

# Habitat Segregation Among Songbirds in Old-Growth Boreal Mixedwood Forest

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The foraging behaviour of ten species of insectivorous songbirds — Boreal Chickadee (*Poecille hudsonicus*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Blue-headed Vireo (*Vireo solitarius*), Tennessee (*Vermivora peregrina*), Blackburnian (*Dendroica fusca*), Magnolia (*D. magnolia*), Yellow-rumped [Myrtle] (*D. coronata*), Black-throated Green (*D. virens*), and Bay-breasted (*D. castanea*) warblers — was observed in the boreal mixedwood forest of Prince Albert National Park in central Saskatchewan. Birds segregated their habitat use by preferentially foraging in different tree species, and through preferential use of different foraging locations (height and position) within trees.

White Spruce (*Picea glauca*) was used more than expected by Yellow-rumped Warblers, and Golden-crowned and Ruby-crowned kinglets. Tennessee and Magnolia warblers used White Birch (*Betula papyrifera*), more than expected and Boreal Chickadees and Blue-headed Vireos used Balsam Fir (*Abies balsamea*) more than expected. Boreal Chickadees, Ruby-crowned Kinglets, and Tennessee, Blackburnian and Yellow-rumped warblers all used the bottom part of trees less than expected, while Blue-headed Vireos foraged near the top of trees less than expected. Large inner branches were avoided by Tennessee, Blackburnian and Yellow-rumped warblers, while Bay-breasted Warblers and Blue-headed Vireos avoided small outer twigs. In conifers, Blackburnian Warblers foraged significantly higher in the trees than all other species except Black-throated Green and Bay-breasted warblers. Blackburnian Warblers also foraged significantly higher than Blue-headed Vireos and Magnolia Warblers in deciduous trees.

Key Words: Songbirds, behaviour, foraging, boreal forest, old-growth, Prince Albert National Park, Saskatchewan.

Behavioural interactions and niche partitioning in songbirds have received much attention in the literature (MacArthur 1958; Sabo 1980; Maurer and Whitmore 1981). For many boreal songbirds, however, much on their basic biology remains poorly understood (Sodhi and Paszkowski 1995). Many of the detailed behavioral descriptions have come from studies conducted in the New England States (Rabenold 1978; Robinson and Holmes 1982; Hunt and Flaspohler 1998). This is likely an incomplete description for some birds, as several of the species discussed have their breeding ranges almost entirely restricted to the Canadian boreal forest (Ficken et al. 1996; Rimmer and McFarland 1998). Studies on the southern fringes of the boreal forest, in Maine or Minnesota, are not adequate on their own to understand boreal ecology as many of the plant and animal species are not the same as further north (Rowe 1972; Acton et al. 1998). Even for wide-ranging species, there is evidence that birds do not behave the same way and do not use the same kind of habitat in all parts of their range (Noon et al. 1980; Collins 1983; Robichaud and Villard 1999).

Recent studies in the boreal forest have focused on habitat associations, and habitat requirements of songbirds (Schieck et al. 1995; Kirk et al. 1996). This information is urgently needed in light of increased pressure from large-scale forestry in this region (Cummings et al. 1994). There is mounting evidence to show that mature and old boreal mixedwood forest support an entirely different suite of species not found in younger

age classes (Stelfox 1995; Cumming and Diamond 2002). These older age classes of forest are currently under a harvesting intensity that is disproportionate to their abundance in the landscape (Cummings et al. 1994; Weyerhaeuser 1998\*).

The goal of this project was to investigate details of within-stand habitat segregation among boreal songbirds, focusing on the foliage-gleaning songbird guild of old (>120 years) boreal mixedwood forest. This type and age of forest was chosen as it was biologically the most diverse and structurally the most heterogeneous habitat in the region (Erskine 1977; Johnson et al. 1995; Robichaud and Villard 1999). In addition, mature to old (80+ years), mixedwood forest will become increasingly rare at the landscape level if current land use practices (i.e., logging, oil and gas exploration and agriculture) continue at their present rate (Cummings et al. 1994; Hobson et al. 2002; Schneider et al. 2002\*).

## Study Area

This study was carried out in the boreal, mixedwood forest of Saskatchewan (Kabzems et al. 1986; Acton et al. 1998), in Prince Albert National Park (53°35'N, 106°00'W) during 1990 and 1991 (see Bayne and Hobson 1997 for description). Three sites were chosen in forest stands that were >40 ha in area and >120 years old. Sites were as similar in topography and vegetative cover as field conditions allowed. Stands were aged by forest inventory maps, and by taking core samples from six of the largest trees on each site. Each study

site was surrounded by continuous forest of similar type, but younger age. None of the study sites had been subjected to forest harvesting, and wildfire was the driving force behind forest succession in this area (Weir et al. 2000).

The study sites were structurally very heterogeneous, with many tree-fall gaps and many standing dead trees. These canopy gaps allowed for regeneration, which resulted in a wide range of tree sizes and ages. Dominant tree species were White Spruce, *Picea glauca*, Balsam Fir, *Abies balsamea*, and Trembling Aspen, *Populus tremuloides*, with scattered White Birch, *Betula papyrifera*. Average canopy height was 21 metres with a maximum height of 38 metres (Cumming 1995). White Spruce was the only species that reached heights of over 30 metres, with some specimens also having diameters in excess of one metre. Understory trees (<12 metres), were mainly Balsam Fir, while the main shrubby species were Balsam Fir, White Birch saplings, and Alder, *Alnus* sp. Shrub distribution was patchy, with dense patches occurring in tree-fall gaps, and scattered shrubs in the rest of the study area. The most abundant ground cover species were various mosses, Bunchberry (*Cornus canadensis*), Wild Sarsaparilla (*Aralia nudicaulis*), Ostrich Fern (*Matteuccia struthiopteris*) and several horse-tail species (*Equisetum* spp.).

## Methods

Observations on bird behaviour took place from late May to early August in 1990 and 1991, and birds were observed between 04:00 (dawn) and 21:00 (dusk). Upon locating a focal bird, continuous observations were made using binoculars until the bird was lost from sight (Altman 1974; Martin and Batson 1986). To avoid possible biases, observations that lasted less than five seconds or longer than two minutes were not used in the analysis. Bird species, behaviour, tree species and bird position in the tree were recorded. Bird height was estimated to within three metres. Linear regression analysis (Zar 1996) was used to ensure that estimates accurately reflected clinometer-measured heights (Cumming 1995).

In addition to behavioural observation, unlimited distance point counts (Bibby et al. 1982) were conducted twice during the breeding season (June), in order to estimate relative abundances of the various bird species. The average number of individuals per point count for each bird species was obtained by taking the maximum number recorded for that species and dividing by the number of point counts. Data from the three sites were pooled and used as a relative index of abundance for the study as a whole. For more details on bird species abundances see Cumming and Diamond (2002).

Following the method of MacArthur (1958), conifers were divided into 15 zones; 5 vertical and 3 horizontal, to determine in which part of the tree birds were foraging (Figure 1). Vertical zones divided the tree into

fifths, with zone 1 at the top and zone 5 at the bottom. Horizontal zones corresponded to the outer part of the branch with new growth, fresh needles and small twigs (zone T), the middle layer of older needles and larger branches (zone M), and the inner part of the branch, largely devoid of needles with large diameter branches (zone B). A similar system was used for deciduous trees except they were divided into three vertical zones due to their more globular shape (Figure 2).

Although many birds exhibit male-female foraging differences (Holmes 1986), data for both sexes were pooled since the focus of the study was on interspecific differences in habitat use and because some species in the study were not sexually dimorphic. Bird foraging behaviour (tree zone use), did not differ significantly between the two species of conifer or between the two species of deciduous trees. Therefore, data for each bird species was pooled based on either coniferous or deciduous trees (Cumming 1995).

Vegetation in the study areas was measured using a modified James and Shugart (1970) method. Ten 0.04 ha circles (22 m diameter) were established in each study area, one centered on each of five point count stations and one at 50 metres in a random direction from that point. Within each circle, species, height in meters and diameter at breast height (dbh) in cm for all trees larger than 7 cm dbh were recorded. Percent basal area for each tree species was calculated using dbh values. Basal area more accurately reflected tree availability to birds than numbers of trees, due to heterogeneity in tree size.

To check for possible visibility biases in the various tree species, simultaneous confidence intervals (Chi-squared with Bonferroni confidence intervals) were constructed by pooling the number of seconds of observation for all bird species (Byers et al. 1984). Simultaneous confidence intervals were also used to assess whether birds preferred or avoided certain tree species. Chi-squared test with Yates correction (Zar 1996) were used *post priori* to determine if birds had a preferred foraging zone within trees. Foraging diversity was analyzed using the Shannon Index (Shannon and Weaver 1949). To assess niche overlap between species, the proportion of observations each bird species spent in each of the 15 possible tree zones (9 zones in deciduous trees) was compared between each species pair using Morisita's Index of overlap (see Diamond 1983). With this index, potential niche overlap can vary from 1 (complete overlap) to 0 (no overlap). Foraging height data were analyzed using a 1-way Anova (Proc GLM; SAS Institute 1988), and the results subjected to a Tukey's HSD pair-wise comparison test (with  $P=0.05$ ).

## Results

### *Tree Species Preference*

By basal area, White Spruce, Balsam Fir, Trembling Aspen and White Birch comprised 46%, 30%, 20%, and 4%, respectively, of the available arboreal habitat.

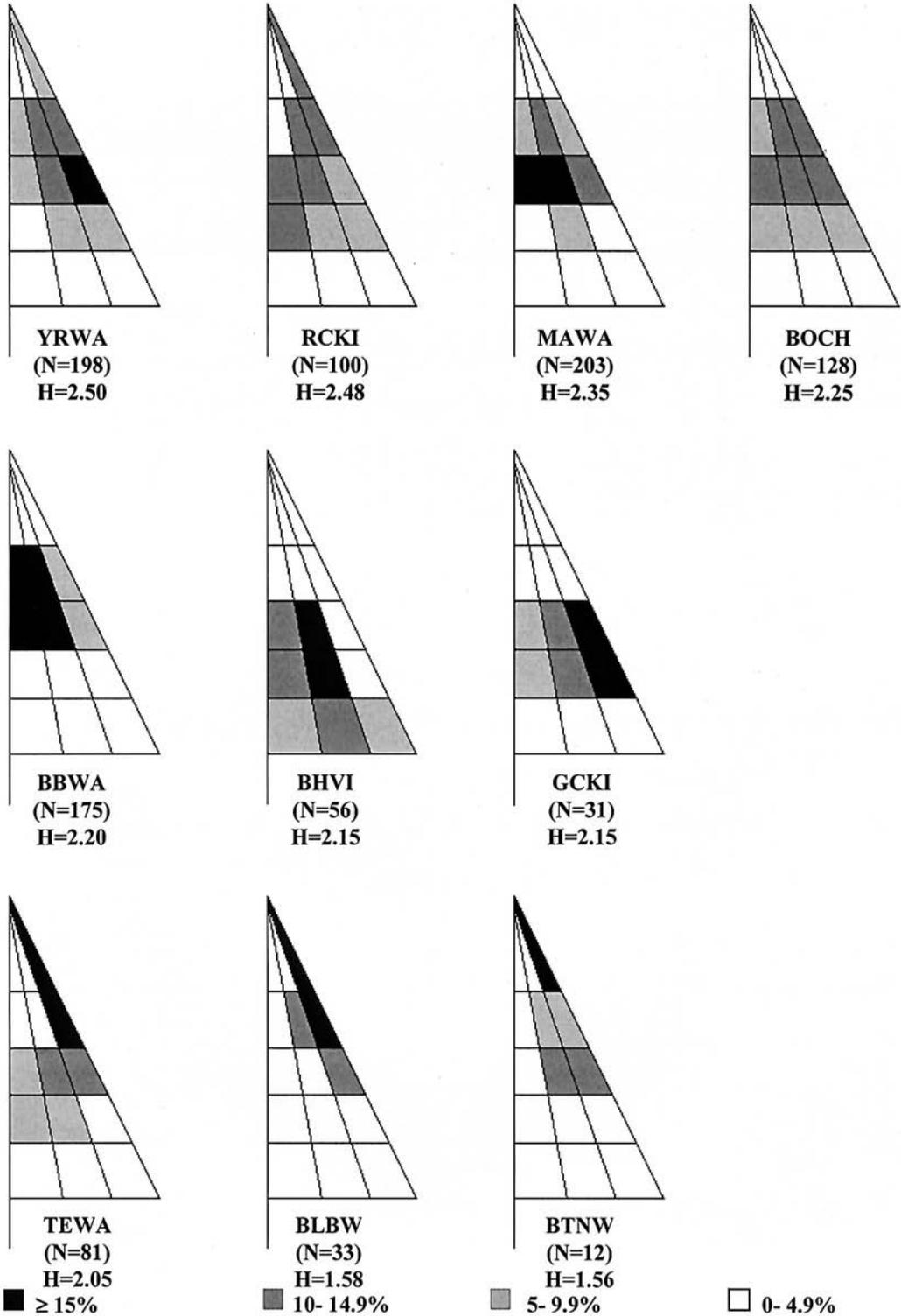


FIGURE 1. Songbird use of zones in coniferous trees. Shadings indicate frequency of observations within a zone (see legend). N= number of observations, H= Shannon diversity index. See Table 4 for species abbreviations.

White Spruce was used more than expected by Yellow-rumped (Myrtle) Warbler, (*Dendroica coronata*), Golden-crowned (*Regulus satrapa*) and Ruby-crowned (*R. calendula*) kinglets and in proportion to its availability by all other species (Table 1). Balsam Fir was used more than expected by Boreal Chickadees (*Poecile hudsonicus*) and Blue-headed Vireos (*Vireo solitarius*) but less than expected by Tennessee Warblers (*Vermivora peregrina*). White Birch was used more than expected by Tennessee and Magnolia (*Dendroica magnolia*) warblers, while Trembling Aspen was used less than expected by Boreal Chickadees, Golden-crowned and Ruby-crowned kinglets, Blue-headed Vireos, Yellow-rumped and Magnolia warblers (Table 1). Bay-breasted Warblers (*Dendroica castanea*) used all tree species in proportion to their availability; however, they did exhibit a tendency to prefer White Spruce and avoid White Birch that was approaching significance. Blackburnian (*D. fusca*) and Black-throated Green (*D. virens*) warblers were not tested due to insufficient sample size (Brennan and Morrison 1990).

#### Point counts

All ten species were found in all three study sites, except Black-throated Green Warbler, which only occurred in one of the three study sites. Average bird abundance per point count from most to least abundant was; Magnolia Warbler (1.2), Yellow-rumped Warbler (0.8), Bay-breasted and Tennessee warblers (0.7), Blackburnian Warbler and Ruby-crowned Kinglet (0.4), Blue-headed Vireo (0.3), Boreal Chickadee and Golden-crowned Kinglet (0.2) and Black-throated Green Warbler (0.1).

#### Foraging Zones

In coniferous trees the most diversely foraging species (in order) were Yellow-rumped Warblers, Ruby-crowned Kinglets, Magnolia Warblers, and Boreal Chickadees (Figure 1). These species were observed in most tree zones and had the highest diversity indices (Shannon and Weaver 1949). The least diversely foraging species were Black-throated Green Warblers, Blackburnian Warblers and Blue-headed Vireos (Figure 1).

In the vertical zones, Ruby-crowned Kinglets, and Tennessee and Yellow-rumped warblers used the bottom of the tree, less than expected, while Boreal Chickadees and Golden-crowned Kinglets used the top and bottom less than expected (Table 2). Blackburnian and Bay-breasted warblers used the bottom two zones less than expected, while Blue-headed Vireos used the top two zones less than expected (Table 2). For the horizontal zones Bay-breasted Warblers and Blue-headed Vireos both used small twigs on the ends of branches (zone T) less than expected, while Tennessee and Blackburnian warblers used small twigs (zone T) more than expected (Table 2). Yellow-rumped Warblers use large inner branches (zone B) less than expected, while Boreal Chickadees, Golden-crowned and Ruby-crowned Kinglets and Magnolia Warblers showed no significant difference in their use of inner and outer branches. Black-throated Green Warblers were not tested due to insufficient sample size (Brennan and Morrison 1990). In deciduous trees, only six of the ten species had a large enough sample size to test foraging zone use (Figure 2). In deciduous trees, Blackburnian Warblers used the top of the trees more than expected. Yellow-rumped, Magnolia and Blackburnian warblers used zone B less than expected, and Tennessee Warblers used zone T more than expected (Table 2).

#### Niche Overlap

In conifers, niche overlap varied from 0% between Blue-headed Vireos and Blackburnian Warblers to 95% between Yellow-rumped Warblers and both Magnolia Warblers and Boreal Chickadees. The four most diversely foraging species, Boreal Chickadees, Ruby-crowned Kinglets, and Yellow-rumped and Magnolia warblers, all overlapped each other by >80%. In deciduous trees, the most foraging overlap was between Yellow-rumped and Blackburnian warblers and between Magnolia and Tennessee warblers; both species pairs overlapped by 88% (Table 3). The least amount of overlap in deciduous trees (40%), was between Black-throated Green and Bay-breasted warblers.

TABLE 1. Bird use of different tree species compared to the tree's availability ( $\chi^2$  test with Bonferroni confidence intervals, DF=3 for all species).

Bird Species	Use		$\chi^2$	P
	> Expected	< Expected		
Boreal Chickadee	Balsam Fir	Trembling Aspen	43.3	***
Golden-crowned Kinglet	White Spruce	Trembling Aspen	10.1	*
Ruby-crowned Kinglet	White Spruce	Trembling Aspen	5.9	*
Blue-headed Vireo	Balsam Fir	Trembling Aspen	6.3	*
Tennessee Warbler	White Birch	Balsam Fir	50.7	***
Magnolia Warbler	White Birch	Trembling Aspen	10.9	*
Yellow-rumped Warbler	White Spruce	Trembling Aspen	21.2	**
Bay-breasted Warbler	–	–	5.0	n.s.

Significance: \* < 0.05, \*\* < 0.01, \*\*\* < 0.001

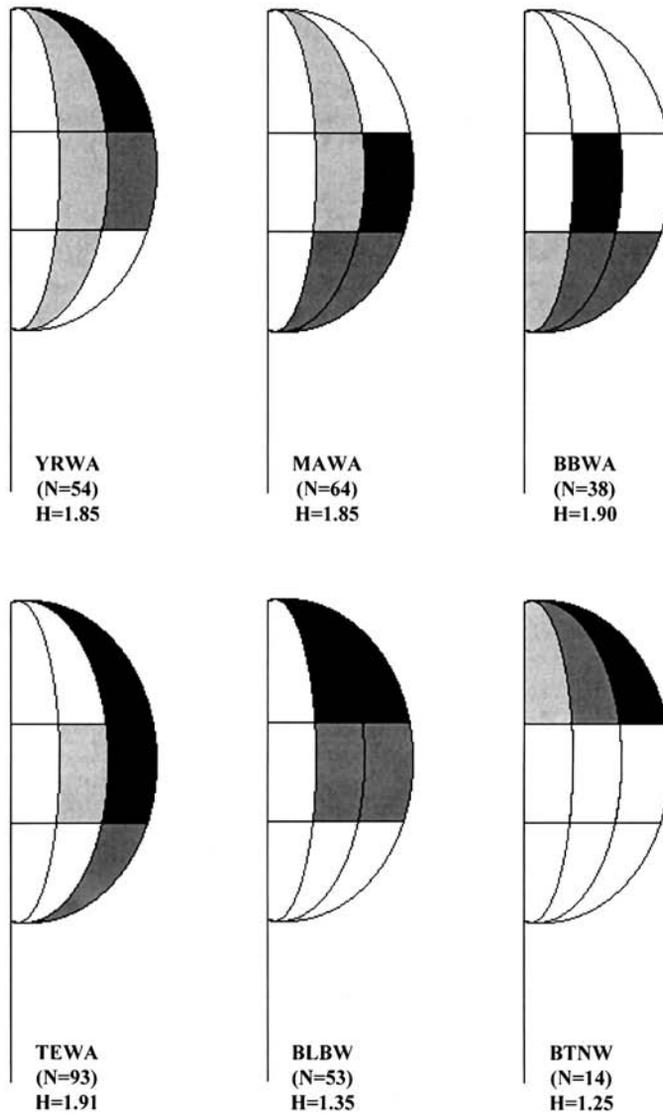


FIGURE 2. Songbird use of zones in deciduous trees. Shadings indicate frequency of observations within a zone (see legend). N= number of observations, H= Shannon diversity index. See Table 4 for species abbreviations.

### Foraging Height

In coniferous trees, the average foraging height of Blackburnian Warblers was significantly higher than all other species except Black-throated Green and Bay-breasted warblers (Table 4). Black-throated Green and Bay-breasted warblers both foraged significantly higher than Magnolia Warblers and Blue-headed Vireos. Foraging heights of all other species were not significantly different (Table 4). In deciduous trees, the

average foraging height of Blackburnian Warblers was significantly higher than that of Blue-headed Vireos and Magnolia Warblers but not significantly different from other species.

### Canopy vs. Subcanopy Use

Blackburnian, Black-throated Green, and Tennessee warblers were seen in canopy level trees (>12 metres) in two-thirds or more of all observations (Table 5). At the other extreme, two-thirds of the observations on

TABLE 2. Bird use of tree zones where zone use was significantly more or less than expected ( $\chi^2$  test with Yates's correction; DF=1 for all species).

Species	Horizontal Zones				Vertical Zones			
	T, M, B	Use	$\chi^2$	P	1 to 5	Use	$\chi^2$	P
<i>In Coniferous Trees</i>								
Boreal Chickadee	n.s.				1, 5	<	20.4	***
Golden-crowned Kinglet	n.s.				1, 5	<	14.5	***
Ruby-crowned Kinglet	n.s.				5	<	16.5	***
Blue-headed Vireo	T	<	20.9	***	1, 2	<	11.1	***
Tennessee Warbler	T	>	14.9	***	5	<	11.2	***
Blackburnian Warbler	T	>	18.5	***	4, 5	<	7.4	**
Magnolia Warbler	n.s.				3	>	13.7	***
Yellow-rumped Warbler	B	<	14.6	***	5	<	10.1	**
Bay-breasted Warbler	T	<	10.5	**	4, 5	<	7.5	**
<i>In Deciduous Trees</i>								
Tennessee Warbler	T	>	30.3	***	n.s.			
Blackburnian Warbler	B	<	24.9	***	1	>	6.6	*
Magnolia Warbler	B	<	15.5	***	n.s.			
Yellow-rumped Warbler	B	<	23.7	***	n.s.			

Significance: \* $<0.05$ , \*\* $<0.01$ , \*\*\* $<0.001$ ; T = outer part of branch with new growth, fresh needles and small twigs; M = middle layer of older needles and larger branches; B = inner part of branch, largely devoid of needles with large diameter branches; 1 to 5: vertical zones, 1 = top, 5 = bottom.

TABLE 3. Average (mean  $\pm$  SD) foraging height (metres) in coniferous and deciduous trees. Species marked with \* foraged significantly higher than other species (1-way Anova with Tukey's HSD test,  $P=0.05$ ).

Bird Species	Coniferous	Deciduous
Boreal Chickadee	6.1 $\pm$ 3.4	9.1 $\pm$ 5.2
Golden-crowned Kinglet	7.0 $\pm$ 2.9	9.2 $\pm$ 3.1
Ruby-crowned Kinglet	7.3 $\pm$ 4.7	9.5 $\pm$ 4.7
Blue-headed Vireo	6.1 $\pm$ 2.0	6.3 $\pm$ 3.8
Tennessee Warbler	8.6 $\pm$ 3.3	9.5 $\pm$ 5.7
Blackburnian Warbler	15.7 $\pm$ 7.8 *	15.7 $\pm$ 3.9*
Magnolia Warbler	5.8 $\pm$ 2.2	6.9 $\pm$ 5.0
Black-throated Green Warbler	12.7 $\pm$ 7.8*	11.4 $\pm$ 3.8
Yellow-rumped Warbler	7.0 $\pm$ 4.2	11.2 $\pm$ 3.8
Bay-breasted Warbler	10.3 $\pm$ 4.8*	11.8 $\pm$ 3.1

**Coniferous:** Blackburnian Warbler foraged significantly higher than all but Black-throated Green Warbler and Bay-breasted Warbler. Black-throated Green Warbler and Bay-breasted Warbler foraged significantly higher than Blue-headed Vireo and Magnolia Warbler.

**Deciduous:** Blackburnian Warbler foraged significantly higher than Blue-headed Vireo and Magnolia Warbler.

Magnolia Warblers and Boreal Chickadees were in subcanopy trees (Table 5). Blue-headed Vireos and Ruby-crowned Kinglets were approximately equal in their use of canopy and subcanopy trees, while Golden-crowned Kinglets and Yellow-rumped and Bay-breasted warblers tended to be observed slightly more often in canopy level trees (Table 5). Yellow-rumped Warblers were observed in canopy level trees significantly more than Magnolia Warblers ( $Z=5.2$ ,  $P<0.001$ ) and Boreal Chickadees ( $Z=3.4$ ,  $P<0.001$ ).

## Discussion

### *Tree Species Preference*

The four main tree species in the study area (White Spruce, Balsam Fir, Trembling Aspen, and White Birch), were not equally abundant, nor equally large (Cumming 1995). If abundance alone had been used as the criteria for tree availability for foraging then Balsam Fir would have appeared to comprise a larger proportion of available habitat than it actually did.

Patches of old, White Spruce-dominated forest are relatively rare in Saskatchewan (Kabzems et al. 1986; Acton et al. 1998); therefore, it was expected that birds which prefer White Spruce would selectively occupy this habitat. The data appear to support this, as all species in the study used White Spruce either in proportion to, or greater than, its abundance. Yellow-rumped Warblers and Golden-crowned and Ruby-crowned kinglets all used White Spruce more than expected. Boreal Chickadees and Blue-headed Vireos used White Spruce in proportion to its abundance and used Balsam Fir more than expected. All five species used Trembling Aspen less than expected (Table 1). This is similar to their behaviour elsewhere, as other researchers have found these five species to be conifer specialists (Keast and Saunders 1991; Ingold and Wallace 1994; Ingold and Galati 1997).

Trembling Aspen was the least favored tree; it was used less than expected by half the bird species in the study. Previous research has suggested differences in insect abundance may exist between aspen and other tree species (Ives and Wong 1988). Holmes and Robinson (1981) suggested structural characteristics of aspen trees and their leaves may impede foraging by insectivorous birds. However, Greenburg (1979) felt that Yellow-rumped and Bay-breasted warblers were phys-

TABLE 4. Foraging overlap between species in coniferous and deciduous trees (Morisita's Index).

Bird species	YRWA	MAWA	BBWA	TEWA	BLBW	BTNW	RCKI	BOCH	GCKI	BHVI	Average % Overlap
In coniferous trees											
YRWA	-	0.95	0.72	0.85	0.50	0.60	0.87	0.95	0.82	0.52	0.75
MAWA		-	0.82	0.71	0.32	0.50	0.84	0.86	0.85	0.61	0.72
BBWA			-	0.50	0.28	0.44	0.72	0.81	0.60	0.47	0.60
TEWA				-	0.78	0.72	0.85	0.91	0.65	0.40	0.71
BLBW					-	0.85	0.52	0.44	0.22	0	0.43
BTNW						-	0.52	0.48	0.40	0.20	0.52
RCKI							-	0.83	0.72	0.50	0.71
BOCH								-	0.63	0.46	0.71
GCKI									-	0.57	0.61
BHVI										-	0.41
In deciduous trees											
YRWA		0.72	0.83	0.86	0.88	0.75					0.81
MAWA		-	0.72	0.88	0.78	0.50					0.72
BBWA			-	0.60	0.66	0.40					0.64
TEWA				-	0.82	0.73					0.78
BLBW					-	0.85					0.80
BTNW						-					0.65

YRWA= Yellow-rumped Warbler; MAWA= Magnolia Warbler, BBWA= Bay-breasted Warbler, TEWA= Tennessee Warbler  
 BLBW= Blackburnian Warbler, BTNW= Black-throated Green Warbler, BHVI= Blue-headed Vireo  
 BOCH= Boreal Chickadee, RCKI= Ruby-crowned Kinglet, GCKI= Golden-crowned Kinglet,

TABLE 5. Bird use of canopy versus subcanopy trees, from most to least canopy using species.

Bird Species	Number of Observations	
	Canopy	Subcanopy
Blackburnian Warbler	62	7
Black-throated Green Warbler	17	5
Tennessee Warbler	80	41
Yellow-rumped Warbler	94	63
Bay-breasted Warbler	73	55
Golden-crowned Kinglet	16	12
Ruby-crowned Kinglet	27	25
Blue-headed Vireo	24	25
Boreal Chickadee	29	50
Magnolia Warbler	60	126

ically adapted to foraging in conifers and both their body size and foraging habits impeded foraging in deciduous trees.

Tennessee and Magnolia warblers both used White Birch more than expected. Morse (1989) felt that many songbirds preferred various *Betula* species for mechanical reasons; they had smaller leaves than other trees (especially *Fagus*, *Acer* and *Populus*) and were easier for gleaning songbirds to reach. Other studies have found various species of birch have higher densities of lepidopteran larvae than other trees (Holmes and Robinson 1981; Holmes and Shultz 1986). An insufficient sample size prevented testing of Black-throated Green Warbler's tree species preference. It is notable, however, that 50% of the foraging observations on this species were in White Birch, even though these trees represented only 4% of the available habitat. Other researchers (Holmes and Robinson 1981; Robichaud and Villard 1999) have also found that Black-throated Green Warblers are partial to birch and use it greater than expected by chance alone.

Tennessee Warblers used Balsam Fir less than expected, while Blackburnian and Black-throated Green warblers were never observed in this tree. Although Blackburnian and Black-throated Green warbler use of this tree could not be tested, the fact that Balsam Fir comprised 30% of the available trees suggests that both birds were avoiding it. Blackburnian and Black-throated Green warblers were consistently observed high in the canopy, so Balsam Fir with an average height of  $11 \pm 5.6$  metres may have been too short to attract these species (Cumming 1995). Branch structure may also have played a role in some birds' avoidance of fir. Differences in branch shape have been attributed to several bird species' preference of Red Spruce (*Picea rubens*) over White Spruce (Morse 1989; Parrish 1995). Balsam Fir branches were less ridged than those of White Spruce (personal observation). Birds which preferentially foraged on thin outer twigs appeared to have more difficulty foraging on the tips of Balsam Fir branches than they did in White

Spruce (personal observation). This was particularly noticeable in Tennessee Warblers because this species focused most of its foraging activities on the outer twigs and new growth in both coniferous and deciduous trees. In contrast, birds which foraged in many tree zones (Yellow-rumped, Magnolia, and Bay-breasted warblers) appeared to be less affected by branch structure and they used Balsam Fir in proportion to its availability.

#### Foraging

Boreal Chickadees were the only permanent residents in the study and one of the few passerines that are resident in the boreal forest (Ficken et al. 1996). It is considered an advantage for birds to be flexible in their foraging habits when they live in an unpredictable environment, like the boreal forest (Hunt and Flaspohler 1998). Boreal Chickadees were diverse foragers, using most tree zones and overlapping more than 80% with Ruby-crowned Kinglets and Yellow-rumped, Magnolia, Bay-breasted and Tennessee warblers. Other studies found Boreal Chickadees had an average foraging height of five metres, and used all parts of the tree branch (Sabo and Holmes 1983; Ficken et al. 1996). Similarly, I found Boreal Chickadees foraged at an average height of six metres and showed no significant difference in their use of inner and outer branches. They did however, use the top and bottom of trees less than expected. Boreal Chickadees may have avoided the tops of trees because this zone was heavily used by several other species. Boreal Chickadees have been shown elsewhere to shift their foraging activity lower in the trees due to competition from Black-capped Chickadees (Vassallo and Rice 1981). Boreal Chickadees also tended to forage in small subcanopy trees more than any other species except Magnolia Warblers.

Ruby and Golden-Crowned kinglets were similar in their behaviour; however, Ruby-Crowned Kinglets were usually higher in the trees and were more diverse foragers. Rabenold (1978) found that where Ruby-crowned Kinglets and Golden-crowned Kinglets occurred together, Ruby-crowned Kinglets were more diverse in their foraging activity and occurred higher in the canopy than Golden-crowned Kinglets. Franzreb (1984) felt this was due to social dominance of Ruby-crowned over Golden-crowned kinglets. No interspecific social interactions were observed in this study; however, Ruby-crowned Kinglets were twice as abundant as Golden-crowned Kinglets and may have influenced the behaviour of the latter through numerical dominance.

Large inner and middle branches were favoured by both Blue-headed Vireos and Bay-breasted Warblers; this was an area of the trees that was seldom used by other species. There was only moderate foraging overlap (47%) between Blue-headed Vireos and Bay-breasted Warblers, as they foraged at significantly different heights. Foraging on large inner and middle

branches is similar to the behaviour these two species have displayed elsewhere (Williams 1996; James 1998).

Both Blackburnian and Black-throated Green warblers foraged high in the trees (significantly higher than most other species), and had larger foraging overlap with each other (85%) than they did with any other species. These warblers appeared to be specialized in a tree-top niche, and have been identified in many studies as feeding, singing, and nesting high in coniferous trees (Morse 1993, 1994). Indeed, Morse (1994) found that Blackburnian Warblers were unlikely to be found in forest without at least some conifers over 18 metres tall. Unlike MacArthur (1958) and Morse (1989), I found no evidence that Black-throated Green Warblers were socially dominant over any other species in the study area. This may have been because Black-throated Green Warblers were the least abundant bird in the study and only occurred in one of three study sites.

Similar to their behaviour elsewhere, Tennessee Warblers were observed at a variety of heights in all tree species, but foraged mainly on the terminal foliage (Rimmer and McFarland 1998). Foraging on the tips of the branches and using many different trees may help Tennessee Warblers (a *Vermivora* warbler) fit into a community (spruce-fir forest) that already has several coexisting species of *Dendroica* warblers (Morse 1989). Tennessee Warblers also used White Birch more than any other species except Magnolia and Black-throated Green warblers. Greenburg (1979) felt that small warblers were better able to forage on deciduous foliage than larger warblers for the physical reasons. Tennessee, Magnolia and Black-throated Green warblers were smaller than most species, except for the two kinglets, and Boreal Chickadees, which were conifer specialists. Therefore, they may have been using a food resource that the larger Yellow-rumped and Bay-breasted warblers would have trouble exploiting.

I found Magnolia Warblers used subcanopy trees more than any other species and had the lowest average foraging height of all species observed. This was similar to Hall (1994), who found Magnolia Warblers used mainly young conifers and were seldom found at any great height. Magnolia Warblers displayed no significant difference in their use of inner, middle and outer parts of branches. This was likely because they most often foraged young trees; there was far less difference in branch structure between inner and outer parts of branches in young trees than there was in large old trees (personal observations).

Yellow-rumped Warbler showed the greatest diversity of foraging habits. They used almost every tree zone in both coniferous and deciduous trees. Yellow-rumped Warblers have been noted elsewhere as being generalists and this flexibility is thought to help them withstand adverse conditions better than their congeners (Rabenold 1978; Hunt and Flaspohler 1998). Unlike their behaviour elsewhere (MacArthur 1958;

Morse 1989), Yellow-rumped Warblers did not use mainly the bottom and inner branches. Yellow-rumped Warblers occurred most often in the middle and outer branches at mid to upper heights in both conifers and deciduous trees, the same zone frequented by Black-throated Green Warblers in other studies (MacArthur 1958; Morse 1989). Morse (1971) and Howe (1979) felt that the presence or absence of Black-throated Green Warblers caused shifts in Yellow-rumped Warbler foraging activity. I observed no social interactions between Yellow-rumped and Black-throated Green warblers, and as Yellow-rumped Warblers were eight times more abundant, there was likely little interspecific competition between these two species. Indeed, Yellow-rumped Warblers experienced the most overlap, and likely the most interspecific competition, from Magnolia Warblers, Boreal Chickadees, and Ruby-crowned Kinglets (Table 4 and Figure 1).

#### *Niche Overlap*

Northern regions, such as the boreal forest, are thought to have such large pulses of seasonally available food that for songbirds food saturation occurs (Rabenold 1983; Wiens 1989). This seasonal pulse of food, combined with a high number of neo-tropical migrants, allows greater niche overlap between songbirds than occurs in other habitats (Rabenold 1978, 1983; Wiens 1989). Rabenold (1978) found that spruce-fir forests in particular had a high number of songbirds which were "...broadly overlapping congeners". Although the present study and Rabenold's were not directly comparable, many of the species were the same between the two studies and results from this study support his theory of generalist stacking. Species with the most generalized foraging behaviour had the highest amount of niche overlap, while those with more specialized foraging behaviour had little niche overlap.

#### *Canopy vs. Subcanopy*

Availability of canopy versus subcanopy trees was not measured; therefore, I could not test whether birds were significantly selecting one over the other. At the two extremes, however, it was apparent that Blackburnian Warblers were using very tall trees almost exclusively, while Magnolia Warblers were using mostly young regenerating trees.

I tested Yellow-rumped Warblers' use of canopy and subcanopy trees against Magnolia Warblers' and Boreal Chickadees' because they had a 95% foraging overlap (in conifers) with both species (83% with Magnolia Warbler in deciduous trees). A Z-test (in results) found Yellow-rumped Warblers used tall (canopy) trees significantly more than the other two species. I felt this was a significant difference between these species, as they used the available habitat in a similar way and they did not forage at significantly different heights. Magnolia and Yellow-rumped warblers were also the two most abundant species in study.

Previous research has shown old-growth boreal mixedwood forest such as those studied here to harbor

unique communities not seen in pre-rotation age forest (Erskine 1977; Kirk et al. 1996; Cumming and Diamond 2002). This diverse songbird community appears to be caused by an interaction between a structurally diverse habitat and a mixture of generalized and specialized foraging behaviours of the bird species involved. Although this study did not examine multiple age classes of forest, it would appear that the community dynamics seen here may be fairly unique due to canopy gap dynamics that tend to be associated with old-growth forest (Hunter 1990). This type and age-class of forest has not received the attention it deserves from either environmental impact studies or long-term management plans for the boreal forest. The scientific community needs to pay greater attention to the contribution old-growth boreal mixedwood forest makes to biodiversity on both a regional and national scale.

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