An Examination of Wood Warblers' Interspecific Interactions in the Forests of Northern Michigan

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Abstract

Resource partitioning between sympatric wood warblers must occur in order for species coexistence. Our study of Blackburnian, Yellow-rumped, and Black-throated Green Warblers investigates niche differentiation between these species, and seeks to compare the warbler partitioning strategies in northern Michigan mixed forests to boreal forests observed in Maine by Robert MacArthur. We tested whether our focal species differ in the percent of time they utilize various tree species and locations in the tree. We collected data at several sites in northern Michigan, with relatively heterogeneous forest communities, by recording the species of tree, position in tree, and amount of time we observed each warbler. Our data showed no difference in percent time in position in tree between warblers but did show that Black-throated Green Warbler utilized tree species differently, as it had a higher percent time in Northern White Cedar than the other species. Our data suggests that the focal warblers differentiate niche by species of tree in northern Michigan mixed forests.

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Introduction

One outcome of competitive exclusion has been a central focus of the ecological sciences. Under this principle, two species cannot coexist indefinitely if they are limited by the same resources. Consequently, coexisting species occupy different niches. This principle began to take form as early as the beginning of the 20th century. In 1904, in a study on the Chestnut-backed Chickadee (*Poecile rufescens*), Joseph Grinnell suggested that the populations of two species with similar food habits will not remain balanced in the same area and that one will crowd out the other (Grinnell, 1904).

Despite this principle, many coexisting species seem to occupy very similar niches, including is the wood warblers of North America; many species of warbler coexist in coniferous and mixed deciduous-coniferous woodlands despite having similar diets and ecological preferences.

In 1958, Robert MacArthur published a study on the minor differences in their behavior and ecology that described how they partition their habitat. MacArthur studied Black-throated Green (*Setophaga virens*), Blackburnian (*S. fusca*), Yellow-rumped (*S. coronata*), Bay-breasted (*S. castanea*) and Cape May Warblers (*S. tigrina*). These five species of warbler have similar general ecological preferences in areas where they overlap - previous studies have revealed only slight differences in niche and considerable interspecific competition (Kendeigh, 1947; Stewart and Aldrich, 1952). MacArthur found that, while the warblers do often feed in the same trees and have similar diets, they tend to forage primarily in different parts of the trees and move in different ways while doing so.

We investigated the resource partitioning of Blackburnian, Black-throated Green, and Yellow-rumped Warblers in northern lower Michigan, and compared our findings to those of

MacArthur to examine the parallels between their relationships in Michigan and Maine, in different habitat types.

We expected to see Blackburnian Warblers to forage largely high in trees, far from the trunk, and mostly in Eastern Hemlocks (Morse, 2004). Yellow-rumped Warblers are have more generalized foraging behavior than most other warblers, so we expected them to forage in more varied parts of trees, but still favoring conifers (Hunt and Flaspohler, 1998). We expected Black-throated Green Warblers would forage mid-level to high in the tree, on outer branches, and to use both deciduous and coniferous trees, as they can be found in a variety of forest types (MacArthur 1958; Collins 1983). Based on the aforementioned expectations, we predicted that the warbler species would selectively forage in different tree species. We also predicted that all would tend toward mid or high levels in trees, with Blackburnian being the most restricted to the upper level of trees, and that Black-throated Green and Blackburnian Warblers would spend a larger percentage of their time on outer branches than Yellow-rumped Warbler.

Therefore, we hypothesized that each species would spend a different proportion of time foraging in different tree species and parts of the tree. Our null hypothesis states that the different species of birds will have equal percent foraging time between tree species and region on the tree.

Methods

We collected data in northern mixed forests in northern Michigan, at Search Bay in Mackinac County, Wilderness State Park in Emmet County, and Grass Bay and the UM Biological Station in Cheboygan County. We typically located birds (Yellow-rumped, Blackburnian, and Black-throated Green Warblers) by their vocalizations. When we were close to the focal warbler, we scanned the trees for movement to find it visually. Once we saw the bird,

we started a timer. We recorded the species of tree the warbler was in and recorded its location in the tree. For location, we split the tree into six sections, based upon height in the tree and distance from the trunk. The sections of the tree were upper/inner (near the top of the tree, close to the trunk), upper/outer (near the top of the tree, far from the trunk near the ends of branches), middle/inner, middle/outer, bottom/inner, and bottom/outer. Any time they changed position, we noted the time they changed position and their new species of tree and position. This was our strategy for the first few sessions of data collection. Subsequently, we located the warblers the same way, but when we sighted them we would record our observations with a tape recorder for future reference. This allowed for one person to record observations without the help of multiple others.

Sample Sizes	
Species:	Sample Size (Number of Individuals):
Blackburnian Warbler (*S. fusca*)	4
Black-throated Green Warbler (*S. virens*)	5
Yellow-rumped Warbler (*S. coronata*)	4

To analyze the data, we conducted a Kruskal-Wallis ANOVA test on the percent of time observed that each warbler spent in each species of tree. The test compared warbler species to determine whether they use different species of trees. We ran the same test, using percent time in each position, to determine whether the warbler species utilize different parts of the tree when foraging. We chose the non-parametric Kruskal-Wallis test because of our small sample size, so our data could not fulfill the assumption of normality of residuals required for the analogous parametric One-Way ANOVA test. A p-value of 0.05 was chosen to denote significance.

Finally, in the case of significant results, we used the Bonferroni test as a post-hoc test to determine which of the warbler species differed from the others. This simple, flexible post-hoc test allows for testing between groups with unequal sample sizes (which was the case with our data).

Parameters Tested		
	Position in Tree:	Species of Tree:
Categories:	Upper/Inner, Upper/Outer, Middle/Inner, Middle/Outer, Bottom/Inner, Bottom/Outer	White Cedar, White Pine, Red Pine, Balsam Fir, White Spruce, Paper Birch, Quaking Aspen, Big-toothed Aspen, Red Oak
Measured As:	% Time, per individual	% Time, per individual
Testing for:	Differences in parts of tree utilized between the 3 Warbler Species	Differences in species of tree utilized between the 3 Warbler Species

Results

Our data for position in tree showed no significant differences between warbler species (all p-values > .05). As such, we fail to reject our null hypothesis that the three focal warbler species do not differ in which parts of trees they utilize (Figure 1).

Kruskal-Wallis Test on Position in Tree, Grouped by Warbler Species

	Upper/Inner	Upper/Outer	Middle/Inner	Middle/Outer	Bottom/Inner	Bottom/Outer
Chi-Square	4.817	.813	.725	1.402	4.875	2.250
df	2	2	2	2	2	2
Asymp. Sig.	.090	.666	.696	.496	.087	.325

Figure 1.

Our data for percent time in each tree species shows that one warbler species was using Northern White Cedar differently than the others (p-value = .033); however, our data showed no significant difference between the warblers for any other species of tree (p-values > .05) (Figure 2). To determine which species of warbler was using Northern White Cedar differently than the others, we ran a Bonferroni Test with White Cedar as the dependent variable.

Kruskal-Wallis Test on Tree Species, Grouped by Warbler Species

	W. Cedar	W. Pine	Red Pine	B.T. Aspen	Q. Aspen	Balsam Fir	Red Oak	Paper Birch	W. Spruce
Chi-Square	6.841	1.600	2.250	4.875	1.375	1.375	1.364	1.600	2.250
df	2	2	2	2	2	2	2	2	2
Asymp. Sig.	.033	.449	.325	.087	.503	.503	.506	.449	.325

Figure 2.

The Bonferroni post-hoc test shows that Black-throated Green Warbler used Northern White Cedar (*Thuja occidentalis*) a significantly larger percent of its time than both Yellow-rumped (p-value = .040) and Blackburnian Warblers (p-value = .006). There was no significant difference between Yellow-rumped and Blackburnian Warblers (Figure 3). The confidence interval for Black-throated Green Warbler percent time minus Yellow-rumped Warbler percent time in Northern White Cedar is (.0246, 1.1054); the same interval for Black-throated Green minus Blackburnian is (.2437, 1.3245) (Figure 3).

Bonferroni Test on White Cedar, Grouped by Warbler Species

(I) species	(J) species	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Blackburnian Warbler	Yellow-rumped Warbler	-.2190968830	.198466901	.886	-.7887112880	.3505175210
	Black-throated Green Warbler	-.7840779040	.188282234	.006	-1.3244615770	-.2436942320
Yellow-rumped Warbler	Blackburnian	.2190968830	.198466901	.886	-.3505175210	.7887112880
	Black-throated Green Warbler	-.5649810210	.188282234	.040	-1.1053646930	-.0245973490
Black-throated Green Warbler	Blackburnian Warbler	.7840779040	.188282234	.006	.2436942320	1.3244615770
	Yellow-rumped Warbler	.5649810210	.188282234	.040	.0245973490	1.1053646930

Figure 3.

Discussion

We saw no significant difference in use of the parts of trees between warbler species. Black-throated Green Warblers utilized tree species differently than the other two warblers. However, there was no significant difference between Blackburnian and Yellow-rumped Warbler.

MacArthur's study illuminated the small differences in ecological preferences which allowed the species he studied to co-occur and is regarded as foundational in understanding the ecology of those warblers. However, it was performed in an area of homogeneous, mature boreal forest. Furthermore, MacArthur's study was performed during a period of relative food abundance, due to a series of spruce budworm (*Choristoneura fumiferana)* outbreaks in the 1940s and 1950s (Webb *et al.*, 1961). Spruce budworm outbreaks may account for more overlap between the species of warblers that were studied, in terms of both niche and geographical range (Stewart and Aldrich, 1952). Because MacArthur's study was performed primarily in one habitat type and during a time of food abundance, the findings may not apply broadly to different regions or outside of periods of relative food abundance.

In comparison, our data was collected in more heterogeneous northern mixed forests. While MacArthur's study sites in Maine had only three species - White Spruce, Balsam Fir, and Black Spruce - our sites had more varied tree communities (MacArthur, 1958). At Search Bay and Wilderness State Park, the primary tree species included White Spruce, Northern White Cedar, Quaking Aspen, Paper Birch, and Balsam Fir. A mixed northern hardwood community was present at the UM Biological Station, with primary tree species including Eastern Hemlock, Big-toothed Aspen, Northern Red Oak, Red Pine, White Pine, and Northern White Cedar, and Sugar Maples. The Grass Bay site contained species from both communities.

These more heterogeneous communities present a broader range of foraging options for the warbler species, allowing them to have more generalized foraging habits. Blackburnian and Black-throated Green Warblers each breed in primarily deciduous forests in the southern regions of their range; while in more northern regions, they inhabit boreal spruce-fir forests (Morse, 2004; MacArthur, 1958). Yellow-rumped Warblers are more restricted to coniferous forests for

breeding but are ecologically generalized (compared to other warblers) and forage in a variety of microhabitats (Hunt and Flaspohler, 1998). Their realized niches in homogeneous forest types are smaller in breadth than their fundamental niche.

The relative heterogeneity of our study sites, compared to MacArthur's sites, may allow warbler species to differentiate ecologically by tree species. Environmental heterogeneity has been shown to interact with species niche breadth (Bar-Massada, 2015). In a more homogeneous forest, with less ability to partition between tree species, the warblers may be forced to reduce niche breadth and forage in different parts of the same tree species.

Furthermore, the relative food abundance due to spruce budworm outbreaks may have allowed more niche overlap and smaller niche breadth of the warblers MacArthur studied; with less concentrated food sources, warblers may need to increase niche breadth and reduce niche overlap (Stewart and Aldrich, 1952).

There are several possible explanations for the lack of significance in our results. Overall, our results were affected by both a small sample size and a short period of time devoted to data collection. However, other factors that may have contributed to our findings were the variable species of trees present in the microhabitats examined and the birds' use of the treetops for song projection.

While the areas explored in our study all represented mixed deciduous-coniferous forests, there was no way to align the forest habitats to have uniform tree species present. Because of the lack of habitat uniformity between sites, there are likely individual variations between birds and their interactions with their environments. Further research must be performed in order to reexamine the notion that inter-habitat characteristics are homogeneous amongst all sites in a region (Barg, 2006).

In addition to lack of uniformity, our results did highlight that each bird species spent most of its time in the tops of the forest canopy (Figure 4). This was likely because each of these bird species have been shown to use the tops of trees to project their vocalizations while foraging (Morse, 1967).

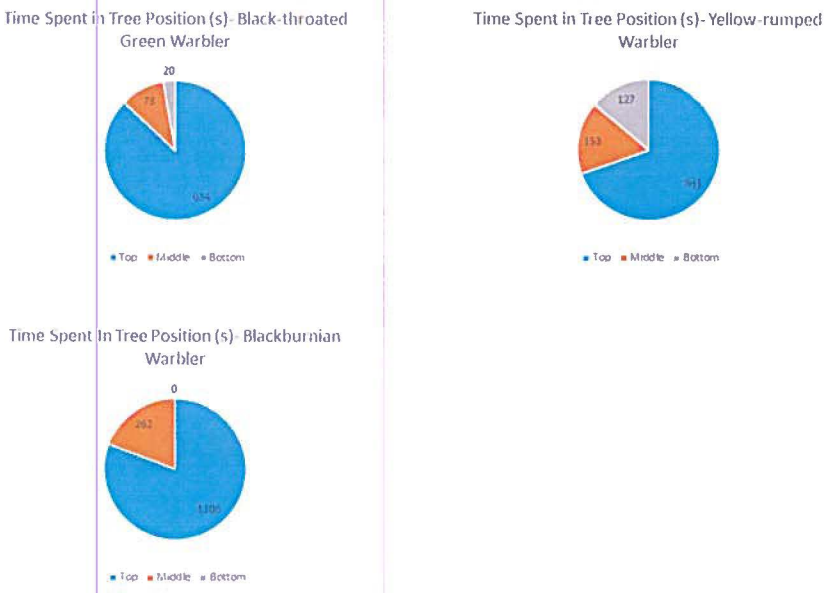

Figure 4 depicts the amount of time in seconds the birds spent in each position on the tree.

Future studies with larger sample sizes comparing warbler niche breadth between different habitats could further investigate whether the three focal warbler species of this study partition resources by tree species, rather than by parts of the same tree species, in northern mixed forests.

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