independent variables were tree species and dbh, study plot, territory where the tree was located, and for the foraging model, sex of the focal bird (Table 1). Intuitively, we would expect that a canopy species like the Black-throated Green Warbler would select trees based on their height rather than their diameter. Because dbh was highly correlated with tree height ($r = 0.86$, $n = 537$) and it could be measured with greater accuracy and speed, we used tree dbh instead in our analyses.

Because some trees were used for more than one behavior, we computed distinct models for each behavior instead of trying to fit a model with behavior as a covariate. This keeps us from comparing model results between behaviors in a rigorous fashion, but this was not our main ob-

TABLE 1. Variables used in the final logistic regression models to predict tree use in Black-throated Green Warblers.

Variable	Type	Description
USE	binary	whether tree was used or not to perform a given behavior
SP	nominal	tree species (four categories)
WS	binary	whether tree was a white spruce or not
DBH	continuous	diameter at breast height (dm)
SITE	binary	North or South Plot
TERR	nominal	randomly assigned bird territory number (17 categories)

jective. For each model, observations were distributed as follows: type A song: 98 used trees, 356 unused trees; type B song: 46 used trees, 146 unused trees; foraging: 74 used trees, 217 unused trees. Some trees used for the same behavior were close enough to each other to have the same nearest unused trees, although they were not necessarily used sequentially on the same day. We only included these unused trees once in the models for each behavior. This explains why the numbers of unused trees are less than four times those of used trees for each behavior.

In the model-building phase, we first examined the effects of each independent variable separately. A "main effects only" multivariate model was built that included the significant variables as well as variables that were nonsignificant but could be involved in interactions. The final model was selected based on the results of likelihood-ratio tests comparing pairs of nested models to determine whether the addition of a term significantly increased the accuracy and fit of the model. The overall goodness-of-fit of the chosen models was assessed with the Hosmer-Lemeshow statistic and the McFadden's rho-squared value (Hosmer and Lemeshow 1989). The Hosmer-Lemeshow statistic indicates whether the model generates estimates that depart significantly from observed values, whereas a high McFadden's rho-squared value confirms that the variables included in the model explain a very high proportion of the variability in the data (Steinberg and Colla 1997). We screened for possible outliers using graphs of standardized changes in the estimated regression coefficients when removing each point (Norušis 1994). Models with and without outliers were compared to determine whether the exclusion of extreme values would significantly alter the logistic regression coefficients and influence the fit of the model. We used a significance level of

0.05. All analyses were performed using SYSTAT 7.0 (SPSS Inc. 1997).

The odds ratio represents the change in the odds of observing the studied response with a unit change in the independent variable. For example, the odds ratio indicates the order of magnitude of the increase in the likelihood that a tree will be used per unit change in dbh. Diameter at breast height, the only continuous variable in our study, was expressed in decimeters to obtain more ecologically meaningful odds ratio estimates (Hosmer and Lemeshow 1989). Some tree and shrub species such as balsam fir, *Abies balsamea,* willows, and green and river alders, were excluded from the analyses because they represented a very low proportion (<2%) of used and unused substrates. Variable SP (tree species; Table 1) thus represents the four species that were most frequently used: white spruce, trembling aspen, balsam poplar, and paper birch. For type A song, variable SP had to be collapsed due to very low observed frequencies in tree species other than white spruce for trees that were used by Black-throated Green Warblers in the North Plot. Thus, for this behavior, we used a binary variable (WS) coded 1 for white spruce and 0 for any of the three other species. Dichotomous variables (WS, SITE, SEX) were treated as interval-scaled (Hosmer and Lemeshow 1989), and the polytomous nominal variables SP and TERR were dummy-coded. White spruce was the species of reference for the coding of SP.

RESULTS

MESOHABITAT USE

Conifer density was significantly higher within Black-throated Green Warbler territories than over the entire plots (Mann-Whitney U-tests, North Plot: $z = -2.55$, $P < 0.01$; South Plot: $z = -1.66$, $P = 0.05$). Figure 1 shows an apparent avoidance of areas without conifers in both

TABLE 2. Results from a logistic regression model predicting tree use by Black-throated Green Warblers as songposts for type B songs. White spruce was used as the species of reference in the coding of SP.

Variable	Estimated coefficient ± SE	P	Estimated Odds Ratio (95% CI)
DBH	0.67 ± 0.21	0.001	1.95 (1.31–2.92)
SP (trembling aspen)	−0.98 ± 0.46	0.03	0.37 (0.15–0.92)
SP (balsam poplar)	−0.86 ± 0.51	0.09	0.42 (0.16–1.15)
SP (paper birch)	0.37 ± 0.81	0.65	1.44 (0.30–6.99)

McFadden's rho-squared = 0.12; Hosmer-Lemeshow statistic = 6.56, df = 6, $P > 0.3$.

study plots. The only exceptions were a territory in the top right corner of the South Plot and two partial territories in the bottom right and left portions (Fig. 1b), where conifers were sparse or absent. In the North Plot (Fig. 1a), areas where conifers reached their highest abundance (top and bottom left) were shared between two territories. Hence, conifers had a strong influence on territory location in Black-throated Green Warblers in our study area.

MICROHABITAT USE

Overview. Both dbh and tree species stand out as important factors to explain tree use by Black-throated Green Warblers (Tables 2–4). Based on the corresponding odds ratios, trees with large dbh, and thus higher trees, were more likely to be used than smaller trees. For foraging, white spruce also was used significantly more frequently than the two poplar species, whereas paper birch was used according to its availability. When considering all trees sampled irrespective of their use, white spruce had significantly larger diameters at breast height than other species (Mann-Whitney U-tests, $P <$ 0.001). However, the fact that the interaction between tree species and dbh did not significantly improve the fit of the models of any of the behaviors (likelihood ratio tests, $P > 0.3$) indicates that the effect of dbh on the probability that a

tree was used did not vary according to tree species. A table showing descriptive statistics for trees used and unused for every behavior and site would have been too cumbersome to present here. These data will be made available upon request.

Type B song. The factors that best explained tree use to sing type B songs were dbh and tree species (Table 2). Diameter at breast height was the most influential variable. For every increase of 10 cm in diameter, the odds of a tree being used increased almost two-fold. Among large-diameter trees, Black-throated Green Warbler males showed a marked preference for white spruce over trembling aspen. Preference for white spruce over balsam poplar was marginally nonsignificant, whereas paper birch was not preferred or avoided. There were no significant differences between plots or individual territories, as the addition of these variables did not significantly improve the fit of the final models.

Type A song. The "best" model in this case included dbh and tree species as independent variables (Table 3). Focal birds showed a preference for trees that were significantly larger than unused trees. For every increase of 10 cm in dbh, irrespective of the species, the odds of a tree being used increased by a factor close to four. Tree species also was an important predictor of use, but its significant interaction with

TABLE 3. Results of a logistic regression model predicting tree use by Black-throated Green Warblers as songposts for type A song.

Variable	Estimated Coefficient ± SE	P	Estimated Odds Ratio (95% CI)
DBH	1.30 ± 0.17	<0.001	3.68 (2.66–5.09)
WS	3.88 ± 1.05	<0.001	48.34 (6.17–378.69)[a]
			2.39 (1.17–4.88)[b]
SITE	2.93 ± 1.05	<0.01	
WS*SITE	−3.01 ± 1.11	<0.01	

McFadden's rho-squared = 0.39; Hosmer-Lemeshow statistic = 3.21, df = 8, $P > 0.5$.
[a] controlled for SITE = North.
[b] controlled for SITE = South.

TABLE 4. Results of a logistic regression model predicting tree use by Black-throated Green Warblers as foraging substrates. White spruce was used as the species of reference in the coding of SP.

Variable	Estimated Coefficient ± SE	P	Estimated Odds Ratio (95% CI)
DBH	0.30 ± 0.15	0.04	1.36 (1.02–1.80)
SP (trembling aspen)	−1.54 ± 0.40	<0.001	0.22 (0.10–0.47)
SP (balsam poplar)	−0.86 ± 0.36	0.02	0.42 (0.21–0.86)
SP (paper birch)	0.76 ± 0.61	0.21	2.13 (0.65–7.04)

McFadden's rho-squared = 0.10; Hosmer-Lemeshow statistic = 3.89, df = 5, $P > 0.5$.

SITE suggests that patterns of use of tree species differed between the two plots. In the North Plot, 97% of all trees used ($n = 39$) were white spruce, whereas this proportion was 64% ($n = 59$) in the South Plot. White spruce represented only 36% ($n = 152$) and 29% ($n = 204$) of unused trees in the North and South Plots, respectively. SITE is an effect modifier of white spruce use because the interaction of these two variables is significant, and as such, the estimated odds ratio of WS has to be adjusted for each level of the effect modifier variable (SITE) that interacts with it (Hosmer and Lemeshow 1989). The territory variable (TERR) did not significantly improve the fit of the chosen model (likelihood ratio test, $G_{14} = 6.55$, $P = 0.95$), and therefore was not retained as a predictor of tree use. Hence, different male Black-throated Green Warblers used trees with similar characteristics.

Foraging. Substrate use for foraging was significantly influenced by tree species and dbh (Table 4). Black-throated Green Warblers preferred to forage in white spruce than in trembling aspen, and to a lesser extent in balsam poplar, but did not prefer or avoid paper birches relative to white spruces. Larger diameter trees were again more likely to be used than smaller trees, as was the case for songposts. SEX was marginally nonsignificant (likelihood ratio test, $G_1 = 3.45$, $P = 0.06$). Finally, there were no SITE or TERR effects on trees used for foraging. When pooling data for the two sites, we found a significant difference in the frequencies of used and unused tree species for males ($G_3 = 22.65$, $P < 0.001$), but not for females, which may explain the near significance of SEX. Males foraged preferentially in white spruce and paper birch, but females only showed a nonsignificant tendency to prefer white spruce.

DISCUSSION

Our results indicate that populations of Black-throated Green Warblers breeding in mixedwood forests preferred to use conifers on at least two scales. At the mesohabitat scale, territory locations coincided with areas where white spruce was present and relatively abundant. Inside their territories, Black-throated Green Warblers were significantly more likely to use white spruce than the more abundant trembling aspen and balsam poplar for singing both A and B song types, and for foraging.

For all three behaviors, both the species of tree and its dbh were significant predictors of tree use. It is difficult to distinguish between the two effects. Black-throated Green Warblers may simply have favored larger trees, which happened to be white spruces in our plots. Tree species also was a significant predictor of tree use in itself, however. Hence, white spruces could have been preferred both for their large size and for other intrinsic characteristics.

Even though we cannot statistically differentiate the effects of tree species and size, we submit that (1) larger and higher trees provide better songposts for Black-throated Green Warblers, and that (2) white spruces may provide better foraging opportunities for this species in our study region. Our first suggestion is based on the fact that, over a given distance, songs broadcast from the canopy have a greater probability of being detected than songs broadcast from the shrub layer (Schieck 1997). Because our plots had a dense shrub layer, it would thus be advantageous for Black-throated Green Warblers to sing near the top of the highest trees, which were white spruces in our study plots. Song frequency is positively correlated with singing height (Lemon et al. 1981), so high-frequency singers like Black-throated Green Warblers may mini-

mize sound attenuation by singing higher in a tree. Holmes (1986) reports an average songpost height of 15.1 m for a deciduous-dominated stand. We did not record precise songpost heights as part of this study, but our qualitative observations indicate that songposts were located in the upper third of trees.

White spruce trees may also provide better foraging opportunities, either because they host more potential prey than the other tree species present or because the Black-throated Green Warbler populations we studied were better adapted to forage in them. The Black-throated Green Warbler is mainly a leaf gleaner (MacArthur 1958, Morse 1968, Robinson and Holmes 1982), a foraging method whose success is closely linked to foliage structure (Holmes and Robinson 1981). Compared to deciduous trees, conifers have stronger branches and offer more support for tip gleaners (Morse 1989a, Parrish 1995a). Deciduous trees species also vary in their leaf morphology and attachment. Among species found in our study plots, paper birch has shorter petioles than either poplar species, which gives foraging Black-throated Green Warblers easier access to prey. Indeed, although the two poplar species were significantly avoided relative to white spruce, paper birch was not. Therefore, the preference for white spruce and to a lesser extent for paper birch for foraging is probably not an artifact of their diameters at breast height.

In this study, sex had a marginally nonsignificant effect on tree use. When comparing used and unused trees for both sites combined, males foraged preferentially in white spruce and paper birch, but females only showed a nonsignificant tendency to prefer white spruce. Holmes (1986) reported a significant difference in the frequency of use of different tree species by male and female Black-throated Green Warblers, with females using yellow birch (*Betula alleghaniensis*) more frequently than males. Our results suggest that trees preferred by males for foraging also were preferred as singing substrates, at least for type B songs. Our nest data are insufficient to determine whether females mainly foraged in the same tree species they used as nesting substrates.

Did deciduous trees provide resources critical to Black-throated Green Warblers in our study plots? In spite of the relatively strong preference for large spruces at the microhabitat scale, de-

ciduous trees were still used as songposts or as foraging and nesting substrates. Of the six nests we found, four were in paper birches, one in a balsam poplar, and one in a white spruce. Such a small sample size does not permit us to draw conclusions about tree species preferences, but these data do indicate that deciduous trees actually can provide nesting opportunities for Black-throated Green Warblers in our study area. Most nests have been reported in conifers (Peck and James 1987, Morse 1993), 1–3 m above the ground (Morse 1993), but the species also nests in deciduous trees, much higher above the ground (Peck and James 1987; pers. observ.). In our study plots, small conifers were rare or absent. Deciduous trees might thus provide important nesting substrates for this species in old boreal mixedwood stands. In other species, vegetation characteristics are very different at nest sites and songposts (Petit and Petit 1988), so this would not be unexpected. However, intensive nest searches would be required to test this hypothesis.

One or many other unmeasured characteristics of old boreal mixedwood stands also might be important for Black-throated Green Warblers. For example, both of our plots were characterized by many treefall gaps. Smith and Dallman (1996) found that Black-throated Green Warbler individuals sang and foraged in gaps of a mixedwood forest more frequently than expected by chance. This suggests that this species favors structurally-heterogeneous stands. The greater light penetration in gaps can create favorable microclimates for arthropods (Smith and Dallman 1996) and thus make foraging more advantageous in a heterogeneous mixedwood forest than in a pure conifer stand, even though white spruce was the preferred foraging substrate in our study. Shrubs were not important foraging substrates in this study, probably because they were mainly used late in the season, at the time when young fledge (pers. observ.). This downward shift in foraging location also has been reported in Red-eyed (*Vireo olivaceus*) and Philadelphia (*V. philadelphicus*) Vireos (Robinson 1981).

Current forest management regulations in Alberta require forestry companies to reestablish the same proportion of conifers that was present in the mixedwood stands they harvest. However, regulations do not specify the spatial arrangement in which conifers should be replanted, and

seedlings are often clumped along access roads for logistical reasons. Over the long-term, this practice will favor pure deciduous or coniferous stands over mixedwood stands. The expected harvest rotations (<70 years) also will reduce the structural complexity of the future forest compared to present old mixedwood stands. Characterizing fine-scale habitat use by the Black-throated Green Warbler in pristine forest stands helped us understand the importance of stand composition and conifer configuration for this and other species that might be affected by the current forestry operations in the boreal mixedwood forest. Even though our populations of Black-throated Green Warblers preferred conifers at the meso- and microhabitat scales, greater concentrations of conifers might not necessarily benefit Black-throated Green Warblers because other potentially important characteristics of mixedwood stands, such as dense layers of deciduous shrubs, may not be found in pure coniferous forests.

Our results suggest that even widely-distributed species may show little plasticity in substrate use on a local scale. This study also confirms that critical habitat components cannot be extrapolated from knowledge of other regional populations, as shown by Collins (1983) and Parrish (1995b). In the boreal mixedwood forest of northern Alberta, Black-throated Green Warblers apparently select territories as a function of conifer distribution, and focus their activities on coniferous trees thereafter. To confirm the importance of white spruce for Black-throated Green Warblers and other species in the boreal mixedwood forest, an experimental study could be conducted by selectively removing mature spruces and monitoring the response of individual birds. Such an experiment should include detailed monitoring of the reproductive performance of territorial males in experimental treatments and control stands, because an increased use of deciduous species in treatments might not necessarily translate into successful reproduction and population persistence. Obviously, performing this type of experiment also would allow examining the response of other species strongly associated with coniferous vegetation in mixedwood stands to broaden the taxonomic scope of the experiment.

ACKNOWLEDGMENTS

LITERATURE CITED

BIBBY, C. J., N. D. BURGESS, AND D. A. HILL. 1992. Bird census techniques. Academic Press, London.

BLOCK, W. M., AND L. A. BRENNAN. 1993. The habitat concept in ornithology, p. 35–91. *In* D. M. Power [ed.], Current ornithology. Vol. 11. Plenum Press, New York.

COLLINS, S. C., F. C. JAMES, AND P. G. RISSER. 1982. Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. Oikos 39:50–58.

COLLINS, S. C. 1983. Geographic variation in habitat structure of the Black-throated Green Warbler (*Dendroica virens*). Auk 100:382–389.

EBERHART, K. E., AND P. M. WOODARD. 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. 17:1207–1212.

FICKEN, M. S., AND R. W. FICKEN. 1962. The comparative ethology of the wood warblers: a review. Living Bird 1:103–122.

HOLMES, R. T. 1986. Foraging patterns of forest birds: male-female differences. Wilson Bull. 98:196–213.

HOLMES, R. T., AND S. K. ROBINSON. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35.

HOSMER, D. W., JR., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York.

LEMON, R. E., J. STRUGER, M. J. LECHOWICZ, AND R. F. NORMAN. 1981. Song features and singing heights of American warblers: maximization or optimization of distance? J. Acoust. Soc. Am. 69:1169–1176.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

MORSE, D. H. 1967. The contexts of song in the Black-throated Green and Blackburnian Warblers. Wilson Bull. 79:62–72.

MORSE, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779–784.

MORSE, D. H. 1970. Differences between courtship and territorial songs. Nature 226:659–661.

MORSE, D. H. 1989a. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, MA.

MORSE, D. H. 1989b. Song patterns of warblers at dawn and dusk. Wilson Bull. 101:26–35.

MORSE, D. H. 1993. Black-throated Green Warbler

(*Dendroica virens*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 55. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

NICE, M. M., AND L. B. NICE. 1932. A study of two nests of the Black-throated Green Warbler. Bird-Banding 3:95–105, 157–172.

NORUŠIS, M. J. 1994. SPSS advanced statistics 6.1. SPSS Inc., Chicago.

PARRISH, J. D. 1995a. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.

PARRISH, J. D. 1995b. Experimental evidence for intrinsic microhabitat preferences in the Black-throated Green Warbler. Condor 97:935–943.

PECK, G. K., AND R. D. JAMES. 1987. Breeding birds of Ontario: nidology and distribution. Vol. 2: passerines. Royal Ontario Mus., Toronto.

PETIT, K. E., AND D. R. PETIT. 1988. On measuring vegetation characteristics in bird territories: nest sites vs. perch sites and the effects of plot size. Am. Midl. Nat. 119:209–215.

ROBINSON, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed Vireos. Condor 83:16–26.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

ROWE, J. S. 1972. Forest regions of Canada. Can. For. Serv. Publ. No. 1300, Ottawa, Ontario, Canada.

ROWE, J. S., AND G. W. SCOTTER. 1973. Fire in the boreal forest. Quart. Res. 3:444–464.

SCHIECK, J. 1997. Biased detections of bird vocalizations affect comparisons of bird abundance among forested habitats. Condor 99:179–190.

SEDGWICK, J. A., AND F. L. KNOPF. 1992. Describing Willow Flycatcher habitats: scale perspective and gender differences. Condor 94:720–733.

SHERRY, T. W., AND R. T. HOLMES. 1985. Dispersion patterns and habitat responses of birds in northern hardwoods forests, p. 283–309. *In* M. L. Cody [ed.], Habitat selection in birds. Academic Press, New York.

SMITH, R., AND M. DALLMAN. 1996. Forest gap use by breeding Black-throated Green Warblers. Wilson Bull. 108:588–591.

SPSS INC. 1997. Systat 7.0: new statistics. SPSS Inc., Chicago.

STEELE, B. B. 1992. Habitat selection by breeding Black-throated Blue Warblers at two spatial scales. Ornis Scan. 23:33–42.

STEINBERG, D., AND P. COLLA. 1997. Logistic regression, p. 67–129. *In* Systat 7.0: new statistics. SPSS Inc., Chicago.

STELFOX, J. B. (ED.). 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre AECV95-R1, Vegreville, Alberta, and Canadian Forest Service (Project No. 0001A), Edmonton, Alberta, Canada.

VERNER, J. 1985. Assessment of counting techniques. Current Ornithol. 2:247–302.