Do Blackburnian Warblers select mixed forest? The importance of spatial resolution in defining habitat

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Abstract

Determining the importance of mixed forests to species diversity has become an important aspect of forest ecology and management. Mixed forests are vulnerable to silvicultural practices that reduce heterogeneity. Thus, species associated with these forest types are of potential concern. To determine if Blackburnian Warblers (*Dendrioca fusca*) select mixed forest, we examined habitat use at two spatial scales and resolutions across the full gradient of forest cover types using spot mapping, point counts, and behavioral observations. We detected no difference in abundance among cover types recognised at the resolution of the provincial air photo forest inventory (deciduous, conifer, and mixed forest). However, at finer resolutions, the species was more likely to occur in stands containing a combination of both deciduous and conifer trees. Territory locations were positively associated with deciduous tree height, conifer live crown width, and mature deciduous and conifer tree density. At the individual tree scale, Blackburnian Warblers were more likely to select mature conifer and deciduous trees for foraging and singing than immature conifers, but did not show preference for any tree type (i.e., deciduous or conifer).
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Keywords: Dendroica fusca; Habitat use; Spatial scale; Deciduous; Conifer

1. Introduction

Examining the importance of mixed forests to species diversity has become an important aspect of forest ecology and management (Freemark and Merriam, 1986; Kirk et al., 1996; Schieck et al., 2000). A mixed forest is characterized as a mosaic of conifer and deciduous tree species and is recognized as a distinct forest type that should be maintained on the landscape because of its floral diversity and structural heterogeneity (Hobson and Bayne, 2000). In forest management planning, tree species composition is the most important characteristic in stand differentiation (Chen and Popadiouk, 2002). MacDonald

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(1995) proposed that a boreal mixed forest should be defined as any site in which no single species comprises 80% or more of the total basal area though the New Brunswick Department of Natural Resources (NBDNR, 2000a) defined the Acadian mixed forest as stands in which neither conifer or deciduous species comprise more than 75% of the basal area.

Mixed forests occupy substantial proportions of the ranges of many neotropical migrant birds and are declining rapidly in the boreal mixed forest of Western Canada and the Acadian forests of Eastern Canada, due largely to timber harvest and subsequent conversion to softwood plantations (Cumming et al., 1994; Betts et al., 2003). Silvicultural practices (e.g., planting, thinning, selection cutting) may result in a reduction in species diversity and simplification of canopy and understory structure in mixed forests (Kirk et al., 1996). This underscores the importance of identifying bird species that specialize in using mixed forests; however, the response of avian communities to conifer–deciduous gradients is still poorly understood (Enoksson et al., 1995).

Despite numerous studies in mixed-forest habitat, few have identified mixed-forest species (but see Mazur et al., 1998; Robichaud and Villard, 1999; Sabine et al., 2001; Girard et al., 2004). However, there may be no particular habitat feature of mixed forests to which species are adapted that does not exist in either pure deciduous or conifer forest; mixed forest may represent a forest type in which generalists can exist alongside deciduous- and conifer-associated species. Alternatively, lack of evidence for mixed-forest species may be due to the paucity of studies that have been designed to address this question explicitly. Here we define a mixed-forest species as one that specializes on, or more frequently uses forest stands that contain both conifer and deciduous trees.

First, very few studies have been conducted across the full gradient from conifer to deciduous stands (but see Kirk et al., 1996; Robichaud and Villard, 1999). If habitat sampling is not conducted across the entire environmental gradient of interest, then there is a risk of making poor or incorrect habitat associations (Vaughan and Ormerod, 2003). Second, failure to identify mixed-forest species may be attributed to inappropriate sampling resolution. The resolution of forest cover categories often used in forest management planning and wildlife habitat classification may

be too coarse to detect a species' association with this forest type. For instance, on New Brunswick Crown land, five cover type categories are used in planning for vertebrate habitat: tolerant hardwood, hardwood, softwood, pine, and mixedwood (NBDNR, 2000b). Forest management policy requires the maintenance of proportions of these cover types in management plans even though it is unknown whether this resolution is fine enough to reflect habitat requirements.

Finally, the spatial extents at which individuals perceive their environment are poorly known (Addicott et al., 1987; Pearson et al., 1996). For many species, patterns of habitat use differ between sampling resolutions and spatial extents (Wiens et al., 1987; Steele, 1992; Jones and Robertson, 2001). Vegetation influencing these patterns can vary across scales and may be structured hierarchically (Urban et al., 1987; Savignac et al., 2000). Results from a community-based songbird study in New Brunswick suggested that Blackburnian Warblers (*Dendroica fusca*) are associated with mixed forests and could serve as a mature mixed-forest indicator (Betts et al., in press). To determine whether this species recognizes and selects mixed-forest habitat we conducted research at multiple spatial scales and across a gradient of forest cover types.

Currently there is an emphasis on community-based research (e.g., Cumming and Diamond, 2002; Stuart-Smith et al., 2002; Drapeau et al., 2003). However, numerous international and national forest management organizations use indicator species for monitoring forest health (Lindenmayer, 1999). In Canada, many forest companies and government organizations use indicator species in their forest management plans (Canadian Council of Forest Ministers, 1995; Betts and Forbes, 2005). NBDNR is attempting to identify indicators of mature mixed-forest health (NBDNR, 2000b). Though decline of mixed forest may negatively influence populations of any species that uses this forest type, species most strongly associated with mixed forest are likely to be at the greatest risk. Despite the widespread use of indicator species, there are few multiscale studies examining habitat use by ecological indicator species.

Blackburnian Warbler is also of conservation interest due to a province-wide decline over the past

20 years (1983–2003) (Sauer et al., 2004). Across its range, the species has been associated with conifer (Macarthur, 1958; Morse, 1976a; Doepker et al., 1992), deciduous (Sherry and Holmes, 1985; Holmes et al., 1986) and mixed forests (Cumming and Diamond, 2002; Girard et al., 2004). Despite this apparent variation in use of coarse cover types, Blackburnian Warbler is strongly associated with mature conifer trees (Collins et al., 1982) because it nests in the higher strata of conifers in all forest types (Morse, 1994). The species exploits a tree top niche and is usually found in the upper third of the canopy singing in a stationary position or foraging by gleaning or pecking on insects along branches in the upper portions of deciduous and conifer trees (Macarthur, 1958; Morse, 1968; Holmes and Robinson, 1981).

This variation in habitat use reported in the literature may be due to the resolution at which forests have been measured and managed. The resolution at which land managers classify forests is often constrained by the information available from air photos (Betts et al., 2003) and may be very different from the resolution at which birds select habitat (Keppie and Kierstead, 2003). Further, much of the previous research on this species may be misleading because it does not encompass multiple scales (Girard et al., 2004). A multiscale approach that incorporates finer resolutions and the full gradient of available cover types should provide a more complete representation of habitat use patterns of potential indicator species.

We examined habitat use at two spatial extents (the territory, and individual trees used for foraging and singing behaviors) and two resolutions (coarse and fine) to determine if Blackburnian Warblers are associated with mixed forest. If Blackburnian Warblers identify mixed forests as a preferred forest type we predicted that, (1) they should exist in highest relative abundances where both conifer and deciduous trees are present and (2) within territories, Blackburnian Warblers will be associated with mixed forest vegetation characteristics (e.g., conifer and deciduous trees). There are numerous potential mechanisms behind these observed patterns in habitat selection including possibilities of lower predation, reduced competition, and greater resource availability in mixed forest (Whelan, 1989; Graham, 2001; Roos and Part, 2004). The species

may require the presence of both conifers and deciduous trees to satisfy life history requirements. Because Blackburnian Warblers require conifers for nesting (Peck and James, 1989; Morse, 1994), increased use of deciduous trees would result in selection of mixed forest. To test this hypothesis, we observed singing and foraging behavior across a hardwood–softwood gradient. We predicted that Blackburnian Warblers would select deciduous trees disproportionately to their availability for foraging and singing behavior.

2. Methods

Our study area encompassed approximately 4000 km^2 in the Acadian Forest Region (Rowe, 1959) of Southeastern New Brunswick, Canada (66.08–64.96 °W, 45.47–46.08 °N). The study area includes Fundy National Park and is characterized by 89% forest cover, a maritime climate and rolling topography (Woodley, 1998). Forest cover types are primarily shade intolerant deciduous stands (white birch [Betula papyrifera], large tooth aspen [Populus grandidentata], trembling aspen [Populus tremuloides], and red maple [Acer rubrum]), shade tolerant deciduous stands (beech [Fagus grandifolia], sugar maple [Acer saccharum], striped maple [Acer pennsylvanica] and yellow birch [Betula alleghaniensis]), mixed-forest communities (either tolerant deciduous trees or intolerant deciduous trees combined with red spruce [Picea rubens] and balsam fir [Abies balsamea]), and conifer communities (red spruce, balsam fir, white spruce [Picea glauca] or black spruce [Picea mariana]) (NBDNR, 1998). Intensive forestry activities (clearcutting and tree planting) are common in all areas except for Fundy National Park.

2.1. Study design

We used territory mapping and the point count method to collect Blackburnian Warbler abundance data (Bibby et al., 1992). Through repeated visits, point counts estimated bird abundance at single points while territory mapping estimated locations and the number of territories. Point counts were more efficient and allowed for a greater number of points to be

visited while territory mapping allowed for the collection of behavioral data. We felt that this dual method would increase the strength of conclusions obtained if results were similar. We collected spot map data in nine stands. Study plots were rectangular in shape (200 × 500, or 330 × 330), at least 50 m from the edge of a stand and over 1 km apart. One study plot was established in each stand. We classified a 'stand' as a group of trees of the same cover type (deciduous, conifer and mixed forest) and age class, bordering either a hard edge (e.g., road) or soft edge (e.g., different cover type). We adopted existing definitions for these cover types; deciduous stands contained >75% deciduous trees, conifer stands contained >75% conifer trees and mixed stands contained <75% of either deciduous or conifer trees (NBDNR, 2000a). Coarse cover types were used a priori to establish sample locations. However, due to heterogeneity among stands, both spot-map plots and point count locations represented the gradient from pure conifer to pure deciduous forest. Spot-mapped stands ranged from a stem density of 1% conifer and 99% deciduous to 93% conifer and 7% deciduous. The most common deciduous species were sugar maple (25%) and yellow birch (19%), and the most common conifer species was red spruce (40%). This allowed sufficient resolution to test the influence of a cover type gradient on habitat selection by Blackburnian Warblers. Study plots were mature, consisting primarily of canopy trees >22 cm in diameter at breast height (dbh) and considered harvestable and near rotation age or past rotation age and losing vigour (Haddon, 1998).

We collected point count data using a stratified random design; with 270 sample points in the three cover types and four age classes ('regenerating': 8 cm maximum dbh, 'young': 16 cm maximum dbh, 'immature': 30 cm maximum dbh, 'mature': >30 cm maximum dbh). In all cases, sample points were at least 200 m apart and 75 m from a stand boundary. A minimum of 13 and a maximum of 29 points were established in each combination of cover type and age class.

2.2. Blackburnian Warbler survey techniques

We measured territory densities using the spot-map method (International Bird Census Committee, 1970; Bibby et al., 1992) seven times between 28 May and 10 July, from 05:30 to 12:30 AST, 2001 and 2002. Starting locations varied daily between and within the nine study plots. Each plot was visited in both time periods (early and mid-morning) an equal number of times across the breeding season. We detected birds by sight, song or call and followed them until they were out of sight or were not detectable by sound. We collected behavioral observations and delineated bird positions on maps of each study plot. Blackburnian Warblers have the highest number of aggressive encounters with conspecifics during the first week of territory occupation (28 May–4 June) and at the end of the third week, from 19 to 25 June (Morse, 1967). During the second time period, we used song playbacks to increase accuracy of territory delineations and we made the assumption that ''floater'' males would not defend an area and that responding males held territories. As territories are well established with nesting females or fledglings at this time, it is unlikely that playbacks affected territory occupation. We played songs from all suspected territory edges, every 15 m, directionally away from territory centers, until males stopped responding or another male appeared. The appearance of another male indicated the territory boundary (Falls, 1981).

We conducted singing and foraging observations of 64 males with observation time standardized by individual. For used trees, we recorded date, song type or foraging behavior, sex and time of day. Trees used for less than 5 s, and not used for foraging or singing were not recorded (Robichaud and Villard, 1999). No more than five trees were collected in one territory. In total, we identified 154 foraging trees and 279 song posts. Each tree was included only once in analysis. Observations were not conducted immediately following playbacks, refraining from collecting observations for at least one day.

We used the fixed-area point count method to sample birds at of each of the 259 sample points (Ralph et al., 1995). Skilled observers visited points three times between 05:30 and 10:30 AST from 05 June to 11 July, for a 5 min duration. We conducted counts in calm (wind speed <20 kph), dry conditions. All male Blackburnian Warblers seen or heard within a 50 m radius were recorded. To avoid observer bias, the

same individual visited each point only once. To limit bias caused by time of day, each point was visited in a different period (early, mid, late morning) in each of the three rounds. Because the majority of point count stations had a single detection, we collapsed Blackburnian Warbler abundance into binomial (presence/absence) data with minimal loss of information.

2.3. Vegetation survey techniques at the territory scale

We determined coarse-resolution forest cover types from forest inventory maps. We delineated age classes based on maximum dbh trees within the stand. At a fine resolution within spot-mapped stands we collected tree density data from prism plots and structural vegetation data from 20 m transect lines to compare occupied territories and randomly selected unoccupied areas (Avery and Burkhart, 1994). Prism plots provide a measurement of tree size and tree density. This technique uses a geometric equation to determine which trees fall within the plot rather than a fixed radius and they more accurately estimate the density of large diameter trees (Philip, 1998). We placed three prism plots with a transect line intersecting the center of the prism plot within each territory as this was the maximum number of plots that could be included without double counting trees. A transect line was laid with 10 m of the line on either side of the prism plot center point. The direction of the line was randomly selected. The transect lines were used to estimate canopy cover and to randomly select trees for structural measurement. Structural data included canopy and subcanopy cover (estimated using an ocular tube along 20 m transect lines), tree height (base of tree to peak growing point), crown height (base of tree to base of crown), crown length (tree height minus crown height), crown width and live crown width. Crown width was the diameter of the crown, measured using the average of two times the radius of the longest and shortest branch in two randomly selected directions (Philip, 1998). Live crown width was the crown width minus the length of branch without live foliage (Franzeb, 1978). Tree species contributing less than 1% of observations were excluded from analysis.

At point count locations we collected fine resolution vegetation data using 20 m × 10 m plots. We recorded species and dbh of all standing live and dead woody vegetation greater than 2 cm dbh. To simplify analysis, tree data were summarized into four dbh categories (2–10 cm, 11–20 cm, 21–30 cm, >30 cm dbh) and two species groups (conifer, deciduous). Based on a priori knowledge of Blackburnian Warbler nesting habits (Morse, 1994), we sampled the number of mature spruce within 50 m of each sample point. This increased spatial scale of sampling is more likely to reflect vegetation composition at the scale of individual territories for this species (territory size = 0.4–0.6 ha; Morse, 1976b). Due to the extensive spatial scale of this sampling (0.79 ha), we allotted each sample point to an ordinal scale representing categories of spruce density (0, 1–5, 6–10, 11–50, 51–75, 76–100, >100 stems/50 m radius point count plot). We used spruce rather than all conifer trees because other species were in low densities (<1% of all trees).

Vegetation data were collected differently between methods because point counts initially addressed community level habitat associations and vegetation data collected were designed for multiple bird species, while spot-map vegetation data were designed to specifically examine Blackburnian Warbler habitat use.

2.4. Statistical analysis at the territory scale

For coarse resolution analysis, we used logistic regression (Mathsoft, 1999) to test the null hypotheses that there was no difference in the likelihood of Blackburnian Warbler occurrence across age classes and no difference across cover types within each age class. We used Tukey multiple contrasts to determine post hoc significant differences among groups (Mathsoft, 1999).

We used logistic regression to model the probability of Blackburnian Warbler occurrence as a function of the interaction between deciduous trees in each of the four dbh categories and the density of mature spruce. Substantial support for these interactions would indicate a higher probability of Blackburnian Warbler occurrence in stands with both conifer and deciduous components. Such interactions can be interpreted as evidence that the existence of conifer trees in a hardwood stand, and vice versa, result in a multiplicative effect on the probability of

occurrence. Models were also built with original mean abundance data using a Poisson error structure with a log link (for Poisson-distributed count data). Model ranks (based on Akaike Information Criterion [AIC]) did not differ, so for ease of interpretation we present logistic regression results.

Logistic regression was also used to determine the probability of territory occurrence based on vegetation characteristics collected within spot-mapped territories and randomly selected unoccupied areas.

In all logistic regression analysis, to avoid multicollinearity we removed vegetation characteristics that were highly correlated ($r > 0.7$). We followed the strategies of Hosmer and Lemeshow (2000) to assess goodness of fit. We used an information-theoretic approach to investigate relationships between habitat models and Blackburnian Warbler occurrence. The information theoretic approach allows one to select a best model and rank the remaining models (Burnham and Anderson, 1998). The advantage of this approach is that it is not founded on arbitrary cut-points to determine statistical significance. Low AIC values indicate best models. We also report 'Nagelkerke's-r^2' as an assessment of explained variation. Unlike deviance, this statistic has a theoretical upper bound of 1 (representing perfect fit; Maddalla, 1983; Nagelkerke, 1991).

2.5. Vegetation survey techniques at the individual tree scale

Within spot-mapped territories, available trees of each species were measured using prism plots to compare use with availability. We recorded tree height, crown height, crown length, mean crown width and live mean crown width on two randomly-selected deciduous and conifer trees within plots to compare the structural difference between used and unused trees. Trees were selected within 1 m of either side of a 20 m transect line.

2.6. Statistical analysis at the individual tree scale

We used Pearson's chi-square to compare dbh and tree type (i.e., deciduous and conifer) of used versus available trees to determine if resources are used disproportionately to availability (Johnson, 1980). The Neu technique determined Bonferroni confidence intervals for observed tree use to ascertain if observed tree use was different from expected tree use (Neu et al., 1974; Byers et al., 1984). In addition, we compared species and tree structure characteristics of used trees to randomly selected trees.

It was not possible to use Pearson's chi-square to compare tree structure characteristics, other than dbh, because these data were collected only from randomly selected trees, and not from all available trees. We applied generalized linear mixed models (GLMMs) using Penalized Quasi-Likelihood to test for differences in characteristics between used versus available trees (Breslow and Clayton, 1993). This allowed us to account for the potential for lack of independence of observations within territories (i.e., multiple observations of a single individual were not necessarily independent). Individual territories were treated as random effects and all other predictor variables as fixed effects. In analysis of all foraging and singing location data, we considered only trees used by males, as the sample size for females was low ($N = 23$).

We developed separate models for song posts and trees used for foraging and segregated by tree type in both analyses because behavioral observations suggested that Blackburnian Warblers did not use tree types indiscriminately (Young, 2004), as is the case in other breeding passerines (Hunter, 1980; Beck and George, 2000). If trees used for both behaviors are not the same, then combining behaviors to create one model of tree use may produce misleading results. Although we limited ourselves to four dbh categories at the territory level, we created more categories of smaller intervals at this level to determine if a threshold tree size exists. If a tree size is avoided, then at some dbh, tree availability should be greater than tree use; using more categories increases the accuracy of identifying avoided or selected tree sizes.

All analyses other than logistic regression were performed using Systat 9.0 (SPSS, 1998). Logistic regression analyses were performed using Splus (Mathsoft, 1999) and GLMM models were fit in R 2.0.1 (R Development Core and Team, 2004). To reduce the chance of including weakly related variables or false effects, we set α at $P = 0.05$. Means are reported ±S.E.
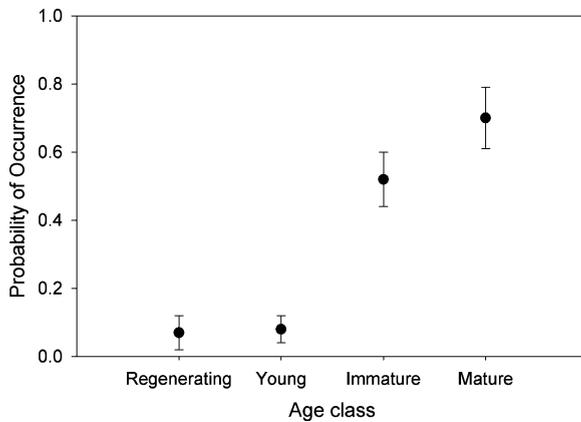
Fig. 1. The probability of Blackburnian Warbler occurrence observed in 50 m radius point count plots in stands of four age classes. Error bars represent S.E.
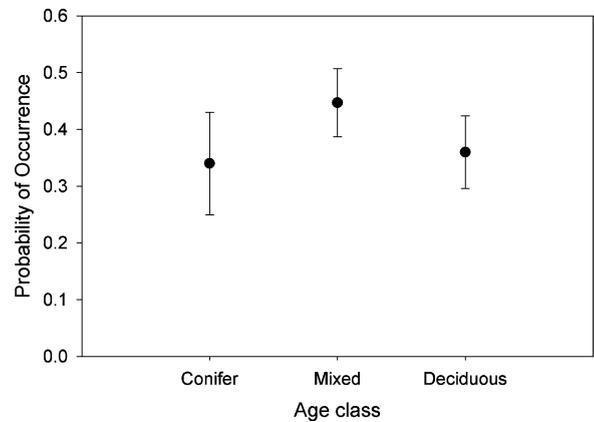

Fig. 2. The probability of Blackburnian Warbler occurrence observed in 50 m radius point count plots in stands of three cover types. Error bars represent S.E.

3. Results

3.1. Territory scale

3.1.1. Coarse resolution

In spot-mapped plots we found territory density to be 0.51 territories/ha in 2001 and 0.71 territories/ha in 2002. Mean territory density was highest in mixed forest stands (2001: 0.67/ha ± 0.09; 2002: 1.0/ha ± 0.01) and lower in conifer (2001: 0.5/ha ± 0.18; 2002: 0.67 ± 0.31) and deciduous (2001: 0.23/ha ± 0.06; 2002: 0.30/ha ± 0.12) stands in 2001 ($H = 5.1$, d.f. = 2, $P = 0.08$) and 2002 ($H = 4.0$, d.f. = 2, $P = 0.14$) with differences approaching statistical significance in 2001. At point count locations, the probability of occurrence of Blackburnian Warbler differed significantly among age classes ($\chi^2 = 53.74$, d.f. = 3, $P < 0.001$) (Fig. 1), but not among cover types ($\chi^2 = 0.71$, d.f. = 2, $P = 0.70$) (Fig. 2). The species was significantly more likely to occur in the mature age class than the regenerating ($P < 0.01$) and young age classes ($P < 0.01$), and in the immature than the regenerating ($P < 0.01$) and young ($P < 0.01$) age classes. There was no significant difference in abundance between immature and mature ($P = 0.32$) or regenerating and young age classes ($P = 0.99$).

3.1.2. Fine resolution

Analysis of spot map data indicated that Blackburnian Warbler territory occurrence was higher with increasing deciduous tree height, conifer live crown width, and mature deciduous tree density and decreasing with immature tree density (Table 1). Models with additional vegetation variables had less support (Appendix A). Analysis of point count data indicated a positive relationship between Blackburnian Warbler presence and the interaction between the density of deciduous trees in larger dbh categories (>10 cm) and spruce trees >20 cm (Table 2; Fig. 3). There was considerably less support for an additive model (deciduous trees >10 cm + spruce >20 cm), and essentially no support for models that included only deciduous or conifer variables.

Table 1
Results of the top-ranked logistic regression model predicting Blackburnian Warbler territory occurrence within fixed area plots

Variable	Estimated coefficient	S.E.	Deviance	P
Deciduous tree height	0.45	0.11	33.72	<0.01
Conifer live crown width	0.02	0.001	22.46	<0.01
Density of immature trees	−0.001	0.0004	8.11	<0.01
Density of mature deciduous trees	0.02	0.007	5.33	0.02

Explained deviance = 0.45, best model $r^2 = 0.51$.

Table 2
AIC values, weights and ranks of logistic regression models used to describe Blackburnian Warbler presence

Model name[a,b]	Rank	W_i[c]	AIC	Δ_{AIC}	Evidence ratio to model 1
DECID > 10 × Spruce > 20	1	0.7022	280.18	0	0.00
DECID > 30 × Spruce > 20	2	0.1732	282.98	2.80	4.06
DECID 11–20 × Spruce > 20	3	0.0666	284.89	4.71	10.54
DECID > 10 + Spruce > 20	4	0.0516	285.40	5.22	13.60
DECID 21–30 × Spruce > 20	6	0.0027	291.32	11.14	262.43
Spruce > 20	7	0.0024	291.57	11.39	297.38
DECID 2–8 × Spruce > 20	5	0.0013	292.82	12.64	555.57
DECID 30	8	0.0000	299.39	19.21	14838.79
DECID 2–8	9	0.0000	304.79	24.61	220797.22
DECID 10–20	11	0.0000	310.32	30.14	3506047.88
DECID 20–30	10	0.0000	311.14	30.96	5282975.30

Models below the dotted line ($\Delta_{AIC} < 10$) have essentially no support given the data. Best model $r^2 = 0.32$.
[a] DECID = deciduous trees.
[b] All values in centimetres, diameter at breast height (dbh).
[c] AIC weights.

3.2. Individual tree scale

3.2.1. Trees that were foraged upon

In deciduous stands, trees that were used for foraging purposes were used in proportion to availability ($\chi_5^2 = 3.20$, $n = 28$, $P = 0.36$). In mixed-forest stands, conifer trees ≤30 cm dbh and deciduous trees <16 cm dbh were used less than expected and deciduous trees >30 cm dbh were used more than expected ($\chi_9^2 = 35.09$, $n = 85$, $P < 0.01$) (Table 3). In conifer stands, conifer trees ≤ 30 cm dbh were used less than expected ($\chi_5^2 = 34.37$, $n = 58$, $P < 0.01$). Use of trees >30 cm dbh was in proportion to availability by species across all cover types (mixed forest: $\chi_2^2 = 5.51$, $P = 0.06$; deciduous: $\chi_2^2 = 2.32$, $P = 0.77$; conifer: $\chi_2^2 = 2.32$, $P = 0.31$). According to AIC, best

Table 3
The proportion of expected and observed foraging observations with Bonferroni confidence intervals for conifer and mixed-forest stands at a significance level of 0.05

Stand type	Tree type[a]	Expected use	Observed use	Bonferroni confidence interval[b]
Mixed	DECID <16 cm	**0.05**	0.01	**−0.01 ≤ p_1 ≥ 0.04**
	DECID 16–20 cm	0.08	0.05	−0.01 ≤ p_2 ≥ 0.11
	DECID 21–24 cm	0.07	0.08	0 ≤ p_3 ≥ 0.16
	DECID 25–30 cm	0.08	0.13	0.03 ≤ p_4 ≥ 0.22
	DECID > 30 cm	**0.25**	0.44	**0.30 ≤ p_5 ≥ 0.58**
	CON < 16 cm	**0.01**	0	**0 ≤ p_6 ≥ 0**
	CON 16–20 cm	**0.08**	0.02	**−0.02 ≤ p_7 ≥ 0.07**
	CON 21–24 cm	0.08	0.07	0 ≤ p_8 ≥ 0.14
	CON 25–30 cm	**0.12**	0.05	**−0.01 ≤ p_9 ≥ 0.11**
	CON > 30 cm	0.17	0.15	0.05 ≤ p_{10} ≥ 0.25
Conifer	DECID < 20 cm	0.07	0.12	−0.01 ≤ p_{11} ≥ 0.22
	DECID 20–30 cm	0.10	0.16	0.02 ≤ p_{12} ≥ 0.30
	DECID > 30 cm	0.14	0.25	0.09 ≤ p_{13} ≥ 0.42
	CON < 20 cm	**0.07**	0.02	**−0.02 ≤ p_{14} ≥ 0.06**
	CON 20–30 cm	**0.18**	0.07	**−0.02 ≤ p_{15} ≥ 0.16**
	CON > 30 cm	0.44	0.38	0.23 ≤ p_{16} ≥ 0.53

Deciduous stands are not included because use was in proportion to availability. Significant differences in expected use and observed use are highlighted in bold.
[a] DECID = deciduous; CON = conifer.
[b] p_i represents theoretical proportions of occurrence and is compared to corresponding proportion of expected use. If the proportion of expected use is outside the confidence intervals of observed use than the hypothesis of proportional use is rejected.
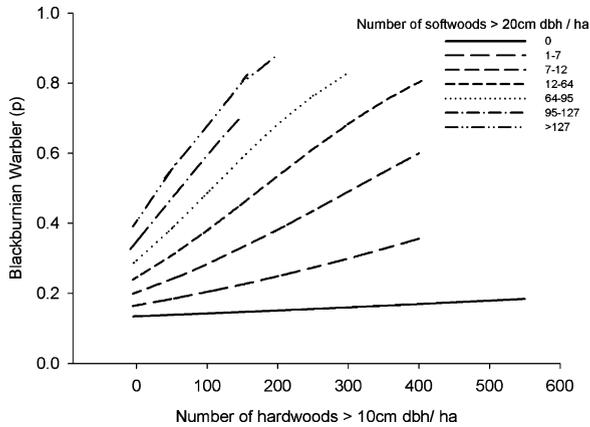
Fig. 3. Fitted line plot of the relationship between probability of Blackburnian Warbler presence and the interaction between the density of mature conifer trees and deciduous trees.

Table 4
Results of top-ranked GLMMs predicting individual tree use by Blackburnian Warblers for foraging and singing behavior

Individual tree use	Random effects	Estimated coefficient	S.E.
Trees that were foraged upon	Live crown width	0.002	0.0005
	Crown length	−0.02	0.01
Song posts	Live crown width	0.002	0.0004
	Tree height	0.08	0.02

model for predicting trees that were foraged upon contained live crown width and crown length (Table 4). Trees with larger live crown widths but smaller crown lengths had a greater probability of being foraged upon.

3.2.2. Song posts

In deciduous stands, deciduous and conifer trees <22 cm dbh were used less than expected

Table 5
The proportion of expected and observed singing observations with Bonferroni confidence intervals for stands at a significance level of 0.05 for song posts

Stand type	Tree type[a]	Expected use	Observed use	Bonferroni confidence interval[b]
Deciduous	DECID < 22 cm	**0.14**	0.04	$\mathbf{-0.03 \leq p_1 \geq 0.12}$
	DECID 22–30cm	0.17	0.17	$0.03 \leq p_2 \geq 0.30$
	DECID > 30 cm	0.30	0.38	$0.20 \leq p_3 \geq 0.57$
	CON < 22 cm	**0.07**	0	$\mathbf{0 \leq p_4 \geq 0.06}$
	CON 22–30 cm	0.08	0.02	$-0.03 \leq p_5 \geq 0.08$
	CON > 30 cm	0.24	0.38	$0.19 \leq p_6 \geq 0.57$
Mixed	DECID 16–20 cm	0.08	0.07	$0 \leq p_8 \geq 0.13$
	DECID 20–24 cm	0.06	0.05	$-0.01 \leq p_9 \geq 0.11$
	DECID 25–30 cm	0.06	0.09	$0.02 \leq p_{10} \geq 0.17$
	DECID > 30 cm	**0.26**	0.45	$\mathbf{0.32 \leq p_{11} \geq 0.58}$
	CON < 16 cm	**0.01**	0	$\mathbf{0 \leq p_{12} \geq 0}$
	CON 16–20	**0.08**	0.02	$\mathbf{-0.02 \leq p_{13} \geq 0.05}$
	CON 20–24 cm	**0.07**	0.02	$\mathbf{-0.02 \leq p_{14} \geq 0.05}$
	CON 25–30 cm	0.08	0.06	$0 \leq p_{15} \geq 0.12$
	CON > 30 cm	0.19	0.27	$0.15 \leq p_{16} \geq 0.38$
Conifer	DECID < 20 m	0.08	0.09	$0.01 \leq p_{17} \geq 0.12$
	DECID 21–24 cm	0.04	0.04	$-0.01 \leq p_{18} \geq 0.09$
	DECID 25–30 cm	0.05	0.05	$-0.01 \leq p_{19} \geq 0.11$
	DECID > 30 cm	0.14	0.18	$0.08 \leq p_{20} \geq 0.29$
	CON < 20 m	**0.06**	0.02	$\mathbf{-0.02 \leq p_{21} \geq 0.05}$
	CON 21–24 cm	0.05	0.01	$-0.02 \leq p_{22} \geq 0.03$
	CON 25–30 cm	**0.11**	0.02	$\mathbf{-0.02 \leq p_{23} \geq 0.05}$
	CON > 30 cm	0.47	0.58	$0.45 \leq p_{24} \geq 0.71$

Significant differences in expected use and observed use are highlighted in bold.

[a] DECID = deciduous; CON = conifer.

[b] p_i represents theoretical proportions of occurrence and is compared to corresponding proportion of expected use. If the proportion of expected use is outside the confidence intervals of observed use than the hypothesis of proportional use is rejected.

($\chi_5^2 = 16.39$, $n = 47$, $P < 0.01$) (Table 5). In mixed-forest stands, deciduous trees <16 cm dbh and conifer trees ≤ 24 cm dbh were used less than expected while deciduous trees ≥30 cm dbh were used more than expected ($\chi_9^2 = 52.95$, $n = 125$, $P < 0.01$). In conifer stands, conifer trees <30 cm dbh were used less than expected ($\chi_7^2 = 24.77$, $n = 47$, $P < 0.01$). Only among trees greater than 30 cm dbh were all tree species used proportionately across all cover types (deciduous: $\chi_2^2 = 0.29$, $P = 0.87$; mixed forest: $\chi_4^2 = 3.1$, $P = 0.54$; conifer: $\chi_2^2 = 2.38$, $P = 0.30$). The best model for predicting song posts using GLMMs contained tree height and live crown width (Table 4). Trees with greater tree height and larger live crown widths had a greater probability of being used as song posts.

4. Discussion

4.1. Territory scale

At a coarse scale of resolution, using forest inventory classifications, we found that Blackburnian Warblers were strongly associated with old forest age classes but did not appear to be strongly associated with mixed forest. Apparent plasticity in cover type use can be interpreted in two ways: (1) Blackburnian Warblers are generalists able to adapt to a variety of cover types and do not prefer mixed forests or (2) the species is present in relatively homogeneous stands if there are mixed-forest components extensive enough to encompass territories. In previous studies, Blackburnian Warblers have been found to be associated with both conifer (Macarthur, 1958; Doepker et al., 1992; Parker et al., 1999) and deciduous forest (Sherry and Holmes, 1985; Holmes et al., 1986) but these studies did not incorporate the full gradient of cover types, which suggests that these inferred habitat associations may be incomplete. For example, if species occurrence is recorded along a single environmental gradient and is sampled only at one end of the gradient (e.g., deciduous stands) then a sigmoid response curve may be fitted when in fact the appropriate relationship is a Gaussian response curve (Vaughan and Ormerod, 2003).

We found that at finer resolutions of measurement, the probability of Blackburnian Warbler presence was highest in stands with a combination of large deciduous and large conifer trees. This was the case in both spot map plots and point counts. These congruent results, using independent methods and data, strengthen the inference that at the territory scale this species selects locations with a mixed forest composition. This suggests a preference for a mixed-forest composition within territories irrespective of coarse-resolution stand cover type. At a fine resolution, a modeling approach using continuous variables rather than categorical variables allowed us to detect Blackburnian Warbler associations with both deciduous and conifer trees. We suggest that if researchers use continuous data based on vegetation measurement, as well as measurements delineated by forest inventories, GIS, or other categorical data, it will increase their power to detect mixed-forest species.

In spot-mapped plots, we found that territory presence increases with deciduous tree height, conifer live crown width, and mature deciduous tree density, but decreases with immature tree density. Further, Blackburnian Warbler avoids immature deciduous trees and conifer trees as foraging and singing substrate. These results indicate that deciduous and conifer tree densities are less influential than tree and stand structure in determining habitat use for this species. Using point count data, we found no relationship with mature deciduous tree densities and Blackburnian Warbler presence, though with the spot-map method we found a positive relationship. The discrepancy between the two census methods and the association with mature deciduous trees can be explained based on study area composition. All spot-mapped stands contained mature trees and at least some conifer trees while point count locations incorporated a wider range of tree sizes and points with no conifer trees.

4.2. Individual tree scale

We found a threshold tree size that is avoided by Blackburnian Warblers for both singing and foraging: <16 cm dbh in deciduous trees and <30 cm dbh in conifers. Although there is more variability in tree sizes used for foraging than for singing, deciduous and conifer trees >30 cm dbh are selected for both behaviors. We hypothesized that as Blackburnian

Warbler requires softwoods for nesting (Peck and James, 1989; Morse, 1994), preference for mixed forest could be a function of increased foraging opportunities or benefits of singing in deciduous trees. However, we found that deciduous trees between small to moderate dbh were used in proportion to their availability. Nevertheless, disproportionate use of large mature conifer and deciduous trees and the avoidance of small and intermediate conifer tree size provide a basis for territory placement in locations with a mature mixed-forest composition. Blackburnian Warblers did select small diameter deciduous trees over small diameter conifer trees, but these deciduous trees had a greater crown width than these conifer trees (Young, 2004). Tree diameter appeared to have a greater influence than tree type. Further, crown length, tree height and crown width were the variables that best predicted tree use in GLMMs, while models containing tree type and species were not supported. Marshall and Cooper (2004) found that Red-eyed Vireos (*Vireo olivaceus*) were more likely to establish territories and return to locations with large crown volumes. Large crown volumes corresponded to locations with high average food availability over multiple years. Similarly, Blackburnian Warblers select territory locations that are characterized by multiple tall trees with large crowns. This species is known to exploit a tree top niche (Macarthur, 1958; Holmes and Robinson, 1981), possibly as a result of exclusion from lower canopy niches by heterospecifics (Morse, 1968). Pure conifer stands throughout NB and the Acadian forest are often characterized by disruptions in canopy cover due to budworm disturbance (MacKinnon and MacLean, 2003). This reduces the total available foraging area for this species. The mixed-forest association that we observed may thus be driven primarily by the structural characteristics of mixed forests (i.e., crown volume) rather than tree species composition per se. Because of an apparently obligate use of conifer trees for nesting (Morse, 1994), pure deciduous stands (also characterized by large crown volumes) are not available for use.

4.3. Management implications

In southern New Brunswick mature mixed forest is the predominant forest type and it is declining at a rate of 0.71% per year (Betts et al., 2003). In the province approximately 79,000 ha is harvested annually, of which 27% is planted with conifer species (Canadian Council of Forest Ministers, 1999), reducing heterogeneity through changes in both stand composition and configuration. Forest management in New Brunswick relies on indicator species, but there is no previous scientific evidence that mixed-forest indicators exist in Acadian forests; there has been little research conducted to determine whether the resolution adopted by managers reflects species habitat requirements. If habitat relationships are examined on a coarse resolution, such as cover type, the Blackburnian Warbler appears to be a generalist. However, at a finer resolution, territory occurrence is predicted by the presence of both deciduous and conifer trees, suggesting that Blackburnian Warblers are mature mixed-forest indicators and will occupy stands that have a mixed-forest component large enough to encompass a territory. Land managers most often classify forests at the resolution of the stand polygon. We have demonstrated that this may be different from the resolution at which birds select habitat. Within-stand habitat variability becomes particularly important if management actions tend to reduce this variability. If stand level models used by forest managers fail to detect changes at this finer scale, species associated with such fine-scale structures may decline. Although we examined one species in one type of mixed forest, our results show that a species can exhibit apparent plasticity at one resolution and yet still select mixed-forest attributes at finer resolutions. Testing for the existence of such patterns is possible only with the collection of vegetation, abundance and behavioral data at finer resolutions. Vegetation characteristics should be measured as gradients rather than as categories. If an indicator approach to forest management is used, then species selected as indicators should be managed using a multi-extent, multi-resolution approach. At all scales, the pattern of habitat use by Blackburnian Warblers suggests that large diameter trees, a characteristic of mature forests, are important factors in determining habitat use. To improve or maintain habitat for this species, mature deciduous and conifer trees should be maintained within a proportion of stands on the landscape. Reduction in mature mixed forest may contribute to further declines in Black-

burnian Warbler populations. This is particularly important in the context of political pressures to double the wood supply in New Brunswick by increasing the rate of conversion to softwood plantation (Jaakko Pöyry Management and Consulting, 2002).

Although Blackburnian Warbler presence is associated with mature mixed forests, we cannot speculate on habitat quality because we did not measure reproductive success or survival. To determine if Blackburnian Warblers have equal success in all cover types, further research should incorporate measures of productivity and survival. We measured behavior but not prey availability. Therefore, we can only speculate on mechanisms driving behavior. Future research should use measures of prey availability to test hypotheses about why mixed forests are selected.

Acknowledgements

Appendix A

See Table A1.

Table A1
AIC values, weights and ranks of logistic regression models used to describe Blackburnian Warbler presence

Model name[a]	Rank	W_i[b]	AIC	Δ_{AIC}	Evidence Ratio to Model 1
DTH + CLCW + ALL 11–20 + D21–30	1	0.4707	108.12	0	0.00
DTH + CLCW + ALL 11–20 + D21–30 + CTH	2	0.2841	109.13	1.01	1.66
DTH + CLCW + ALL 11–20 + D21–30 + CTH + D > 30	3	0.1127	110.98	2.86	4.18
DTH + CLCW + ALL11–20 + D21–30 + CTH + D > 30 + YBIRCH > 30	4	0.0736	111.83	3.71	6.39
DTH + CLCW + ALL 11–20 + D21–30 + CTH+D > 30 + YBIRCH > 30 + CCL	5	0.0381	113.15	5.03	12.37
DTH + CLCW + ALL 11–20 + D21–30 + CTH + D > 30 + YBIRCH > 30 + CCL + AVDI	6	0.0151	115.0	6.88	31.19
DTH + CLCW + ALL 11–20 + D21–30 + CTH + D > 30 + YBIRCH > 30 + CCL + AVDI + DCL	7	0.0057	116.95	8.83	82.68
DTH + CLCW + ALL 11–20 + D21–30 + CTH + D > 30 + YBIRCH > 30 + CCL + AVDI + DCL + DLCW	8	0.0021	118.9	10.78	219.20

[a] DTH = deciduous tree height; CLCW = conifer live crown width; ALL11–20 = density of trees between 11 and 20 cm dbh; D21–30 = density of deciduous trees 21 and 30 cm dbh; CTH = conifer tree height; D > 30, density of deciduous trees > 30 cm dbh; YBIRCH > 30 = density of yellow birch > 30 cm dbh; CCL = conifer crown length; AVDI = average diameter; DCL = deciduous crown length; DLCW = deciduous live crown width.
[b] AIC weights.

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