CHAPTER SIX

Influence of Plant Species Composition on Golden-winged Warbler Foraging Ecology in North-Central Pennsylvania*

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Abstract. Golden-winged Warblers (*Vermivora chrysoptera*) have experienced significant population declines in the Appalachian Mountains for more than 40 years and are currently a focal species for management of young forests throughout their breeding distribution. Avian fitness has been linked to the quality and quantity of insect food supplies, but little information is available on foraging ecology of Golden-winged Warblers. We evaluated shrub and tree species selection by foraging Golden-winged Warblers in north-central Pennsylvania during the 2011 breeding season. Additionally, we compared caterpillar abundance among 13 woody plant species present within breeding territories. Golden-winged Warblers selectively foraged on black locust (*Robinia pseudoacacia*), pin cherry (*Prunus pensylvanica*), white oak (*Quercus alba*), and blackberries (*Rubus* spp.). Tree and shrub species composition differed between Golden-winged Warbler territories and adjacent, unoccupied areas of early successional forest cover, and habitat use was consistent with patterns of caterpillar abundance. Whereas vegetation structure generally dominates management guidelines for breeding habitat of insectivorous songbirds, including Golden-winged Warblers, our research clearly demonstrated the need for land managers to also consider plant species composition. In the case of habitat management for breeding Golden-winged Warblers in north-central Pennsylvania, our assessment suggested favoring the presence of black locust, pin cherry, white oak, and blackberry, over sassafras (*Sassafras albidum*), mountain laurel (*Kalmia latifolia*), and blueberry (*Vaccinium* spp.).

Key Words: black locust, breeding territory, caterpillar, early successional habitat, habitat selection, Neotropical migrant, pin cherry, prey abundance, *Rubus* spp.

Prey availability has a strong effect on reproductive success of breeding songbirds (Martin 1987, Nagy and Holmes 2005). Selection of a breeding territory that provides abundant food resources necessary for rearing young has important consequences for an individual's fitness (Simons and Martin 1990, Rodenhouse and Holmes 1992, Verhulst 1994). Considering the importance of prey availability and provisioning rates to songbird reproductive

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success (Goodbred and Holmes 1996, Moorman et al. 2007), it is not obvious why songbird foraging has received little research attention compared to other aspects of avian ecology. In fact, habitat conservation of imperiled avian species has often focused on vegetative structure (Rotenberry and Wiens 1980, Vale et al. 1982), which herein we define as the physical arrangement of vegetation, irrespective of plant species composition (Wiens 1969). MacArthur and MacArthur (1961) and Diaz et al. (2005) argued that bird community dynamics have little to do with plant species composition. However, several published studies indicate that insectivorous birds selectively search for prey on certain tree species (Holmes and Robinson 1981, Gabbe et al. 2002, George 2009), which may be linked to prey density, an important component of prey availability. Additionally, arthropod densities have been shown to vary among tree species (Marshall and Cooper 2004). In efforts to increase habitat quality to the level where breeding bird populations are self-sustaining, it is equally important to consider both the physical structure of breeding habitat (MacArthur and MacArthur 1961, Gregg et al. 2000, Wood et al. 2006) and foraging ecology of focal species (Weikel and Hayes 1999). Although much work has been done to elucidate breeding habitat structure for many avian species (Recher 1969, Fink et al. 2006, A. M. Roth et al., unpubl. plan), detailed information regarding foraging ecology is often lacking.

Much is known about the structural components of breeding habitat of Golden-winged Warblers (*Vermivora chrysoptera*), but there is little information on foraging ecology. Golden-winged Warblers are an insectivorous, Neotropical migrant that breed in higher elevations of the Appalachian Mountains, the northeast and north-central regions of the U.S., and scattered areas across adjacent southern Canada (Confer et al. 2011; A. M. Roth et al., unpubl. plan; Chapter 1, this volume). Breeding populations of Golden-winged Warblers in the Appalachian Mountains occur in predominantly forested landscapes (A. M. Roth et al., unpubl. plan). Within these forested landscapes, areas used by breeding pairs include patches of young forests, forest and shrub wetlands, managed shrublands, and the edge portions (<55 m) of surrounding unharvested forest (saw timber; >80 years old: Chapter 5, this volume). The Appalachian breeding-distribution segment of Golden-winged Warblers has experienced a population decline for more than 40 years (Sauer et al. 2011; Chapter 1, this volume) and Golden-winged Warblers are now considered a species of management concern (U.S. Fish and Wildlife Service 2009). Reasons for the species' decline include reduced abundance of breeding habitat, hybridization with Blue-winged Warblers (*V. cyanoptera*), and nest parasitism by Brown-headed Cowbirds (*Molothrus ater*, Buehler et al. 2007). The availability of young forest across the Appalachian landscape has declined during the past century due to ongoing succession of abandoned farmland to closed-canopy forest (Gill 1980).

Many aspects of Golden-winged Warbler biology have been examined but little is known about the species' foraging ecology. There is little documentation of which arthropods are consumed by Golden-winged Warblers but caterpillars and spiders appear to be common prey. Anecdotal evidence suggests that caterpillars, particularly leafrollers (Lepidoptera: Tortricidae), are one of the most important components of the diet of Golden-winged Warblers, and adults provision nestlings with caterpillars (Jacobs 1904, Forbush 1929, Will 1986, Confer et al. 2011). Based on the limited available information on the diet of Golden-winged Warblers (Jacobs 1904, Forbush 1929, Will 1986), we assumed that caterpillars were the dominant prey in our study area.

Forage-site selection, or the plant species on which a bird forages, is a key aspect of avian breeding ecology and has been linked to prey abundance (Willson 1970, Holmes and Robinson 1981, Gabbe et al. 2002, George 2009). Many songbirds are thought to select territories based on plant species composition and selectively search for prey on certain plant species within their territories (Holmes and Robinson 1981, Gabbe et al. 2002, George 2009). If Golden-winged Warblers behave similarly, information regarding the abundance and distribution of prey, foraging-site selection, and vegetative composition and structure associated with territories can improve understanding of the breeding ecology of Golden-winged Warblers. Herein, we describe Golden-winged Warbler foraging ecology, prey abundance, and tree and shrub species use in north-central Pennsylvania. Specifically, our objectives were to (1) examine whether Golden-winged Warblers selectively search for prey on tree and shrub species disproportionate to tree and shrub species availability within their breeding territories, (2) relate Golden-winged Warbler foraging site selection to abundance of caterpillars, and (3) identify plant species composition and vegetation structure associated with Golden-winged Warbler territories compared to unoccupied areas of seemingly appropriate breeding habitat.

METHODS

Study Area

We examined foraging ecology of Golden-winged Warblers at the Sproul State Forest located in north-central Pennsylvania (41.245° N, 77.877° W) from 1 May through 10 July 2011. Sproul State Forest lies in western Clinton and northern Centre counties at an elevation of 600–620 m and encompasses 1,120 km^2. Sproul State Forest is entirely in the Mountainous High Plateau section of the Appalachian Plateau's physiographic province (Briggs 1999). The region is characterized by high ridges and deep valleys created via headwater erosion of the West Branch of the Susquehanna River (Briggs 1999). There is little human development in the region with the exception of sparsely distributed primitive cabins, natural gas pipelines, a major roadway (State Route 144), several gated and ungated gravel roads, and numerous natural gas wells.

We monitored Golden-winged Warblers in Sproul State Forest at three study sites (140, 60, and 70 ha) within a 1,619-ha area burned by an arson fire in 1990. Sproul State Forest is dominated by northern hardwood and dry oak forests (Johnson et al. 2009). Most forest stands in Sproul State Forest were 80–100-year-old, closed-canopied forest that lacked the structural characteristics used by nesting Golden-winged Warblers. Rather, breeding Golden-winged Warblers in Sproul State Forest were associated with disturbance-generated plant communities adjacent to unharvested forest (saw timber; >80 years old) including areas influenced by timber harvests, wildfire, and abandoned natural gas wells (Larkin and Bakermans 2012). Young forest cover available to breeding Golden-winged Warblers was characterized by a patchy mosaic of saplings, shrubs, herbaceous openings, and scattered trees (approx. basal area: 2.3–9.2 m^2/ha). Golden-winged Warbler territory density across the three study sites averaged 1.75 territories/10 ha over a 4-year period (range: 1.08–2.52 territories/10 ha; 2008–2011, J. Larkin, unpubl. data). Common shrub species in descending abundance included blackberry (*Rubus* spp.), mountain laurel (*Kalmia latifolia*), blueberry (*Vaccinium* spp.), and sweet fern (*Comptonia peregrina*). Common tree species in descending abundance included red maple (*Acer rubrum*), black locust (*Robinia pseudoacacia*), pin cherry (*Prunus pensylvanica*), black cherry (*P. serotina*), chokecherry (*P. virginiana*), sweet birch (*Betula lenta*), sassafras (*Sassafras albidum*), white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. montana*), and white pine (*Pinus strobus*).

Field Methods

Golden-winged Warbler Foraging Observations and Territory Mapping

We uniquely banded every territorial male Golden-winged Warbler monitored in our sample to assure individual identification. Our study area was the focus of a larger concurrent study of Golden-winged Warblers beginning in 2008. As such, several males were previously banded with U.S. Geological Survey aluminum leg bands and a unique combination of colored leg bands. To capture and mark unbanded males we used one 6-m mist net, a recording of Golden-winged Warbler type I and II songs (Lang Elliott with Donald and Lillian Stokes: Stokes Field Guide to Bird Songs), and a model of a male Golden-winged Warbler (Ward and Schlossberg 2004). Our study protocol was approved by the Indiana University of Pennsylvania's Animal Care and Use Committee (IACUC #03-0708).

We observed color-banded male Golden-winged Warblers for up to 30 min every other day between the hours of 05:00 and 18:00 Eastern Standard Time (EST) from 9 May 2011 to 20 June 2011. Golden-winged Warblers are rapid fliers and can traverse their territories almost instantaneously; thus, we considered observations on one substrate (shrub or tree) followed by observations on another substrate to be statistically independent (Holmes et al. 1979a). We therefore included each foraging observation recorded from a sequence of foraging observations in our analysis (Holmes et al. 1979a, Morrison 1984, George 2009). When making observations, we randomized the order of individuals observed to account for potential variation in behavior throughout the day (Shields 1977). We recorded behavioral data using field notebooks and digital voice recorders (Olympus VN-5000, Center Valley, PA). During each observation session, we recorded study site, date, time of day, individual identification, individual's sex, geographic coordinates, plant species, observed activity (singing, perching, or foraging), duration of time spent foraging, and forage-site category (shrub or tree). Shrubs were defined as a woody low-growing plant containing multiple stems originating near the base of the plant and trees were defined as >0.5 m tall and >1 cm dbh.

We also conducted territory mapping of male Golden-winged Warblers concurrently with foraging observations using the methods of Wakeley (1987). We delineated territories by following males on ≥8 occasions during the breeding season. Song posts, defined as locations where a bird sang at least once, and foraging sites were marked with flagging tape and geographic coordinates were recorded with a handheld GPS receiver (Garmin eTrex H, North American Datum 1927). We used territory mapping data (geographic coordinates) and the Hawth Tools extension (Beyer 2004) in ArcGIS 9.2 (ESRI 2009) to estimate the area of each male's territory (ha) using Minimum Convex Polygons (Mohr 1947). For the purpose of this manuscript, we delineated territories based on geographic coordinates of observed song posts and foraging sites, which may underestimate the size of home ranges used by breeding Golden-winged Warblers because long-distance foraging is excluded (Streby et al. 2012; Chapter 5, this volume).

Vegetation Sampling

We characterized vegetation from late June through early July 2011, after we had collected Golden-winged Warbler observations. Some vegetation characteristics, such as amount of herbaceous cover, may have changed between when we observed foraging Golden-winged Warblers and when we conducted vegetation surveys but the composition and structure of woody plants remained the same through the period of our study. Within each male's territory we sampled vegetative structure and species composition within 5-m-radius circular plots along transects (Morrison 1981, Canterbury et al. 2000). The number of transects and 5-m-radius sampling plots per territory varied depending on territory size to achieve 10 sampling plots per ha, to ensure that we sampled all territories proportional to size and that we adequately characterized the patchy nature typical of nesting habitat of Golden-winged Warblers (Confer et al. 2011). To plan appropriate plot spacing we calculated a total transect length by obtaining a random compass bearing (rotation of a handheld compass until a helper indicated "stop") and starting point (north, south, east, or west side of territory, chosen randomly from folded papers). To determine the number of transects and distance between plots along each transect, we then divided total transect length by the number of 5-m-radius plots needed to achieve 10 sampling plots per ha of a warbler territory.

In each 5-m-radius plot, we recorded the number and species of all trees and saplings, which were characterized by the presence of one or a few apical stems or trunks that supported a branching structure. We defined saplings as ≥0.5 m tall and 1.0 cm ≤ dbh < 10.0 cm, whereas trees were ≥10 cm dbh. We did not differentiate between saplings and trees during Golden-winged Warbler foraging observations so we combined those two categories. We also visually estimated to the nearest 1% the percent cover of herbaceous vegetation, tree seedlings, bare ground, and each shrub species within each 5-m-radius plot. To assist with visual estimates, we divided each 5-m-radius circular plot into four quadrants and summed the percent of each cover type in each quadrant to estimate the percent of each cover type in the entire plot. A team of observers surveyed all vegetation plots to avoid variation due to multiple observers. Each team member estimated and the team came to an agreement on the percent cover of each cover type within each quadrant (each quadrant totaling 25% of the area of the plot). We summed the percent cover for each cover type across the four quadrants to create the final percent cover estimates for each cover type within the entire 5-m-radius plot.

We used the same vegetation sampling protocol to characterize adjacent areas of young forest cover that were unoccupied by Golden-winged Warblers. We surveyed these areas for Golden-winged Warblers and detected no birds after listening and visually searching each area two to three times weekly throughout the breeding season; hereafter, we refer to these areas as "unoccupied areas." We used ArcGIS to create random points throughout areas of young forest unoccupied by Golden-winged Warblers. We randomly selected 12 points and used these random points as the center of a 1.7-ha square polygon, as this was the average size of our spot-mapped Golden-winged Warbler territories. Unoccupied areas were located 0.5–3.7 km from known territories of Golden-winged Warblers in our study area.

Arthropod Sampling

We used exclosure netting and branch clippings to estimate arthropod abundance for 13 focal woody plant species present within territories of Golden-winged Warblers. Exclosure netting and branch clipping are effective ways to evaluate arthropod abundance in the absence of bird predation (Holmes et al. 1979a,b; Atlegrim 1989; Johnson 2000), and dietary analyses have been used to verify that this method captures nearly all items eaten by insectivorous birds (Johnson 2000). We constructed exclosure nets using rolled plastic mesh (1-m-wide roll with 2 cm × 2 cm gaps), cut into 2.4-m sections. We folded the mesh and sewed the sides (with cotton string) to create a bag with final exclosure dimensions of 1.2 m × 1 m.

We placed exclosure netting on branches of individual plants of each target species that was common within our study area: blackberry ($n = 15$), black locust ($n = 15$), blueberry ($n = 10$), mountain laurel ($n = 10$), sweet fern ($n = 10$), black cherry ($n = 10$), pin cherry ($n = 10$), chestnut oak ($n = 10$), red maple ($n = 10$), sassafras ($n = 10$), sweet birch ($n = 10$), white oak ($n = 10$), and white pine ($n = 10$). We placed exclosure nets on branches from 22 May through 24 June 2011 throughout our three study sites. Netting remained on branches for a minimum of two weeks to allow arthropods, including caterpillars, to repopulate vegetation in the absence of bird predation. We clipped all branches from 8 June through 9 July 2011; we timed branch collection to coincide with the nestling stage of Golden-winged Warblers when the demand for food resources was expected to be greatest. To minimize arthropod loss during branch clipping, we gently placed a 147 L, heavy duty plastic bag over each branch, cinched the end of the bag, then clipped the branch and tightly tied the bag shut. To determine if bird predation had an effect on caterpillar densities, we clipped additional, nonnetted branches of black locust ($n = 10$), pin cherry ($n = 5$), and blackberry ($n = 10$), which we compared to additional, paired exclosures placed on these species. We randomly selected nonnetted branches near the paired exclosure branch using two observers: one observer selected the three closest branches within sight of the branch in the exclosure and assigned them numbers 1–3, then the second observer chose a number from 1 to 3, corresponding to the branch that we subsequently clipped.

Within two days of branch collection, we carefully searched through leaves on all branches to find all arthropods visible to the naked eye, then counted and identified individuals to Order using identification guides (Borror and White 1970, Milne and Milne 1980). We assumed that all caterpillar-like insect larvae acted as one functional group regardless of taxonomic classification and referred to this category as "caterpillars." We collected and stored leaves from each branch clipping in paper bags and hung them to allow air flow and to keep moisture within the bags at a minimum (reducing the risk of rotting and mildew of leaves) until we oven dried (40°C for 48 hr) and weighed samples to determine dry mass (Butler and Strazanac 2000, Marshall and Cooper 2004). We scaled caterpillar abundance to dry leaf mass (number of caterpillars/10 g dry leaf mass) as a measure of relative abundance (Futuyma and Gould 1979).

Statistical Analyses

Plant Species Use versus Availability

Assessment of third-order resource selection compares used and available resources for individual animals within their respective territory (Johnson 1980), which in this study we considered to be the spot-mapped territory. We considered individual Golden-winged Warblers as the sampling units and used compositional analysis based on the function `compana` in the `adehabitat` package (Aebischer et al. 1993, Calenge 2006) in Program R (ver. 2.13.0, R Foundation for Statistical Computing, Vienna, Austria). We tested whether Golden-winged Warblers foraged on certain tree and shrub species disproportionate to their availability within a spot-mapped territory. For both tree and shrub compositional analyses, we converted time spent foraging on and availability of each species to a proportional use and availability; using the relative proportional use and availability of resources avoids the problem of the unit-sum constraint, where avoidance of one resource leads to an apparent preference for other resources (Aebischer et al. 1993). To account for nonnormality in our use and availability data, we conducted both tree and shrub analyses based on data randomization with 10,000 repetitions (Aebischer et al. 1993). We maintained an alpha level of 0.05 and controlled for experiment-wise error between two MANOVA tests (Multivariate Analysis of Variance) of shrub and tree composition with the Holm method in Program R (`p.adjust`; Package: `stats`).

To reduce the number of resource categories in our analyses, we included only shrubs and trees present in >50% of spot-mapped territories and utilized for foraging on ≥2 occasions. With these criteria, our results reflect relative preference among used plant species within Golden-winged Warbler territories, and not avoidance. Our analyses did not allow us to make inferences about avoidance of trees or shrubs because we only analyzed the subset of plant species used by Golden-winged Warblers.

Caterpillar Abundance

We compared the abundance of caterpillars among woody plant species using a Kruskal–Wallis rank sum test (`kruskal.test`) in Program R. We used a Kruskal–Wallis test rather than a one-way analysis of variance because our data were not normally distributed (Shapiro–Wilk test) and standard transformations did not result in normally distributed data (Zar 1999). We analyzed caterpillar abundance on trees and shrubs separately because we recorded tree and shrub species use by Golden-winged Warblers separately. If the Kruskal–Wallis test indicated an overall difference in abundance, we conducted multiple comparisons for a Kruskal–Wallis test (`kruskalmc`) in Program R within the `pgirmess` package (Siegel and Castellan 1988, Giraudoux 2011) to determine species-specific differences among caterpillar abundances, with an across-comparisons alpha level of 0.05 (Giraudoux 2011). We maintained alpha levels of 0.05 between the two Kruskal–Wallis tests (shrubs and trees) using the Holm method in Program R (`p.adjust`; Package: `stats`).

Additionally, we compared caterpillar abundance between netted and unnetted branches of three plant species (blackberry, black locust, and pin cherry) using separate independent-samples t-tests in SPSS (ver. 19.0.0, SPSS Inc., Chicago, IL). Caterpillar abundance on blackberry was slightly nonnormally distributed (based on a Shapiro–Wilk test) so we $\log_e$ transformed $[\ln(x + 1)]$ the count data to meet assumptions of normality (Zar 1999). We combined caterpillar data from netted and unnetted treatments for further analysis of caterpillar abundance because we found no differences in caterpillar abundance between netted and unnetted branches for any tree or shrub species. However, our sample sizes were small with 10 unnetted pairs per species of black locust and blackberry, and five unnetted pairs of pin cherry, which may have limited our ability to detect differences in caterpillar densities between netted and unnetted treatments.

Analysis of Territories versus Unoccupied Areas

We compared vegetative structure and ground cover of Golden-winged Warbler territories to that in adjacent, unoccupied areas of similar stand age. To evaluate vegetative structure, we compared percent cover of shrubs, number of saplings, and number of trees between territories and unoccupied areas using an independent-sample *t*-test (Zar 1999). Both tree and sapling counts were nonnormally distributed (based on a Shapiro–Wilk test) and we $\log_e$ transformed $[\ln(x + 1)]$ both datasets prior to analysis (Zar 1999). Data for percent ground cover were also nonnormally distributed (based on a Shapiro–Wilk test) and standard transformations did not result in normally distributed data. We therefore used Mann–Whitney U tests in SPSS to compare differences in ground cover between Golden-winged Warbler territories and adjacent unoccupied areas (Zar 1999). Ground-cover variables included percent cover of bare ground, percent cover of tree seedlings, percent herbaceous cover, and percent cover of each shrub species (blackberry, blueberry, mountain laurel, and sweet fern). We maintained an overall alpha level of 0.05 across all independent sample tests by adjusting the resulting *P*-values using the Holm method in Program R (`p.adjust`; Package: `stats`).

To determine which tree species were associated with territories of Golden-winged Warblers, we conducted an indicator species analysis (Dufrêne and Legendre 1997) in PC-ORD (ver. 6.0, MjM Software, Gleneden Beach, OR). The method is a form of cluster analysis and combines data on the concentration of species abundance in a particular group and faithfulness of species occurrence in a particular group (Dufrêne and Legendre 1997).

The two components are combined to produce indicator values (IV), which range from zero (no group indication) to 100 (perfect group indication). Indicator values are then tested for statistical significance by Monte Carlo randomizations (Dufrêne and Legendre 1997). A statistically significant result indicated that a plant species was characteristic of either territories or unoccupied areas and was present in the majority of the plots in either category (Dufrêne and Legendre 1997). We considered species to be indicative of territories or unoccupied areas when $P < 0.05$.

RESULTS

Plant Species Use versus Availability

We observed 14 male Golden-winged Warblers searching for prey on trees and shrubs for 253.2 and 51.0 min, respectively. On average, we observed each individual searching for prey on trees for 18.1 min (range: 0.9–76 min) and on shrubs for 4.6 min (range: 0.1–20.7 min). We observed Golden-winged Warbler males searching for prey an average of seven days (range: 4–12 days).

We recorded a total of 25 tree species within Golden-winged Warbler territories. Of 25 tree species, only seven met our criteria for inclusion in compositional analysis (present in ≥50% of territories and at least two observations of foraging visits). Golden-winged Warbler use of these seven tree species differed from their availability ($\Lambda = 0.052$, $P = 0.02$; Table 6.1). Black locust and pin cherry were both foraged on more than black cherry, whereas white oak was foraged on more than sassafras and sweet birch, compared to their respective availabilities.

We did not observe three of the 14 Golden-winged Warblers we monitored searching for prey on shrubs; we therefore excluded them from our shrub selection analysis. We recorded four shrub species within territories: blackberry, blueberry, mountain laurel, and sweet fern. We only observed birds foraging on mountain laurel and blackberry. Therefore, these two species were the only shrubs we included in our analysis. Golden-winged Warblers selectively foraged on blackberry compared to mountain laurel ($\Lambda = 0.067$, $P = 0.02$; Table 6.1).

Structure and Composition of Territories versus Unoccupied Areas

Vegetative structure differed between Golden-winged Warbler territories ($n = 14$) and unoccupied areas ($n = 12$; Table 6.2). Territories had a higher percent of herbaceous cover, fewer saplings, and more trees compared to unoccupied areas. Unoccupied areas had a higher percent cover of blueberry and mountain laurel, and a lower percent cover of blackberry and herbaceous plants (Table 6.2). We detected

TABLE 6.1

Simplified ranking matrix from compositional analysis for territories of Golden-winged Warblers based on proportional tree species use (foraging) and proportional tree species availability.

	White oak	Black locust	Pin cherry	Sweet birch	Red maple	Sassafras	Black cherry	Rank
White oak		—	—	—	—	—	—	1
Black locust	ns		—	—	—	—	—	2
Pin cherry	ns	ns		—	—	—	—	3
Sweet birch	$P < 0.05$	ns	ns		—	—	—	4
Red maple	ns	ns	ns	ns		—	—	5
Sassafras	$P < 0.05$	ns	ns	ns	ns		—	6
Black cherry	ns	$P < 0.05$	$P < 0.05$	ns	ns	ns		7

We observed 14 Golden-winged Warblers foraging at the Sproul State Forest in north-central Pennsylvania during the 2011 breeding season. Cells in the matrix with a significant difference in log ratios (calculated from proportions) of used and available tree species are indicated by $P < 0.05$. Ranks represent the importance of each tree species in ascending order from most important (1) to least important (7). Significant P-values indicate a difference between the ranking of two tree species.

TABLE 6.2

Differences in vegetation structure and ground cover composition between Golden-winged Warbler territories (n = 14) and unoccupied areas (n = 12) during the 2011 breeding season in Sproul State Forest, Pennsylvania.

Structural variables		Mean	SD	t_{24}	$P \leq$
% Shrub cover[a]	Territory	62	14.9	0.28	1.000
	Unoccupied	64	20.8		
No. saplings[b]	Territory	14.1	6.9	5.42	0.001***
	Unoccupied	58.5	53.3		
No. trees[b]	Territory	2.3	1.2	−3.54	0.010**
	Unoccupied	0.9	0.8		

Percent ground cover composition variables		Median (%)	Interquartile range	Mann–Whitney U	P[c]
Bare ground[a]	Territory	4	0.0–7.5	61.0	0.705
	Unoccupied	9	1.4–14.8		
Tree seedlings[a]	Territory	2	1.1–3.9	40.0	0.095
	Unoccupied	7	1.8–9.3		
Herbaceous cover[a]	Territory	33	20.9–36.1	33.0	0.044*
	Unoccupied	11	5.1–25.6		
Blackberry[a]	Territory	39	31.3–54.8	0	0.001***
	Unoccupied	0	0.0–0.1		
Mountain laurel[a]	Territory	2	0.0–6.7	7.0	0.001***
	Unoccupied	29	14.1–46.3		
Blueberry[a]	Territory	7	3.9–13.8	13.0	0.002**
	Unoccupied	33	23.3–35.2		
Sweet fern[a]	Territory	4	1.4–7.2	71.5	1.000
	Unoccupied	1	0.6–6.3		

Significant differences are indicated with asterisks; * $P \leq 0.05$, ** $P \leq 0.010$, *** $P \leq 0.001$.

[a] Indices based on visual estimates.

[b] No. of saplings and trees were $\log_e$ transformed for analyses; means and standard deviations (SD) are shown for untransformed variables.

[c] P-values are corrected for multiple comparisons using the Holm method.

no difference in percent shrub cover between territories and unoccupied areas.

We detected several floristic differences between Golden-winged Warbler territories and unoccupied areas, based on indicator species analysis. Six tree species were indicative of territories: black locust (IV = 85.7%, $P = 0.001$), chokecherry (IV = 70.6%, $P = 0.001$), pin cherry (IV = 64.5%, $P = 0.048$), black cherry (IV = 63.9%, $P = 0.002$), white pine (IV = 50.0%, $P = 0.005$), and red pine (IV = 35.7%, $P = 0.041$). Three species were indicators of unoccupied areas: sassafras (IV = 99.6%, $P < 0.001$), chestnut oak (IV = 90.6%, $P < 0.001$), and red oak (IV = 44.0%, $P = 0.044$).

Caterpillar Abundance on Woody Plant Species

Caterpillar abundance did not differ between netted and unnetted branches of black locust ($t_{23} = 1.731$, $P = 0.097$), pin cherry ($t_{13} = 1.353$, $P = 0.199$), or blackberry ($t_{23} = 0.185$, $P = 0.855$); therefore, we pooled netted and unnetted treatments for analyses of caterpillar abundance across tree and shrub species. Caterpillar abundance differed among tree species (Kruskal–Wallis test: $\chi^2_8 = 64.142$, $P < 0.001$), with black locust, pin cherry, and black cherry having the highest caterpillar abundances among trees, and sassafras, sweet birch, and white pine having the lowest (Figure 6.1). Black locust had a higher

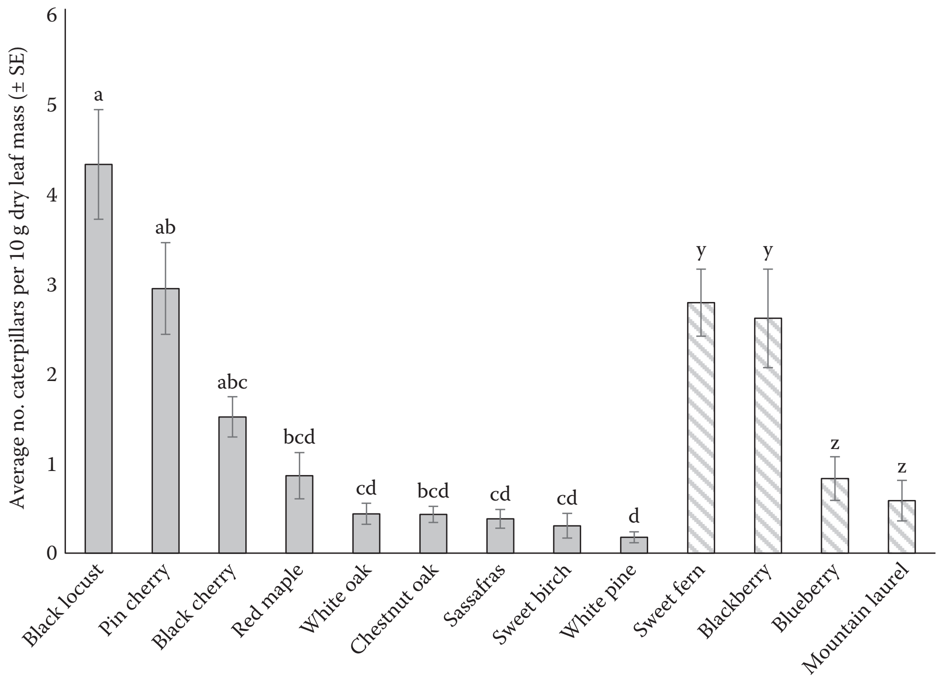

Figure 6.1. Estimated caterpillar abundance on tree and shrub species collected at Sproul State Forest, Pennsylvania, 2011. Means for species with the same letters are not statistically different. Trees (solid fill) and shrubs (line fill) were analyzed separately. $n = 10$ for all species except black locust ($n = 25$), blackberry (*Rubus* spp.: $n = 25$), and pin cherry ($n = 15$).

abundance of caterpillars than red maple, chestnut oak, sassafras, sweet birch, white pine, and white oak. Pin cherry had a higher abundance of caterpillars than sassafras, sweet birch, white oak, and white pine, whereas black cherry had a higher abundance of caterpillars than white pine. Caterpillar abundance also differed among shrub species (Kruskal–Wallis test: $\chi^2_3 = 20.169$, $P < 0.001$). Both blackberry and sweet fern had higher caterpillar abundances than mountain laurel and blueberry, whereas blackberry and sweet fern had similar caterpillar abundances (Figure 6.1).

DISCUSSION

Golden-winged Warbler foraging locations and territory placement were influenced by plant species composition and associated prey abundance. Woody plant species that had the highest caterpillar abundances were also selectively foraged on by Golden-winged Warblers and were indicators of Golden-winged Warbler territory locations. Specifically, white oak, blackberry, pin cherry, and black locust were selectively foraged on by the male warblers monitored during this study. Pin cherry and black locust were also indicators of Golden-winged Warbler territories. Last, black locust and pin cherry had the highest abundance of caterpillars, the primary food source for many breeding insectivorous birds including Golden-winged Warblers (Jacobs 1904). A recent study reported that stomach contents of nestling and young fledgling Golden-winged Warblers in the western Great Lakes region were composed of 89% (based on mass) of leafroller caterpillars (*Archips* spp., Streby et al. 2014). Whereas habitat structure generally dominates management guidelines for Golden-winged Warbler breeding habitat (A. M. Roth et al., unpubl. plan), our research suggests that land managers also need to consider plant species composition, as this habitat characteristic appears to influence prey availability for Golden-winged Warblers.

Black locust is a nitrogen-fixing legume and its leaves have been reported to contain high concentrations of nitrogen (4.0%–5.5% dry leaf mass; Day and Monk 1977, Bassam 1998). Foliar nitrogen content is an important determinant of growth and survival for larval Lepidoptera (Mattson 1980, Schowalter and Crossley 1988). Herbivorous insects selectively feed on nitrogen-rich foliage (Athey and Connor 1989, Marquis and Lill 2010) and grow larger and produce more fecund adults when raised on higher nitrogen diets (Scriber and Slansky 1981). As such, Golden-winged Warblers may have established territories in areas with more black locust, and preferentially foraged on this tree species to access more abundant and higher quality caterpillar prey (Schoener 1971). A previous study in Kentucky reported that black locust was an indicator of Golden-winged Warbler territories on reclaimed surface mines, and that males were often observed gleaning insects from locust leaves (Patton et al. 2010). The importance of black locust to passerine foraging ecology has been reported in Illinois where four of eight passerine species preferred to search for prey on black locust (Hartung and Brawn 2005). However, the Kentucky and Illinois studies did not quantify caterpillar abundance, and thus did not provide a mechanistic explanation for the observed use of black locust by breeding songbirds. Our finding that black locust had the highest abundance of caterpillars among woody species sampled provides the first mechanistic explanation of the Golden-winged Warbler's close association with this early successional tree species in the Appalachian portion of its breeding distribution.

Similar to black locust, pin cherry had high caterpillar abundance, was selectively foraged on by Golden-winged Warblers, and was an indicator of territory use. Interestingly, black cherry was also an indicator of territory use and had a caterpillar abundance similar to that of pin cherry; however, Golden-winged Warblers selectively foraged on pin cherry over black cherry. This observation may be explained by differences in degree of herbivore defense exhibited by these two closely related species. Both black and pin cherry employ chemical defenses against herbivory via alkaloids, sterols, triterpenes, and benzenoids (Ricklefs 2008), but black cherry mounts a higher defense (Burns and Hankala 1990, Eisner and Siegler 2005). Black cherry supported a high caterpillar abundance, but Golden-winged Warblers may have foraged on black cherry less than expected based on its availability because associated prey were less palatable. Further research that examines specific prey species consumed by Golden-winged Warblers would be helpful in explaining observed differences in use of these closely related tree species as foraging substrates.

White oak was the only other tree species that was selectively foraged on by Golden-winged Warblers in our study. The selection of white oak by foraging Golden-winged Warblers was somewhat surprising because white oak had one of the lowest caterpillar densities among the 13 woody plant species that we sampled. We hypothesize that Golden-winged Warblers may have been forging in white oak to access alternative prey. For example, white oak supported the highest abundance of Hymenoptera (3.53 Hymenoptera/10 g dry leaf mass, SE = 2.90) and spiders (1.41 spiders/10 g dry leaf mass, SE = 0.43) among all woody plant species we sampled (Bellush 2012). White oak exhibited approximately two times the abundance of both these arthropod groups compared to black locust, which had the second highest abundance of both Hymenoptera and spiders (Bellush 2012). Golden-winged Warblers have been documented to consume other arthropods, including spiders and winged insects (Jacobs 1904, Forbush 1929) and it is plausible that Golden-winged Warblers were selectively searching for prey on white oak due to the abundance of alternative prey.

Of the four shrub species that dominated our study sites, only two shrubs (blackberry and mountain laurel) were used by foraging Golden-winged Warblers we monitored. Blackberry was selectively foraged on by Golden-winged Warblers and had one of the highest caterpillar abundances (Table 6.1; Figure 6.1). Furthermore, there was considerably more blackberry within Golden-winged Warbler territories compared to unoccupied areas. Previous studies elsewhere have identified positive relationships between songbird communities and blackberry (Kroodsma 1982, 1984; Nur et al. 2008). Our findings support the recommendations within recently published Golden-winged Warbler habitat management guidelines (Bakermans et al. 2011; A. M. Roth et al., unpubl. plan; Chapter 7, this volume) that blackberry provides an important component of Golden-winged Warbler breeding habitat.

Similar to blackberry, sweetfern supported a high abundance of caterpillars. The high number of caterpillars we found on sweetfern is unsurprising given this species' nitrogen fixing properties (Schemnitz 1974). However, we never observed Golden-winged Warblers searching for prey on sweetfern and its abundance did not differ between territories and unoccupied areas. Sweetfern is a low-growing shrub (~0.5 m in height) and was relatively uncommon in both territories and unoccupied areas compared to other shrub species (Table 6.2). Thus, low abundance and short stature may have limited our ability to observe Golden-winged Warblers searching for prey on sweetfern. Determining the degree to which Golden-winged Warblers take advantage of the high caterpillar abundances that occur on sweetfern is worthy of future investigation.

Several woody plant species that we examined appeared to provide limited-to-no benefits for breeding Golden-winged Warblers. Sassafras, mountain laurel, and blueberry were all indicators of areas unoccupied by Golden-winged Warblers, were not selectively foraged on, and had some of the lowest caterpillar densities of all woody species we sampled. It is unsurprising that sassafras was an indicator of areas unoccupied by Golden-winged Warblers as this species is known to have chemical defenses that deter herbivorous insects (Gant and Clebsch 1975). Oils extracted from sassafras leaves contain the monoterpene geraniol (Gant and Clebsch 1975), and various monoterpenes are toxic to herbivorous insects and serve as a feeding deterrent (Barnard and Xue 2004, Gershenzon and Dudareva 2007).

Mountain laurel comprised almost seven times and blueberry about three times the percent ground cover of unoccupied areas compared to Golden-winged Warbler territories. Specifically, these two shrub species alone accounted for over 60% of the ground cover in unoccupied areas (Table 6.2). As such, we speculate that the dominance of mountain laurel and blueberry prevented the development of other vegetation components known to be important to breeding Golden-winged Warblers (i.e., herbaceous plants and blackberry). We propose that low caterpillar abundance we observed on these woody plant species combined with their dominant influence on the presence of other important vegetation components likely explains why they were associated with areas unoccupied by Golden-winged Warblers.

In summary, selective foraging by male Golden-winged Warblers, along with high caterpillar abundances, indicated that black locust, pin cherry, white oak, and blackberry provided important foraging resources to breeding Golden-winged Warblers in north-central Pennsylvania. Thus, we urge land managers intending to create or improve quality of Golden-winged Warbler breeding habitat to consider the potential influence of plant species composition on prey abundance. Vegetation structure generally dominates management guidelines for Golden-winged Warbler breeding habitat, but our findings suggest preferentially maintaining or encouraging the presence of black locust, pin cherry, white oak, and blackberry, while eliminating or discouraging dominance of sassafras, mountain laurel, and blueberry in the High Allegheny Plateau physiographic region. Last, reforestation efforts on drastically disturbed areas in our study region such as reclaimed surface mines should consider including pin cherry, black locust, white oak, and blackberry in revegetation strategies. By doing so, extensive areas of nonforested, reclaimed surface mines in the region could be restored to young forests with high value for breeding Golden-winged Warblers. It is important to recognize that our findings are only applicable to a relatively small portion of the Golden-winged Warbler's breeding distribution. However, they highlight the need for further research that incorporates multiple study sites that represent a diverse group of vegetative communities to determine if plant species composition has a similar influence elsewhere on Golden-winged Warbler foraging ecology and territory placement. Our findings are based on the quantification of all caterpillar types, and that a study concurrent with ours provided the first empirical evidence that tortricid moth larvae (leafrollers, Lepidoptera: Tortricidae) are a major component of Golden-winged Warbler diets in Minnesota (Streby et al. 2014). As such, we strongly encourage future research to specifically quantify tortricid moth larvae to determine the degree to which Golden-winged Warblers depend on this caterpillar group.

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