

**FORAGING NICHES AND RESOURCE PARTITIONING BETWEEN THREE  
CO-OCCURRING SONGBIRDS IN THE SOUTHERN APPALACHIANS**

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## ABSTRACT

KATIE BECRAFT: Foraging Niches and Resource Partitioning Between Three Co-occurring Songbirds in the Southern Appalachians  
(Under the direction of Dr. Allen Hurlbert)

The Black-throated Blue Warbler (*Setophaga caerulescens*), Black-throated Green Warbler (*Setophaga virens*), and Blue-headed Vireo (*Vireo solitarius*) inhabit mixed hardwood and cove forests of the southern Appalachian Mountains. They are similar in that they are small, insectivorous, Neotropical migrants which obtain most of their food primarily from foliage arthropods. In the southern Appalachians, they co-occur frequently, and during the breeding season when energetic demands are high, they could be competing for limited resources. I quantified the foraging niches of these bird species and found that they have different foraging niches and that the presence of each species affects the behavior of the other species for some of the foraging characteristics studied. This suggests that competition is an important factor in determining resource partitioning between these species. These findings have implications for understanding community structure and for informing land management strategies for avian communities in the southern Appalachian Mountains.

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## CHAPTER 1: BACKGROUND

### *Competition and the Niche*

Understanding mechanisms of species coexistence is a key issue in community ecology. Within ecological communities, species interactions such as predation, parasitism, mutualism, and competition have all been invoked as explanations for community structure (Wiens 1989), but the degree to which these interactions contribute to community assembly is highly debated and undoubtedly variable between systems. Perhaps one of the more contentious issues is the role of competition in structuring ecological communities.

For many decades, the conceptual framework of the ecological niche has been important in examining species co-existence and providing a foundation on which to consider competition (Chase & Leibold 2004, Elton 1927, Grinnell 1917, Hutchinson 1957). The idea of the niche was critical in placing a focus on species' differences as important determinants of coexistence. Early studies demonstrated that competition affected where and how organisms could establish and persist (e.g., Connell 1961). Diamond's (1975) study of New Guinea island bird communities argued for the importance of interspecific interactions in community assembly and found co-occurring species to show less distributional overlap than expected at random. Yet another class of evidence for interspecific competition comes from cases of ecological release such as the

broadening of niches seen in Caribbean island bird assemblages in response to the absence of a competitor (Cox & Ricklefs 1977).

While scientists increasingly began to study competition through quantitative and qualitative differences in niche characteristics, various concerns were raised about such approaches. Starting in the 1970s, a large body of literature developed pointing out that much of the evidence for competition which had been presented thus far was circumstantial and that proving the importance of competition as a structuring mechanism was quite difficult (Strong et al. 1979, Weiher et al. 2011, Wiens 1989). Emerging from this period of debate was a better understanding and more rigorous sense of what evidence was necessary and sufficient in order to document competition. As recently summarized by Dhondt (2012), necessary conditions include: resources must be limiting, intraspecific competition must occur, and resource use must overlap. Evidence that would be sufficient for proving the existence of competition includes: use of a resource by one species affects the use by another species, the presence of one species reduces the fitness of another species, and the presence of one species reduces the abundance of another.

By examining meaningful axes of variation which may be related to differences in resource use, one can look for the patterns which suggest that competition is playing a role in determining species' niches. Furthermore, if competition is shaping ecological niches, we might expect two possible scenarios. First, that competition was historically important in driving nonplastic niche differences (that is, differences in average behavior), but it is no longer ongoing. In this scenario, it is difficult to distinguish between the case where niche differences arose in a non-competitive context. (Connell 1980). The second scenario is that competition continues to be an important process

structuring communities, and that species exhibit flexibility in foraging behavior and adapt to the contemporary competitive environment. Plastic niche shifts in response to a potential competitor could provide one type of evidence sufficient for inferring competition.

### *Interspecific Competition in Songbirds*

The coexistence of many seemingly similar songbird species has led to a number of classical studies on competition and resource partitioning in birds (Holmes et al. 1979, MacArthur 1958, Noon 1981). Resource partitioning is thought to be especially important when resources are limiting (Dhondt 2012, Wiens 1989), and there are several key resources for which species might compete. One limiting resource is space. Most songbirds are territorial, especially during the breeding season, and high-quality territories for nesting and feeding chicks are highly desirable. Nesting and roosting sites can also be in limited supply, particularly for secondary cavity nesters which depend on existing cavities for nesting. Although interspecific competition for space and nesting sites has been documented in some cases (Dhondt et al. 1982, Garcia 1983), intraspecific competition for these types of resources is likely more important. While conspecifics avoid overlapping territories, a species is much more likely to have a territory that overlaps with heterospecifics, increasing the chances that they will be foraging in the same area (Sherry 1979). If these species are similar in their use of resources, this could result in interspecific competition for food.

Ways in which songbirds might alter their foraging behavior in response to competition include foraging at different heights within the environment, searching different substrates, using different prey attacking maneuvers, different sections within a tree, or different tree species. Some species can adjust foraging behavior in accordance with environmental changes which occur regularly or sporadically, such as insect outbreaks (Airola & Barrett 1985, Morris et al. 1958, Morrison et al. 1987). Additionally, Morse (1971) found evidence that species of warblers on islands in the northeastern United States demonstrated differing degrees of plasticity in their foraging niches. The role that competition plays in shaping foraging niche differences between most similar groups of songbirds remains unknown.

### *Study Species and Habitat*

The Black-throated Blue Warbler (*Setophaga caerulescens*), Black-throated Green Warbler (*Setophaga virens*), and Blue-headed Vireo (*Vireo solitaries*) inhabit mixed hardwood and cove forests of the southern Appalachian Mountains. They are similar in that they are small, insectivorous, Neotropical migrants which obtain most of their food primarily from foliage-dwelling arthropods. Along Breeding Bird Survey (BBS; Bystrak 1981) routes in the southern Appalachians, co-occurrence of these species is high, which suggests that they cue in to similar landscape level variables. Their similar habitat and dietary preferences make them good candidates for potential competitors.

All three of these species have a range limit which roughly extends from the southern Appalachians up into the northeastern United States and into southern Canada.

The behavior of each of these three species has been examined to some extent in the northern part of their ranges, but not as much is known about populations in the south (Holmes et al. 1979, Holmes & Robinson 1981, MacArthur 1958, but see Rabenhold 1978), where these species are presented with a more diverse array of tree species when foraging. Compared to their northern counterparts, southern populations of these birds experience longer breeding seasons and less dramatic peak of food availability and may be more resource-limited during the breeding season than northern communities (Rabenhold 1978). On the other hand, southern bird communities are less diverse than northern communities, which may be related to the seasonal overabundance of food in the north (Rabenhold 1978). Because of this, birds in southern populations experience a different community structure wherein each bird species may be more specialized in foraging behavior.

#### Black-throated Blue Warbler

The Black-throated blue warbler (BW from here on) typically weighs 10 grams and is 10.8 cm in length. Males are blue with a black throat, white underside, and distinctive white wing patch, and females are gray with a white underside, wing patch, and eyebrow. They occur in large tracts of unfragmented forest and appear to select habitat with a dense understory of shrubs for nesting (Holmes et al. 2005, Steele 1993). Density of breeding BWs appears to be correlated with shrub density (Steele 1992). Males defend territories of 1-4 ha (Steele 1992) and adult BWs usually show high site fidelity, returning each spring to an area within 100 m of territories occupied in previous years (Holmes & Sherry 1992). Pairs are typically monogamous (Holmes et al. 1992).

Studies of BWs in New Hampshire have found that females laid an average of 4 eggs per clutch and often attempted a second brood (Holmes et al. 1992). BWs are insectivorous and Lepidoptera larvae, Coleoptera, Homoptera, Hymenoptera, Diptera, and Arachnida are reported prey items during the breeding season (Robinson & Holmes 1982). Long-term studies at Hubbard Brook in New Hampshire have demonstrated effects of intraspecific competition for this species but interspecific competition has not been examined. Densely populated areas have lower fecundity, and habitat heterogeneity also results in subordinate individuals being forced into lower quality habitat (Rodenhouse et al. 2003). The BW forages primarily in the understory and moves rapidly, gleaning prey from the surfaces of leaves and branches nearby (Robinson & Holmes 1982).

#### Black-throated Green Warbler

The Black-throated Green Warbler (GW from here on) is approximately 12 cm long and 9 grams. Males have a distinctive black bib and yellow face, with a gray body, olive back, white underparts streaked with black, and two white wingbars. Females are similar but duller, with a less distinctive black bib. There is a coastal plain race, *Setophaga virens waynei*, which is restricted to the coast from Virginia to South Carolina. They occupy mixed deciduous to coniferous forest, and preference for hardwoods or conifers may be intrinsic and differ between populations (Parrish 1995). Males defend small territories of 0.25-1 ha, and previous studies in Maine have not found evidence that density of congenics affects territory size (Morse 1976). Multiple broods have not been reported for this species (Morse & Poole 2005). Lepidoptera larvae, Homoptera, and Coleoptera, and Diptera are reported prey items, and they move rapidly when foraging,

searching nearby substrates (Robinson & Holmes 1982). Previous studies have found that the GW is a socially dominant species in some situations (Morse 1971, Morse 1974), and in Maine it partitioned resources with four other warbler species along spatial dimensions (MacArthur 1958).

### Blue-headed Vireo

The Blue-headed Vireo (BV from here on) is larger than the two warblers, weighing on average 16 grams and is 12.7 cm in length. It has a grayish-blue head, olive body with white underparts, yellow wing bars, and a bold white eye ring. Males and females have very similar plumage and size. Two subspecies, *Vireo solitarius solitarius* and *Vireo solitarius alticola* are recognized, with the latter inhabiting the southern Appalachians north to Maryland and wintering in the southeastern United States. Males defend territories of 1.5-6.5 ha and pairs are highly monogamous (Morton et al. 1998). Nests are built in tall shrubs to mid-canopy trees, and females lay 3-5 eggs. Although they use a variety of trees, they are often associated with conifers, especially when foraging (Kendeigh & Fawver 1981, Tingley et al. 2002). They feed on Lepidoptera, Coleoptera, and Arachnida, and (Robinson & Holmes 1982). They forage slowly and are likely to attack prey from a greater distance than the warblers (Robinson & Holmes 1982). This searching behavior also allows them to capture larger, more cryptic prey items such as adult Lepidoptera, and they also search large branches and trunks in addition to foliage (Robinson & Holmes 1982).

An examination of the foraging niches of these three foliage gleaning species in the southern Appalachians has the potential to shed insight into their foraging behavior in

this understudied region, and to provide a better understanding of the importance of interspecific interactions in resource partitioning.



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## **CHAPTER 2: FORAGING NICHES AND RESOURCE PARTITIONING BETWEEN THREE CO-OCCURRING SONGBIRDS IN THE SOUTHERN APPALACHIANS**

### **Abstract**

The Black-throated Blue Warbler (*Setophaga caerulescens*), Black-throated Green Warbler (*Setophaga virens*), and Blue-headed Vireo (*Vireo solitarius*) inhabit mixed hardwood and cove forests of the southern Appalachian Mountains. This trio presents an interesting situation for understanding resource partitioning and interspecific competition. They are similar in that they are small, insectivorous, Neotropical migrants which obtain most of their food primarily from foliage arthropods. In the southern Appalachians, they co-occur frequently, and during the breeding season when energetic demands are high, they could be competing for limited resources. I quantified the foraging niches and examined tree species preferences of these three bird species in order to determine how they make use of similar food sources in the same habitat and whether they affect each other's foraging behavior. I found that the three species have different foraging niches and that the presence of each species affects the behavior of the other species for some of the foraging characteristics studied. This suggests that competition is an important factor in determining resource partitioning between these species. These findings have implications for understanding avian community structure in the southern Appalachian Mountains.

## **Introduction**

The identity and persistence of individual species within a community are affected by the manner in which limited resources are partitioned within that community. Among resources that may be limiting, food is an important factor which strongly affects a species' growth, reproduction, and survival. In songbirds, studies of resource partitioning have received attention due to the apparent paradox that many seemingly similar species are able to coexist (MacArthur 1958, Holmes et al. 1979, Noon 1981). These studies and others have identified a number of foraging and habitat-related niche axes along which species differ in a manner consistent with resource partitioning (Holmes 1979, Sabo & Holmes 1983, Sodhi & Paszkowski 1995). To the extent that species exhibit niche differences, such differences can arise from different circumstances. If competition was historically intense among species, then niches may have diverged through time in such a way as to reduce overlapping resource use. However, distinct niches could also have resulted from evolutionary trajectories that were unaffected by competition, and differentiating between these two processes may be quite difficult (Connell 1980). Alternatively, species may exhibit plastic niche shifts in response to the competitive environment. For example, birds exhibit greater habitat breadth on species poor islands than species rich islands with other similar species (Brown & Wilson 1956, Cox & Ricklefs 1977, Lack 1947). Similarly, songbird species have been found to shift foraging and behavioral niches as well in response to the presence of potential competitors (Alatalo et al. 1986, Morse 1967, Morse 1971). Thus, key to understanding resource partitioning is the simultaneous examination of both mean niche differences

between species in a community as well as niche shifts which may occur between similar species in each other's presence.

In the Southern Appalachian Mountains, three songbirds frequently co-occur in mixed hardwood forests. The Black-throated Blue Warbler (*Setophaga caerulescens*; BW hereafter), Black-throated Green Warbler (*Setophaga virens*; GW), and Blue-headed Vireo (*Vireo solitarius*; BV) are among the most spatially correlated in abundance and co-occurrence ( $0.35 < r < 0.50$ , unpublished analyses of North American Breeding Bird Survey data) of any set of songbird species in this region. Previous studies have found that foliage arthropods comprise the majority of each species' diet during the breeding season (Robinson & Holmes 1982). Given their co-occurrence and similar diet, an obvious question is whether these species are partitioning resources in some way. While some work has been done characterizing the foraging behavior of these species at the Hubbard Brook Experimental Forest in New Hampshire (Holmes 1979, Holmes & Robinson 1981, Robinson & Holmes 1982), little is known from the Southern Appalachian region, where forest structure and composition are considerably more diverse. Lastly, what work has been done has examined the foraging niches of these species as non-plastic behaviors and failed to appreciate that competition could lead to niche shifts under certain contexts.

My goal in this study is two-fold. First, I address whether the foraging niches of the Black-throated Blue Warbler, Black-throated Green Warbler, and Blue-headed Vireo in the Southern Appalachians are distinguishable from each other. In line with previous studies, I consider foraging height, horizontal position within the tree, foraging substrate, prey attacking maneuver, and tree species as the primary axes of the foraging niche

(Airola & Barrett 1985, Holmes et al. 1979, Sodhi & Paszkowski 1995). My second focus is to examine whether the foraging niches of these species shift with competitive context. To examine niche shifts, I compared each species' behavior in areas with and without the other two species, with the expectation of observing one of three possible scenarios: 1) no niche shifts occur, suggesting that competition is unimportant and/or foraging behavior is nonplastic, 2) species exhibit niche shifts, but those shifts are convergent such that species' foraging niches are more similar in each other's presence, suggesting that they are cueing in on similar environmental variables, or 3) species exhibit divergent niche shifts, such that foraging niches are more different from each other in each other's presence, which is consistent with the effects of competition.

## Methods

### *Study area*

The study was conducted at 20 sites located throughout the southern Appalachian Mountains extending from northern Georgia to central Virginia, USA (Figure 1) and ranging from 304 to 1280 m in elevation. Sites were centered on selected point counts from existing North American Breeding Bird Survey (BBS; Bystrak 1981) routes. National Landcover Data (Jennings 2000) was used to select BBS sites which contained >20% dry-mesic oak or cove forest within 400m of the BBS site location. Within sites, forest composition varied with topography. Along sheltered and north-facing slopes, dominant species included *Rhododendron* sp. (primarily *R. maximum*), *Tsuga canadensis*,



*Liriodendron tulipifera*, and *Betula lenta*. Dry-mesic areas contained mixed *Quercus sp.* (primarily *Q. rubra*, *Q. montana*, and *Q. alba*), *Carya sp.*, *Tsuga canadensis*, *Hamamelis virginiana*, and patches of *Rhododendron sp.*. Areas of nutrient-rich soils contain *Halesia carolina*, *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Tilia Americana*. The most xeric areas are characterized by *Quercus sp.* (*Q. rubra*, *Q. montana*, and *Q. alba*), *Pinus strobus*, and *Kalmia latifolia*. A complete description of study sites is provided in Appendix 1.

#### *Avian point counts*

Study sites were visited 3-5 times between mid-May and the first week of July during 2011 and 2012. Point count stations were established at least 250 m apart at 3 and 5 locations in 2011 and 2012, respectively (Figure 1). Counts were conducted at these stations during each visit to the site within 5 hours of sunrise. Each point count was performed by a single observer and all avian species detected were recorded for 10 consecutive minutes. Point count data was used to calculate presence/absence, occupancy, and mean number of detections for each of the focal species at each point count station for the season. For a description of the number of point count stations with each species combination, see Table 2.

#### *Foraging data*

At each site, a single observer searched the area methodically for actively foraging birds. Occasionally two observers would search the same site but would remain in separate areas so as not to observe the same individuals. All observations were

recorded before 13:00, and most observations were recorded within 5 hours after sunrise. Once a foraging individual was detected, foraging behavior was recorded continuously using a handheld voice recorder until the bird was lost, which was usually less than one minute and no more than 15 minutes. Because birds were not banded, individuals could not be positively identified, so it is likely that some individuals were observed more than once throughout the season. Sample sizes for each species and a conservative estimate of unique individuals observed are provided in Table 1. Foraging data were collected following procedures used by similar studies of insectivorous songbirds (Holmes et al. 1979, Robinson & Holmes 1982). The observer recorded the location, species, and sex (when possible), as well as characteristics used to define the foraging niche. This included foraging height, tree or shrub species being used, horizontal position within tree (inner 1/3, middle 1/3, or outer 1/3), substrate (leaf, twig, branch, or trunk), and prey attacking maneuvers. Maneuvers which involved a reaching movement to capture prey without flight were defined as a glean, and movements which required the use of flight or hovering to capture prey off a substrate were defined as a hover (Holmes et al. 1979). Maneuvers directed at aerial prey were rare and accounted for <1% of all observations, so they were ignored in subsequent analyses described here.

Data were transcribed from the digital recordings into a database, and each foraging maneuver (glean, hover) was treated as an individual unit. I will refer here to each unit, or foraging maneuver, as a “movement” and the collection of one or more movements by a single individual as an “observation.” Some individuals were only observed long enough to perform one foraging movement, while others were seen doing many consecutive movements. Because of issues of non-independence with these

sequences of movements, I have accounted for differences between individuals in the overall foraging niche models as well as differences between study sites using a hierarchical approach (see below).

### *Foraging Niche Models*

The goal of the foraging niche models was to determine if the foraging height or category count distributions (for categorical variables) on any of the foraging niche axes differed by species. First, I examined whether the three species used horizontal sections of trees (inner third, middle third, outer third) differently. This mixed effects model was constructed as follows:

Let  $Y_{jk}$  denote the horizontal section that bird  $j$  was observed to occupy during the  $k^{\text{th}}$  observation of that bird:

$$Y_{jk} = \begin{cases} 2, & \text{if "outer third"} \\ 1, & \text{if "middle third"} \\ 0, & \text{if "inner third"} \end{cases}$$

The predictor of interest is the bird species, BV, BW, or GW. Let  $x_1$  and  $x_2$  be binary indicator variables denoting whether the species being observed is BW or GW, respectively:

$$x_{1j} = \begin{cases} 1, & \text{if bird } j \text{ is BW} \\ 0, & \text{otherwise} \end{cases}, x_{2j} = \begin{cases} 1, & \text{if bird } j \text{ is GW} \\ 0, & \text{otherwise} \end{cases}$$

The assignment  $x_{1j} = x_{2j} = 0$  corresponds to the BV.

The regression model for horizontal position then, can be written as follows:

$$\log \frac{P(Y_{ijk} = 1)}{P(Y_{ijk} = 0)} = \beta_{01} + \beta_{11}x_{1ij} + \beta_{21}x_{2ij} + u_{1j} + v_{1i}$$

$$\log \frac{P(Y_{ijk} = 2)}{P(Y_{ijk} = 0)} = \beta_{02} + \beta_{12}x_{1ij} + \beta_{22}x_{2ij} + u_{2j} + v_{2i}$$

The parameters in this regression model act like ordinary regression parameters except the interpretation is on a log odds scale. The intercepts  $\beta_{01}$  and  $\beta_{02}$  are the two log odds (logit) of position for the reference species (BV here). The coefficients of the two dummy variables represent deviations from these log odds for the other two species. For instance  $\beta_{11}$  represents how much the BW differs from the BV in the first logit. Here  $u_{1j}$  represents all the first logit characteristics shared by the observations made on individual bird  $j$ . Similarly  $u_{2j}$  represents all the second logit characteristics shared by the observations made on individual bird  $j$ . In a similar fashion  $v_{1i}$  and  $v_{2i}$  represent the first and second logit characteristics, respectively, shared by birds observed at the same location  $i$ . Solving for the individual probabilities and using the fact that the three probabilities must sum to 1, one is able to obtain probability estimates for the categories of horizontal section (inner, middle, and outer third).

In addition to the categorical horizontal position variable described above, mixed effects logistic regression models were constructed in a similar fashion for the other categorical variables: substrate (leaf, twig, branch, or trunk), maneuver (glean or hover), and surface side (upper or lower). A multinomial distribution was assumed for substrate and a binomial distribution was assumed for maneuver and surface side.

A mixed effects multinomial logistic regression model is not easily fit with currently available frequentist software, but estimates can be obtained using Bayesian methods. The Bayesian approach is extremely flexible and readily permits the inclusion of random effects to account for heterogeneity across sites and individuals. Bayesian models are particularly well-suited for modeling complex ecological data (Clark 2007).

To obtain Bayesian estimates that approximate frequentist estimates, I used diffuse, non-informative priors in all the models so that the posterior distributions are primarily data-driven and only minimally affected by prior information. Normal priors with a mean of zero and a low precision (large variance) were used for all regression coefficients. Selecting a non-informative prior for the random effects covariance matrix is complicated by the fact that the prior distribution for the entries of the matrix needs to be a joint distribution to guarantee that a valid covariance matrix is obtained. Following the guidelines outlined in Gelman and Hill (2007) and Peterson (2007) I used a scaled inverse Wishart distribution with degrees of freedom set to its minimum allowable value.

Bayesian estimation was carried out using Markov chain Monte Carlo as implemented in WinBUGS 1.4.3 (Lunn 2000). All other calculations were carried out with R 2.15.1 (R Core Development Team 2012). The *arm* package (Gelman et al. 2012) was used to call WinBUGS from R. The BUGS code for the basic multinomial model (without random effects) was adapted from Ntzoufras (2009).

Three Markov chains were run simultaneously for each model in order to assess convergence. A 20,000 iteration burn-in period plus 70,000 additional iterations proved to be adequate for each model. Graphical examination of the individual chains revealed that all three chains had converged to the same posterior distribution for each parameter.

Graphically the chains exhibited good mixing, the  $\hat{R}$ (mixing index) diagnostics were all less than 1.1, and the effective sample sizes for the posterior distributions of the individual parameters were all large.

Using the returned samples of the posterior distributions of the individual parameters, the median and 95% credibility and/or highest probability density intervals were obtained. Posterior distributions were also obtained for the probabilities of the use of horizontal sections, substrate, side, and maneuver by each species, using the equations described previously.

Foraging height was analyzed using a linear mixed-effects model with the nlme package in R (Pinheiro et al. 2009), with bird species as a fixed effect and site and individual as random effects.

### *Tree Species Preferences*

Data on vegetation composition was collected during 2012. At each site, six 400 square meter vegetation plots were laid out as in Figure 1. Relative cover estimates for all tree and shrub species within each plot were recorded as dominant (>50%), moderate (20-50%), sparse (5-20%) or trace (<5%) within each strata of the forest (shrub, tall shrub, subcanopy, canopy). These cover estimates were converted to numerical values based on category midpoints and were calculated by summing over the strata for each plant species at each site to estimate total cover of each species.

For each site, I also calculated the proportion that each bird was observed foraging in each tree species. Because some birds were seen in more than one tree during an observation, I counted each unique tree used in an observation for this analysis. For

example, an individual bird with three foraging movements in tree species 1 and one foraging movement in tree species 2 would have a single count for each tree species in this analysis. Unique tree counts were used because consecutive movements of a bird are not independent and birds were often observed performing several maneuvers within the same tree. Further, this method eliminates observer bias resulting from differences in the ability to detect birds between tree species. If foraging randomly, birds would be expected to use each tree species according to its availability in the environment (Holmes & Robinson 1981, Gabbe et al. 2002). To obtain a preference index (PI) for each tree species and each bird, I calculated a weighted mean of the difference between observed and expected use. This mean was weighted by the number of observations from each site, due to the fact that sites differed in vegetation composition and the number of observations was not equal across sites. A negative PI indicates that a bird species was observed foraging in a particular tree species less frequently than expected, while a positive PI indicates the tree species was used more frequently than expected. A PI of 0 means that a tree species is being used in accordance with its availability in the environment. Chi-square tests were used to assess the degree to which observed use differed from expected use. Many tree species were uncommon in this environment and had expected counts  $<5$ , so chi-square tests were also done excluding these uncommon species.

#### *Assessing Possible Effects of Competitors*

To assess the effect of one species on the foraging behavior of another, I compared foraging behavior of the focal species between sites differing in the presence,

abundance, or occupancy of the two potential competitors. Occupancy was calculated based on the percentage of surveys in which each species was detected at a point count station over the 3-5 visits per season. These different approaches were used in models of foraging height which was the most flexible model to deal with and interpret. Based on AIC values, model interpretability, and with the goal to compare behavior between sites with and without competitors, presence/absence was used as the predictor, and all further discussion will be based on presence/absence. Foraging data was associated only with the point count data during the year it was collected, to ensure that presence/absence data reflects the distribution of birds during the current year.

Each foraging observation was assigned to the nearest point count station (typically within 70m), and presence/absence data established by point counts was used to determine if a bird was co-occurring with a competitor or not. The rarity of certain species combinations leads to a sparse data matrix, and so a different approach was used for this set of analyses to account for quasi-separation in the data. For example, when the GW was absent, the BV was always observed foraging on the upper side of the branch. On the other hand, when the GW was present foraging on both upper and undersides was observed. The absence of GW is a perfect predictor of “Side,” but many models fail to detect this. I used the Firth method (Firth 1993, Heinze & Schemper 2002) in the *logistf* package in R (Ploner et al. 2010) to account for the separation in these analyses. Firth regression is identical to Bayesian logistic regression with a non-informative Jeffreys prior (Fijorek & Sokolowski 2012). Model structure and in some cases small sample sizes did not allow the incorporation of random effects of sites and individuals. Counts of each categorical foraging behavior (horizontal tree section, substrate, surface side, and



maneuver) were used as the response, with presence/absence of a potential competitor as a predictor. Models for each species were run separately. Competition models for foraging height were treated differently because height is a continuous rather than categorical response. These models were similar to the foraging niche models for height, except that each species was run separately and the presence of a competitor was used as the predictor. Random effects for site and individual were included in these models.

## **Results**

### *Foraging Niches*

Foraging height was an important factor differentiating these species (mixed effect model, species as a predictor of foraging height,  $p < 0.001$ ). Although each species used a wide range of heights, each focused its foraging activity within a specific range. BWs foraged at a mean height of 8.6 m, BVs occupied the midstory and subcanopy at a mean height of 10.9 m, and BGs preferred the highest foraging heights of all three species, at a mean height of 14.9 m (Figure 2; Appendix 2). Differences also exist in the position used most often within trees between these species. Most striking is the GW's heavy use of the outer third of trees, foraging in the tips of branches two-thirds of the time (Figure 2; Appendix 2). The B W uses the outer and middle areas of trees in nearly equal proportions, and the BV follows similar tendencies, although it forages in the

middle section more so than the BW (Figure 2; Appendix 2). All three species forage least often in the inner 1/3 of trees (Figure 2; Appendix 2).

Substrate use by these species differed most noticeably between the BV's use of branches and trunks (51% of foraging) and the warblers' preference for foliage (62% and 66% for the BW and GW, respectively; Figure 2). Similarly, both warblers used a gleaning maneuver to capture prey most often (66% and 70%; Figure 2), whereas the BV gleaned and hovered in nearly equal proportions. The GW is distinguished from the others in its tendency to capture prey on the upper side of surfaces (64% of foraging; Figure 2; Appendix 2).

### *Tree Species Preferences*

These three bird species all used tree species in a nonrandom fashion ( $p \leq 0.005$  for each species; Figure 3). The BV showed strong preferences for *Tsuga canadensis* and *Pinus strobus*, and moderate preferences for *Liriodendron tulipifera*, *Acer saccharum*, and *Quercus montana*. The BV avoided *Rhododendron sp.*, *Fagus grandifolia*, *Magnolia sp.*, *Kalmia latifolia*, and *Acer pensylvanicum*. The BW exhibited the strongest preference for *Tsuga canadensis*, with a slight preference for *Pinus strobus*, while it appeared to avoid *Acer rubrum*, *Fagus grandifolia*, *Quercus rubra*, and *Acer saccharum*. The GW foraged preferentially in *Liriodendron tulipifera*, *Pinus strobus*, and *Quercus montana*, while *Rhododendron sp.*, *Fagus grandifolia*, and *Kalmia latifolia* were among the most avoided species. All three birds showed preferences for *Pinus strobus*, the BV and BW both strongly preferred *Tsuga canadensis*, and the BV and GW both preferred *Liriodendron*

*tulipifera*. All three species avoided *Rhododendron sp.*, *Fagus grandifolia*, and *Kalmia latifolia*.

### *Effect of Competitors*

Each of the three focal species shifted its foraging niche along at least one dimension in response to the presence of a competitor (Figure 4). The BV foraged less in the inner sections of trees when the BW was present (20% vs. 32% of foraging;  $p = 0.05$ ; Figure 4, Appendix 3). When the GW was present, the BV used foliage substrates, under surfaces of leaves, and hovering more often ( $p = 0.01, 0.02, 0.01$ , respectively; Figure 4, Appendix 3). The BW used middle sections more (38% vs. 30%;  $p = 0.05$ ; Figure 4, Appendix 3) when the BV was present, and hovered more when the GW was present ( $p = 0.03$ ; Figure 4, Appendix 3). The GW used outer sections less (72% vs. 55%;  $p = 0.01$ ; Figure 4, Appendix 3) when the BV was present, but used outer sections more and inner and middle sections less when the BW was present ( $p = 0.06, 0.08, 0.02$ , respectively; Figure 4, Appendix 3). Foraging height did not vary in response to the presence of competitors for any focal species ( $p > 0.10$  for all comparisons).

## **Discussion**

### *Foraging Niches*

I studied the foraging behavior of three foliage gleaning birds that frequently occur together in the Southern Appalachians. I found evidence that their foraging niches

are distinguishable in the characteristics examined, and that these niches exhibit some plasticity in response to the presence of the other species. These findings imply that these species may have evolved different foraging niches in order to partition resources, and that the observed niche shifts are a response to current, ongoing competition.

Overall, differences in foraging niche characteristics suggest that these three species are partitioning niche space along certain axes more than others. Similar to MacArthur's (1958) findings, spatial characteristics of the niche such as foraging height and horizontal position are important in partitioning resources between these species. However, use of substrates and maneuvers also differed between species, indicating that behavioral foraging niche characteristics are also important in partitioning resources, as others have pointed out (Morse 1971, Holmes et al. 1979). One aspect of the foraging niches of these species which is reflected in some of their differences is their body size and relatedness. The two warblers are smaller and congeneric (*Setophaga*), whereas the BV is larger and in a different genus (*Vireo*). The two warblers are similar in substrate use and maneuvers and being smaller are more likely to forage in small twigs and leaf petioles, while the BV is more likely to use sturdier branches and limbs. BVs are also known to take larger prey items, especially moths, beetles, and other cryptic prey on branches and trunks, although caterpillars are an important food source for all of these birds (Robinson & Holmes 1982). Despite size differences and relatedness, the BW and BV are similar in use of horizontal sections and in capturing prey on the under sides of surfaces. The BW stands apart from the other two species primarily in its use of lower foraging heights, although the BV and GW differ from each other in this regard as well.

Comparisons of foraging behavior observed in the southern Appalachians to previously studied northern populations in Hubbard Brook reveal which niche differences are geographically conserved and which are more variable. For example, foraging height appears to be strongly conserved between north and south, with the BW foraging at the lowest heights, the GW at the highest, and the GW at intermediate heights in both regions (Table 3). Also, the BV consistently used bark substrates more often and foliage less compared to the two warbler species, and the GW was the species that foraged most frequently by gleaning in both regions (Table 3). Differences between northern and southern populations included the relative use of foliage and bark substrates by GWs and BWs, and in the relative frequency of gleaning between BWs and BVs (Table 3). Some differences between regions were exhibited by all three species, such as an increased foraging height and greater use of bark substrates in the southern Appalachians (Table 3). Likely some of these differences can be attributed to differences in habitat composition and structure between the northern and southern forests. For example, the presence of *Rhododendron maximum* and *Tsuga canadensis* in the understory of the southern Appalachians may provide more opportunities to search for prey on bark substrates than in northern hardwoods forests. In addition, the Hubbard Brook forest has several more species of foliage gleaning birds compared to the southern Appalachians, and this difference in competitive environment might explain some of the differences seen. In general, I found that the three focal species differ consistently along several foraging niche axes across their range, but that some foraging characteristics are more variable and may be responding to competitors, habitat structure, or other variables. This could

suggest a plasticity in foraging behavior or a difference between northern and southern populations.

### *Tree Species Preferences*

Another niche axis by which the BV, BW and GW vary is in tree species preference. These birds used tree species in a nonrandom fashion (Figure 3), which is consistent with other studies of tree species preferences in foliage-gleaning songbirds (Gabbe et al. 2002, Holmes & Robinson 1981). Some of these preferences and aversions may indicate that tree species are an important axis for resource partitioning.

It is not surprising that the GW showed a strong preference for *Pinus strobus*, as it has been associated with conifers in previous studies (Holmes & Robinson 1981, Robichaud & Villard 1999, Tingley et al. 2002). In the far northern part of its range where it is most abundant, the GW inhabits coniferous spruce-fir forests, which may be an indication of its innate preference for conifers. However, Parrish (1995) showed that GWs tended to have a preference for conifers or hardwoods based on geographic location, so the reason for these preferences are unknown. GWs also preferred *Liriodendron tulipifera* (Figure 3), which is probably related to their use of high foraging heights. BVs used *Quercus sp.* more than expected at random, while the BW avoided *Quercus sp.*, which may be an indication of resource partitioning between these bird species. Similarly, the BV preferred *Acer saccharum*, while the BW avoided it (Figure 3).

Foliage-gleaning birds, including BWs and BVs at Hubbard Brook were also found to avoid *Fagus grandifolia*, possibly due to a low availability of resources on this tree species. Recently, Singer (2012) found that *Fagus grandifolia* was among the poorest

hosts for arthropod communities, which suggests that these birds avoid *Fagus grandifolia* due to a low availability of resources on this species. Preliminary arthropod data (unpubl. data) collected at the study sites shows a positive relationship between mean individual arthropod size and tree species preferences by these birds. This suggests that resource availability is an important factor in determining tree species preferences, and future research in this area should account for resources when considering tree preferences.

### *Effect of Competitors*

Many of the shifts in foraging behavior observed in our three focal species due to the presence or absence of the others are consistent with changes expected from interspecific competition. For example, the BV uses the undersides of surfaces and hovering more often in the presence of the GW, which is expected because the GW prefers to glean the upperside of surfaces. The BW also hovers more often when the GW is present, which may suggest that BWs and BVs are hovering more in order to take advantage of prey not as easily captured by the GW's rapid movement and gleaning. The GW also uses the inner and middle sections of trees less and the outer section more when the BW is present, which may suggest that the BW is excluding the GW from these sections. However, there are other shifts seen which are inconsistent with these expectations. The BV forages in foliage more often in the presence of the GW, which also prefers foliage. The GW also uses the outer sections of trees less often when the BV is present, but based on overall foraging niches, we would expect the GW to use these sections more often when the BV is present. Why the BV uses the inner sections less and the BW uses the middle sections more in each other's presence is unknown. These shifts

are not inconsistent with competition, but would be more suggestive if they were reciprocal. Given that the BV foraged in the inner sections less often, the BW might be expected to use the inner sections more, but this was not observed.

Some of the observed changes could also be attributed to underlying, unmeasured variables. Although sites were accounted for in models, some unmeasured differences between sites occupied and unoccupied by each species could be affecting behavior and contributing to these patterns. Habitat selection by these species might result in more foraging opportunities in foliage versus branches, or in the outer sections which could affect the foraging behavior of other species when they are co-occurring.

Foraging height is documented to be an important factor in differentiating niches of many species (MacArthur 1958, Holmes et al. 1979) and appears to be important overall for these birds. Changes in foraging height in response to the presence of other species was not observed, however. Noticeably, the GW seems to maintain a very consistent mean foraging height despite the presence of the other species. As mentioned previously, this supports previous findings of the GW's relatively nonplastic foraging behavior. Furthermore, because the mean foraging height is already quite different between these species, there may be less pressure to change in response to competition.

One interesting pattern emerging from these data is the tendency for each species to have an effect on the foraging behavior of another species. No obvious dominance hierarchy was apparent, in which one species affects the others but is not affected by them. Furthermore, each species affected each of its competitors by either a) causing it to shift its foraging spatially, or b) causing it to shift behaviorally (substrate choice, maneuver), but not both (Figure 5). The presence of either BW or BV resulted in a spatial



change (horizontal sections used) in the foraging niches of its two competitors, while the GW's presence resulted in behavioral shifts in the BV and BW (Figure 5). If foraging niches shift in response to competition, we might expect that they will shift by only the minimum amount necessary to relieve competitive pressure. The observed pattern of niche shifts in these species suggests that shifting both spatial and behavioral aspects of the foraging niche may be unnecessary and that shifts in only a single dimension may be sufficient to reduce competition.

### *Caveats*

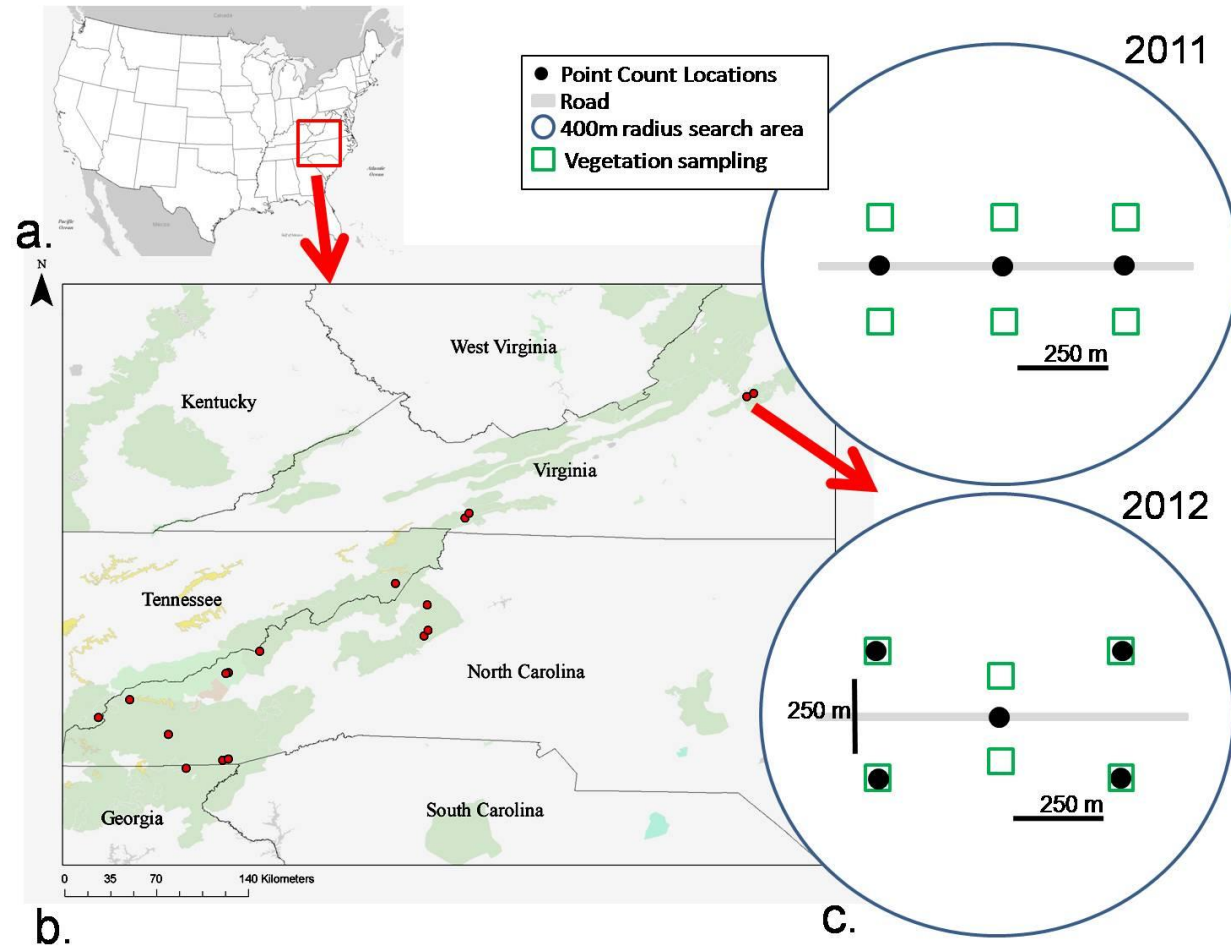
These data presented here have certain limitations in addressing interspecific competition, which is notoriously difficult to demonstrate conclusively (Wiens 1989, Dhondt 2012). Dhondt (2012) categorized the different types of evidence that might be put forward in support of competition as either "necessary" or "sufficient". With respect to the former, we found these species employ foraging strategies with substantial overlap making them likely competitors. With respect to the latter, we found that resource use of one species affects the resource use by others. Although these patterns are suggestive of competition, many other types of evidence were not addressed such as whether resources are limited in this environment, if intraspecific competition occurs for these species (necessary evidence), and effects on the fitness and distribution of each species on the others (sufficient evidence). Thus, the findings here are a useful starting point for further study.

Other limitations of these data exist due to the nature of collecting behavioral data in an uncontrolled environment. Sites with certain combinations of the focal species were

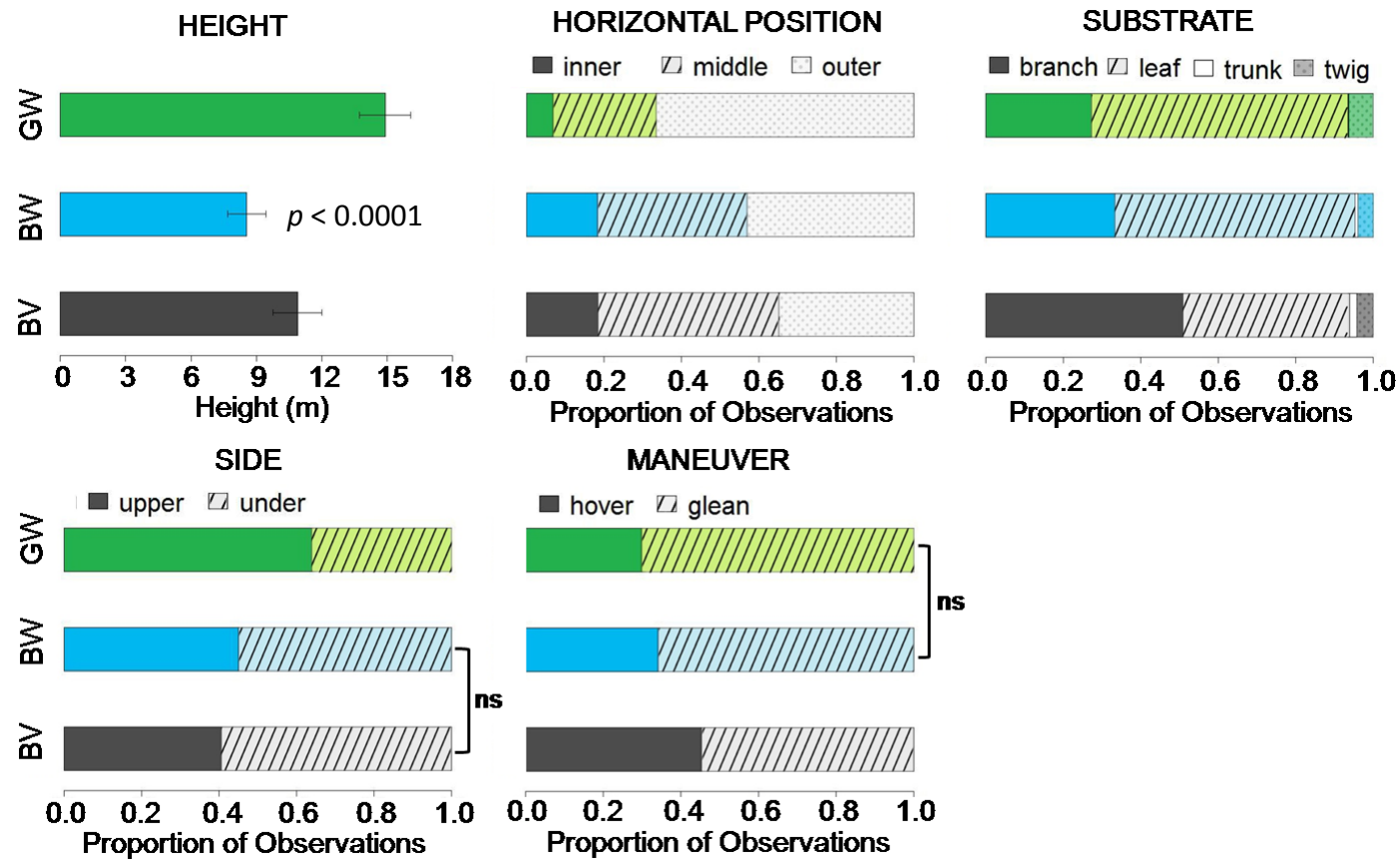
few in number (e.g., sites with BVs but without GWs, and vice-versa), hindering the types of comparisons that could be made. In fact, sites with an abundance of one species usually supported a high abundance of the other species, suggesting that these species are cuing into similar habitat characteristics. I characterized the competitive environment based on the presence or absence of potentially competing species, but such a characterization ignores variation in the abundance of both the focal species and its competitors. Furthermore, two species could both be recorded as present at a station but they might not interact with one another if their territories were far apart. Although the extent of these biases is unknown, they would be expected to add noise to and hence obscure any effects of the competitive environment. Given that many of the niche shifts observed are consistent with patterns of competitive interactions between these species, in the absence of these biases an even stronger pattern might emerge.

### *Conclusions*

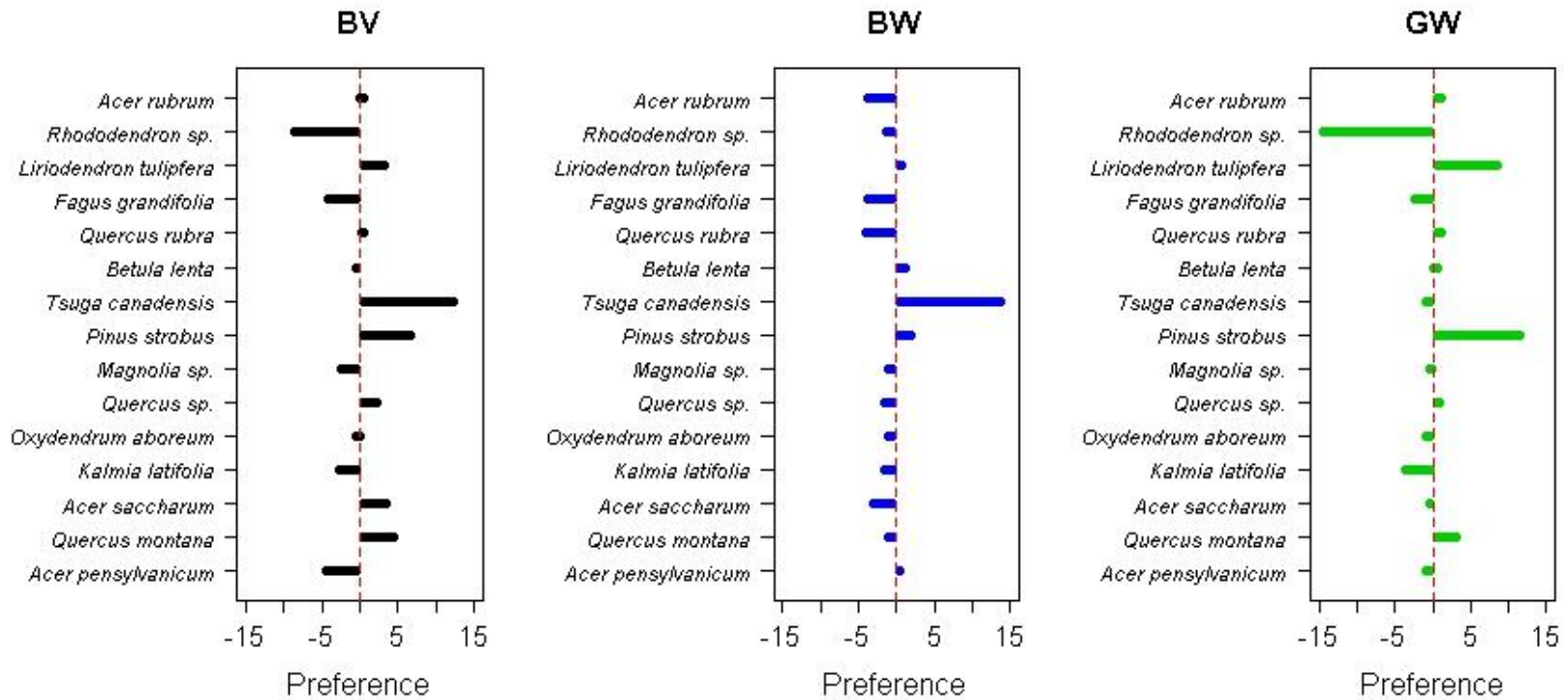
The Blue-headed Vireo, Black-throated Blue Warbler, and Black-throated Green Warbler have foraging niches which largely overlap but differ in mean position. These niches are plastic in response to the presence of the other species and although some convergent changes were seen, the majority of observed shifts were divergent. This suggests that 1) competition between these species in the past may have shaped their foraging niches in such a way as to partition resources, and 2) that the observed niche shifts are a response to current, ongoing competition. These results demonstrate the utility of an approach which assesses both average differences in the foraging niches of potential competitors as well as niche shifts in response to different competitive contexts.



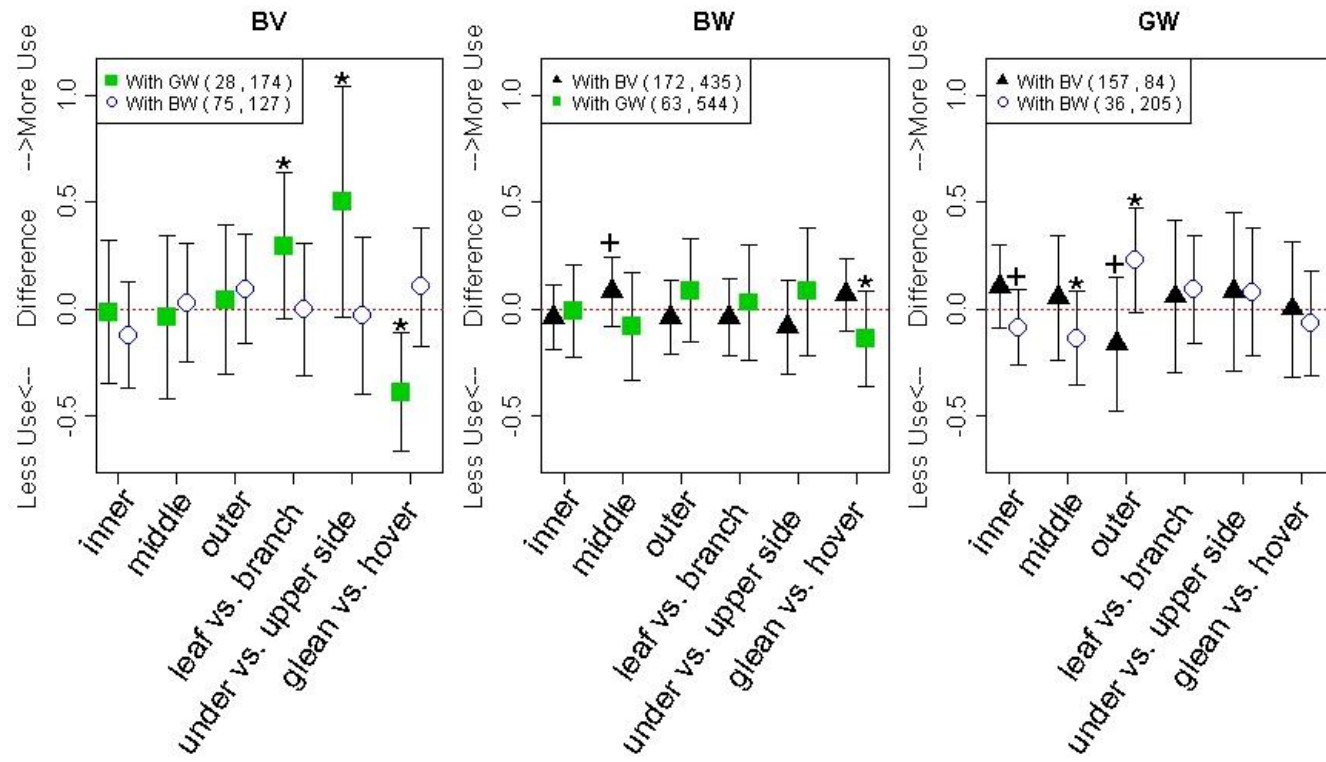
**Figure 1.** a. Map of the United States, showing study range for the project (inset) b. Study range with sites depicted as red dots c. Sampling design layout for 2011 and 2012



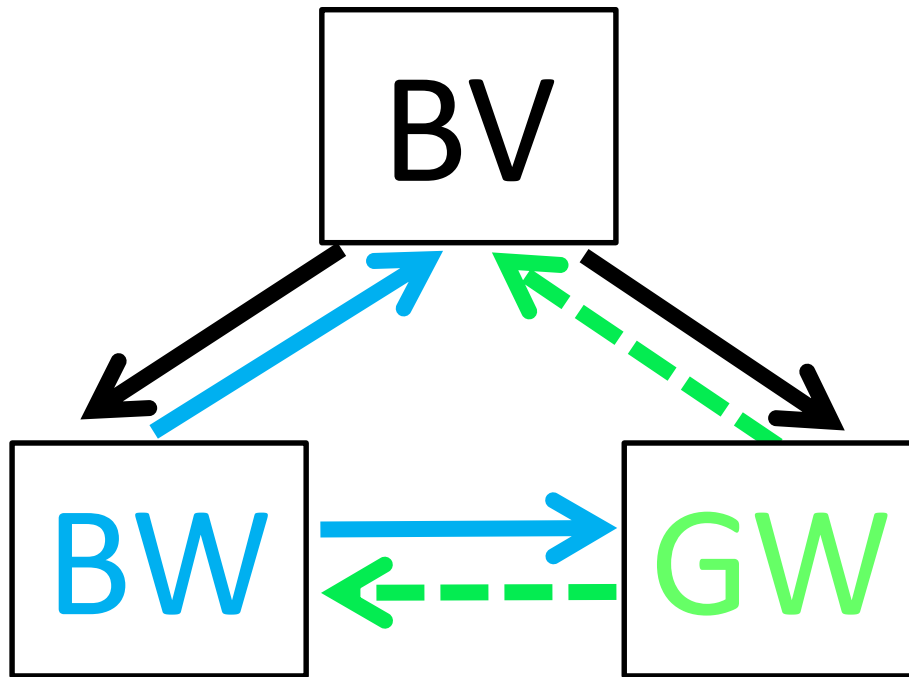
**Figure 2.** Mean foraging niches of the Blue-headed vireo (BV), Black-throated Blue Warbler (BW), and Black-throated Green Warbler (GW) independent of competitive environment. Foraging height analyzed using a mixed effects model and other variables analyzed using Bayesian mixed-effects models. Comparisons for variables other than height significant by Bayesian log odds ratios (as described in text) unless otherwise noted (ns). Individuals: BV=78, BW=157, GW=73; n observations: BV=198, BW=606, GW=240.



**Figure 3.** Tree species preferences for the Blue-headed vireo (BV), Black-throated Blue Warbler (BW), and Black-throated Green Warbler (GW). Preference indexes calculated as difference between observed and expected use for each tree species. Negative values indicate less use than expected at random, while positive values indicate more use than expected at random.  $p$ -values  $< 0.05$ .  $\chi^2_{BV} = 0.005$ ,  $\chi^2_{BW} = 0.001$ ,  $\chi^2_{GW} = 0.001$ . Tree species listed in order from highest %cover to lowest, with total cover  $> 3\%$  and sufficient foraging observations.



**Figure 4.** Effect of competitors on the Blue-headed vireo (BV), Black-throated Blue Warbler (BW), and Black-throated Green Warbler (GW). Values shown are differences in the proportion that a behavior is used when a given competitor is present versus absent. Number of foraging movements used in analyses without and with a given competitor is shown in parentheses. \*  $p < 0.05$ , +  $0.10 < p < 0.05$



**Figure 5.** Summary of effects of competitors on the Blue-headed vireo (BV, black arrows), Black-throated Blue Warbler (BW, blue arrows), and Black-throated Green Warbler (GW, green arrows). Arrows point from the competitor to the species it is affecting with the arrow color indicating which competitor is causing the effect. Solid lines indicate a spatial change in foraging niche (which horizontal section is used), while dashed lines represent behavioral changes in foraging (substrate used, maneuver type, or surface side used).

**Table 1.** Sample sizes showing the total foraging movements, number of individuals (observations), and a conservative estimate of the minimum possible number of unique individuals observed.

	<b>Foraging Movements</b>	<b>Individuals</b>	<b>Min. Unique Individuals</b>
<b>BV</b>	202	81	48
<b>BW</b>	607	158	48
<b>GW</b>	241	74	36

**Table 2.** Number of point count stations in each year within study range with each combination of the three focal species. Based on presence/absence data collected at point count stations, which is further described within the text. Species codes as in Table 1.

<b>Species Present</b>	<b>2011</b>	<b>2012</b>
BV, BW, GW	23	36
BV, BW	1	5
BV, GW	8	28
BW, GW	3	6
BV	4	5
BW	2	4
GW	3	6

**Table 3.** Comparison of northern (Hubbard Brook, NH; Holmes et al. 1979, Robinson and Holmes 1982) and southern populations (this study) of focal species. Heights shown are in meters, and all other variables are percent use when foraging. Species codes as in Table 1.

<b>Foraging axis</b>	<b>Study</b>	<b>Species</b>		
		<b>BV</b>	<b>BW</b>	<b>GW</b>
Height (m)	Holmes et al. 1979	10.5	5.8	13.9
	This study	10.9	8.6	14.9
Leaf (%)	Robinson & Holmes 1982	55.2	78.8	73.9
	This study	43.0	61.9	66.3
Bark (%)	Robinson & Holmes 1982	31.6	8.3	13.6
	This study	57.0	38.1	33.7
Hover (%)	Robinson & Holmes 1982	60.8	60.7	35.4
	This study	45.2	34.1	29.8
Glean (%)	Robinson & Holmes 1982	34.5	33.4	54.2
	This study	54.8	65.9	70.2



**Appendix 1.** Description of study sites. A vegetation description characterizing each site based on National Land Cover Data is provided in far right columns.

Site Number <sup>1</sup>	Latitude <sup>2</sup>	Longitude <sup>2</sup>	Elevation (m)	Visited 2011	Visited 2012	% Cove	% Dry-Mesic Oak	% Northern Hardwoods	% Xeric Oak	% Other
2704132	34.972008	-83.46505	833	X	X	32	45	0	16	8
6302205	35.4416	-83.8522	618		X	20	32	8	22	18
6303117	36.090936	-81.810806	1251	X	X	11	34	2	15	38
6390627	35.737317	-83.04095	711		X	20	47	2	10	20
6390644	35.7753	-82.9594	1137	X	X	11	44	0	24	21
6390909	35.87949	-81.8331	606		X	9	32	0	37	22
6390944	35.91901	-81.8046	472		X	13	40	0	10	37
6391006	35.0275	-83.2122	1027	X	X	7	25	12	26	31
6391028	35.0357	-83.1746	997	X	X	24	44	1	9	22
6391108	35.2041	-83.5848	1199	X	X	17	46	0	13	24
8204219	36.2383	-82.0275	1101		X	12	32	7	16	32
8290243	35.32195	-84.0661	921		X	4	17	17	26	36
8290339	35.628	-83.174	1280	X	X	19	42	6	17	16
8290344	35.623	-83.1914	1260	X	X	18	39	1	21	22
8890009	37.738689	-79.270728	548	X	X	51	39	5	0	6
8890029	37.727003	-79.244753	761	X	X	12	79	4	0	5
8890236	37.516956	-79.617772	304	X	X	40	44	4	0	12
8890223	37.540154	-79.56831	443	X		42	33	15	0	10
8892025	36.684619	-81.550561	1067	X	X	12	44	1	14	29
8892036	36.717633	-81.522403	1073	X	X	41	29	0	14	17

<sup>1</sup> Site number is of the form SSRRRPP where SS is the BBS state code, RRR is the BBS route number, and PP is the point count stop along the survey route at which the study site was centered.

<sup>2</sup> Latitude and longitude are given in NAD83.

**Appendix 2.** Models estimates showing the mean foraging behavior for each niche axis, followed by 95% confidence or credibility intervals in parentheses. Blue-headed vireo (BV), Black-throated Blue Warbler (BW), and Black-throated Green Warbler (GW) estimates shown are independent of competitive environment. Foraging height analyzed using a mixed effects model and other variables analyzed using Bayesian mixed-effects models, as described in text.

		BV	BW	GW
Height(m)		10.89 (9.77, 12.00)	8.56 (7.68, 9.44)	14.91( 13.73, 16.08)
Horizontal Section	% inner	19 (10, 29)	19 (12, 28)	7 (3, 14)
	% mid	46 (34, 59)	38 (29, 49)	27 (17, 38)
	% outer	35 (24, 46)	43 (33, 52)	66 (54, 76)
Substrate	% branch	50 (40, 61)	33 (27, 41)	27 (20,36)
	% leaf	43 (31, 54)	62 (54, 69)	66 (56, 75)
	% trunk	2 (0, 6)	1 (0, 3)	0 (0, 1)
	% twig	5 (2, 10)	4 (2, 7)	7 (3, 12)
Surface Side	% upper	40 (29, 55)	45 (34, 55)	64 (51, 76)
	% under	60 (45, 71)	55 (45, 66)	36 (24, 49)
Maneuver	% hover	45 (36, 54)	34 (29, 40)	30 (22, 38)
	% glean	55 (46, 64)	66 (60, 71)	70 (62, 78)

**Appendix 3.** Effect of competitors on the BV, BW, and GW. Values shown are the percentage that a behavior is used when a given competitor is present (+) versus absent (-). For height, foraging height in meters is shown with and without a competitor. Number of movements and individuals used in each comparison is also shown. +  $p < 0.10$ , \*  $p < 0.05$ , \*\*  $p < 0.01$

			Height (m)	Horizontal Section			Substrate	Surface Side	Maneuver	Movements	Individuals
				% inner	% mid	% outer	% leaf	% upper	% hover		
BV	-	BW	10.80	<b>32*</b>	41	27	48	40	52	75	34
	+	BW	11.13	<b>20*</b>	44	36	48	43	42	127	48
	-	GW	9.09	26	47	29	<b>23**</b>	90	<b>12**</b>	28	13
	+	GW	11.29	24	43	33	<b>53**</b>	40	<b>51**</b>	174	69
BW	-	BV	7.96	26	<b>30*</b>	44	67	42	41	172	43
	+	BV	8.63	22	<b>38*</b>	40	63	51	35	435	116
	-	GW	7.56	24	43	34	61	55	<b>24*</b>	63	18
	+	GW	8.58	23	35	42	64	47	<b>38*</b>	544	141
GW	-	BV	14.54	<b>7+</b>	<b>23*</b>	<b>72**</b>	63	70	31	157	49
	+	BV	15.40	<b>17+</b>	<b>28*</b>	<b>55**</b>	68	62	31	84	25
	-	BW	14.74	<b>19+</b>	32	<b>50+</b>	64	66	29	36	9
	+	BW	16.01	<b>10+</b>	18	<b>72+</b>	73	59	36	205	65

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