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Foraging Ecology of the Golden-Winged Warbler (Vermivora Chrysoptera): Does Plant Species Composition Matter?

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FORAGING ECOLOGY OF THE GOLDEN-WINGED WARBLER

(*VERMIVORA CHRYSOPTERA*):

DOES PLANT SPECIES COMPOSITION MATTER?

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The Golden-winged Warbler (*Vermivora chrysoptera*) has experienced significant population declines over the past 50 years and is currently a focal species for young forest management in the eastern United States. While bird fitness has been linked to the quality and quantity of insect food supplies, research on Golden-winged Warbler foraging ecology has been limited. I evaluated shrub and tree species selection by foraging Golden-winged Warblers in northcentral Pennsylvania during the 2011 breeding season. Additionally, I compared prey (caterpillar) abundance among 13 woody plant species present within breeding territories. Golden-winged Warblers selectively foraged on black locust, pin cherry, white oak, and *Rubus* spp. Tree and shrub species composition differed between Golden-winged Warbler territories and adjacent, unoccupied areas of early successional habitat; findings were consistent with patterns of caterpillar abundances. Findings from this research provide land managers with insight for creating breeding habitat that considers the foraging ecology of this imperiled species.

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CHAPTER I

INTRODUCTION

Background

Historically, habitat conservation of imperiled avian species often focused on vegetation density and foliage structure of the environment (Rotenberry & Weins 1980; Vale et al. 1982). In fact, it was argued that bird community dynamics had little to do with plant species composition (MacArthur & MacArthur 1961, Diaz et al. 2005). However, recent studies have shown that insectivorous birds exhibit selection for tree species as forage substrates (Holmes & Robinson 1981; Gabbe et al. 2002; George 2009), which may be linked to prey density. While creating the optimal physical structure of a species' environment is an integral part of avian habitat management (MacArthur & MacArthur 1961; Gregg et al. 2000; Wood et al. 2006), it is equally important to incorporate knowledge of foraging ecology (Weikel & Hayes 1999). As such, managers should combine species-specific foraging preferences with information about vegetative composition and structure to provide improved habitat conditions for imperiled species. While much work has been done to elucidate habitat structure needs of many avian species (for example: Recher 1969; Fink et al. 2006; Roth et al. 2012), detailed information regarding foraging ecology is often lacking.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a neotropical migrant that has been experiencing population declines for more than 40 years (Sauer et al. 2011) and is considered a species of management concern (U.S. Fish and Wildlife Service 2009). The species declined 8.4% per year throughout its northeastern U.S. breeding range from 1966 to 2010 (Sauer et al. 2011). There have been drastic reductions in Golden-winged Warbler populations throughout the Appalachian region in states such as Virginia (-8.6%), Pennsylvania (-6.8%), West Virginia (-8.9), and Tennessee (-7.7) (Sauer et al. 2011). Reasons for these declines include reduced availability of breeding habitat, habitat loss on wintering grounds, hybridization with the Blue-winged Warbler (*V. cyanoptera*), and nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) (Buehler et al. 2007).

Research concerning Golden-winged Warbler breeding ecology has primarily focused on issues deemed conservation priorities (Buehler et al. 2007) such as nesting success (Confer et al. 2003), habitat use (Kubel & Yahner 2008), distribution (Ficken & Ficken 1968a; Confer et al. 2010), and its relationship with the Blue-winged Warbler (Ficken & Ficken 1968a; Confer & Knapp 1981, Confer & Larkin 1998; Reed et al. 2007; Patton et al. 2010). In 2008, a 3-year study was initiated to relate Golden-winged Warbler demographics and habitat characteristics throughout its breeding range. Findings from this range-wide study were used to identify "manageable habitat variables" and to create site-specific habitat prescriptions intended to guide future habitat management (Bakermans et al. 2012; Roth et al. 2012).

Evaluation of Golden-winged Warbler response to habitat prescriptions is the first step in creating habitat specifically for Golden-winged Warblers, although other high-risk, shrub-scrub species (i.e. American Woodcock, *Scolopax minor*; Eastern Whip-poor-will, *Caprimulgus vociferous*) may also benefit from these habitat modifications (Keppie & Whiting 1994; Cink 2002; Bakermans et al. 2011). Results from the range wide study provided the initial framework necessary to guide land managers with specific habitat variables important to the Golden-winged Warbler and associated shrub-scrub species (Roth et al. 2012).

While the recent range wide study has provided extensive insight into habitat influences on Golden-winged Warbler demographics, other aspects of the species' ecology are poorly understood. For example, little is known about Golden-winged Warbler foraging ecology (Jacobs 1904; Forbush 1929; Will 1986). Golden-winged Warblers may select territories based on plant species composition and selectively forage on certain tree species within their territory (Holmes & Robinson 1981; Gabbe et al. 2002; George 2009). Forage-site selection is a key aspect of avian breeding ecology and has been linked to abundance of prey (Holmes & Robinson 1981). Thus, determining the abundance and distribution of prey, foraging-site (i.e. plant species) selection, and vegetative composition and structure of occupied vs. unoccupied areas are important aspects of Golden-winged Warbler foraging ecology that are in need of study. Insight gained through Golden-winged Warbler foraging ecology research will provide valuable information to incorporate into recently developed Golden-winged Warbler conservation plans (Bakermans et al. 2011; Roth et al. 2012).

This research was designed to characterize the foraging ecology of the Golden-winged Warbler in northcentral Pennsylvania. Specifically, my study compared Golden-winged Warbler foraging behavior to 1) vegetative composition, and 2) cruciform larvae (i.e. caterpillar) availability. I examined foraging site selection to determine if there were particular plant species used by Golden-winged Warblers as forage sites and if this selection was associated with caterpillar prey abundance. I also surveyed adjacent, similarly aged, yet unoccupied areas to evaluate floristic and structural differences between used and unused habitat.

Objectives

1. Examine whether Golden-winged Warblers forage on plant species in proportion to availability within their breeding territory.
2. Quantify cruciform larvae abundance on branches of focal tree and shrub species with and without bird-exclosure netting.
3. Relate Golden-winged Warbler foraging site selection to cruciform larvae availability.
4. Evaluate plant species composition and structural habitat differences between early successional habitat occupied and unoccupied by Golden-winged Warblers.

CHAPTER II

LITERATURE REVIEW

The Golden-winged Warbler is distributed throughout its breeding grounds in the higher elevations of the Appalachian Mountains, the northeast and north-central regions of the United States, and scattered areas in Canada (Confer et al. 2011; Roth et al. 2012). The species winters in southern Central America and northern South America, from southern Nicaragua to Costa Rica, Panama, Venezuela, and Colombia. The Golden-winged Warbler arrives at their North American breeding grounds from the end of April through the end of May (Confer et al. 2011).

The Golden-winged Warbler is an imperiled, ground-nesting passerine with grey plumage and bright patches of yellow on its head and wings (Earley 2003). This species breeds in early successional, heterogeneous habitat with a combination of herbaceous and woody patches (Ficken & Ficken 1968a; Confer et al. 2011; Roth et al. 2012). Territories are typically located along edges between forest and natural or man-made early successional habitat resulting from timber harvests, fire, wind events, wildlife openings, utility rights-of-way, shrub wetlands, and abandoned beaver meadows (Short 1963; Klaus & Buehler 2001). Because Golden-winged Warblers breed in habitats that are ephemeral in nature, the availability of adequate habitat depends on periodic disturbances (Confer & Knapp 1981).

Golden-winged Warbler Decline

Of all the factors thought to be contributing to the decline of the Golden-winged Warbler, breeding habitat loss in areas devoid of Blue-winged Warblers is likely the most significant cause (Confer et al. 2003; Buehler et al. 2007). The Golden-winged Warbler expanded into the northeastern United States in the past 150 years, occupying secondary successional shrubby habitat on abandoned farms and clear-cut forests (Confer et al. 2010). The initial stages of farmland abandonment in the eastern United States most likely provided the early successional habitat necessary for the expansion of the Golden-winged Warbler (Confer & Knapp 1981; Confer & Larkin 1998). Golden-winged Warblers experienced the loss of vast amounts of habitat (tens of millions of hectares) as abandoned farm land passed through the early stages of shrub succession (Confer et al. 2003).

Loss of early successional habitat is not the only reason for decline because even in areas where breeding habitat exists, Golden-winged Warblers are no longer present (Confer et al. 2003). Golden-winged Warblers are experiencing hybridization with the Blue-winged Warbler that reduces "pure" Golden-winged Warbler genotypes (Gill 1980; Vallender et al. 2009). Hybrids between the two species were not reported until 1874 when the two main phenotypes (Brewster's Warbler, *V. leucobronchialis*; Lawrence's Warbler, *V. lawrencei*) were described as new species (Gill 2004). This hybridization has been correlated with the northeast spread of Blue-winged Warblers in the past 150 years into the historic range of the Golden-winged Warbler (Parkes 1951; Ficken & Ficken 1968b; Gill & Murray 1972). Both species have exhibited northward range expansions within the past 150 years, but Golden-winged Warbler expansion preceded Blue-winged Warbler expansion (Confer & Knapp 1981). This expansion lag may have occurred because of relatively recent farmland abandonment and the Golden-winged Warbler's habitat preference for higher herb-cover values than the Blue-winged Warbler (Confer et al. 2003).

Hybridization of the two species could eventually lead to the extinction of the Golden-winged Warbler (Vallender et al. 2009). Blue-winged and Golden-winged Warblers were allopatric in North America before European settlement but they are now sympatric over a wide area because of regional habitat changes, such as abandonment of old fields and reforestation (Gill 1980). Increased anthropogenic changes often cause genetically similar, previously isolated species to come into secondary contact (Rhymer & Simberloff 1996). When a declining species experiences genetic introgression by a closely related species, extinction often results (Wolf et al. 2001).

On the other hand, recent research has questioned the Blue-winged Warbler's role in the decline of Golden-winged Warbler populations (Shapiro et al. 2004). Intensified sampling (compared to original genetic research [Gill 1980, 1987, 1997]) in West Virginia showed equally proportioned introgression of each species' mtDNA into the others species' mtDNA, while smaller samples in Michigan and Ohio also failed to show any evidence of asymmetrical introgression (Shapiro et al. 2004). Thus, hybridization with the Blue-winged Warbler may have less of an effect on Golden-winged Warblers population declines than initially suspected.

Several other factors contribute to the population decline of the Golden-winged Warbler (Buehler et al. 2007). Blue-winged Warblers occupy habitats similar to those of the Golden-winged Warbler (Will 1986; Patton et al. 2010), and may have a competitive advantage over Golden-winged Warblers with respect to foraging (Ficken & Ficken

1968a). Blue-winged Warblers foraged faster and probably more efficiently than Golden-winged Warblers, exhibiting higher rates of feeding patterns per minute, locomotory patterns per minute, locomotory and feeding patterns per minute, and feeding patterns per locomotory patterns (Ficken & Ficken 1968a). Blue- and Golden-winged Warblers obtained their prey in the same manner and at the same relative height; while Golden-winged Warblers tended to feed higher than Blue-winged Warblers, foraging height differences were not statistically significant between the two, which may increase interspecific competition (Ficken & Ficken 1968a). On the other hand, conflicting research has demonstrated that interference competition between the two species for territorial space does not limit Golden-winged Warblers and the two species generally ignore each other (Gill & Murray 1972; Confer & Larkin 1998). That being said, the bills of Golden-winged and Blue-winged Warblers are adapted for gleaning and probing buds and leaf clusters; similarities in feeding locations and methods seem to suggest that the two species eat similar food (Ficken & Ficken 1968a), even if they do not aggressively compete for prey resources.

Research has shown that Golden- and Blue-winged Warblers compete with each other for space and food resources because of similar ecological requirements (Ficken & Ficken 1968a). One might infer that because the two warbler species seem to forage in such a similar manner, they may not be able to partition resources as efficiently as other ecologically similar species (e.g. resource partitioning, MacArthur 1958). In fact, since Blue-winged Warblers tend to replace Golden-winged Warblers within 50 years of establishment in an area (Gill 1980), it can be deduced that effective partitioning of resources is unlikely and their niches are too similar to allow indefinite coexistence in most areas although one exception has been documented (Sterling Forest, New York, Confer et al 1998).

Golden-winged Warbler populations are also declining in some regions due to brood parasitism by Brown-headed Cowbirds (Coker & Confer 1990; Confer et al. 2003). In central New York, cowbirds parasitized about 30% of Golden-winged Warbler nests, which reduced fledging success by about 17% (Confer et al. 2003). Because Golden-winged Warblers prefer to nest in areas that are relatively open, one might hypothesize that they are naturally more susceptible to brood parasitism by Brown-headed Cowbirds, which often parasitize nests along field and forest edges (Brittingham & Temple 1983). In fact, Golden-winged Warblers nesting in earlier stages of succession were more likely to be parasitized by Brown-headed Cowbirds (Confer et al. 2003). On the other hand, Brown-headed Cowbirds seem to be uncommon in the eastern United States where there are areas of large, unbroken forests (Wilcove 1988; Coker & Confer 1990) and it has been suggested that land managers should maintain and/or establish large areas of continuous forest cover to guard breeding neotropical migrants against Brown-headed Cowbird parasitism (Robinson et al. 1993). Many of the remaining populations of Golden-winged Warblers in the eastern United States occur in extensively forested landscapes (Roth et al. 2012). As such, nest parasitism by Brown-headed Cowbirds may have minimal impacts remaining Golden-winged Warbler populations.

Golden-winged Warbler Foraging Ecology

Interestingly, the genus name "*Vermivora*" is Latin for "worm-eating" where the root "verm-" translates to "worm" and "vora-" translates to "swallow" (Smeaton 1843).

This, however, is somewhat of a misnomer because members of the genus *Vermivora* do not eat worms, but do commonly prey on caterpillars (Griscom 1947).

While biologists understand much of the Golden-winged Warbler's basic life history, its feeding preferences are almost completely unknown. Researchers agree that they prefer arthropods of some kind but exactly what species they consume has only been identified in a few instances (Jacobs 1904; Forbush 1929; Will 1986). Although no formal analysis was conducted, Will (1986) observed Tortricid moths and their larvae to be the main prey of Golden-winged Warblers, but noted that various moths and their pupae, as well as other winged insects and spiders are also part of their diet. Forbush (1929) noted that Golden-winged Warblers preyed on many destructive caterpillars (such as: canker-worms, genus and species unidentified; brown-tail moth larvae, *Euproctis chrysorrhoea*; gypsy moth larvae, *Lymantria dispar*) but acknowledged that little was actually known about the Golden-winged Warbler's diet.

Golden-winged Warblers in Kentucky were often observed gleaning insects from black locust (*Robinia pseudoacacia*) leaves, possibly because it experiences heavy browsing by many insects, including the locust borer (*Megacyllene robiniae*) (Patton et al. 2010). Though no data was provided to support tree species preferences, Ficken & Ficken (1968a) noted that apple (*Pyrus malus*), black cherry (*Prunus serotina*), and hawthorn (*Crataegus* sp.) were the main small trees on which Golden-winged Warblers searched for prey. In Maryland, Nelson (1933) observed an individual Golden-winged Warbler feeding on a low shrubby growth of pawpaw (*Asimina triloba*) containing Lepidoptera larvae of *Talponia plummeriana*. McDonald (1976) observed Blue-winged Warblers feeding on two occasions: 2 adults and 1 juvenile were seen gleaning

Lepidopteran mimosa webworm larvae (*Homadaula anisocentra*), a probable apple aphid (probably *Aphis pomi*, Order Homoptera), and a walnut parasite (*Corythucha* sp. nymph, Order Hemiptera).

In Pennsylvania, Jacobs (1904) observed Golden-winged Warbler foraging behavior but conducted no formal investigation or analysis. Nonetheless, Jacobs' (1904) accounts are detailed and provide an interesting look into Golden-winged Warbler foraging ecology. He observed males foraging among the tips of branches and tops of saplings. He assumed that the males were obtaining leaf lice and small caterpillars that reside in the tips of branches and the underside of leaves because they constantly searched and picked at emerging buds and leaves on twig-ends. Jacobs (1904) noted that it was not possible to see what the Golden-winged Warblers caught because they were foraging relatively high in the vegetation. After personally examining foraging sites, he found many brown and green "leaf-lice" and small "hump-back winged mites" on the leaves and twigs. He was not able to discern identity and therefore concluded that food brought back to the young must be miniscule. However, several times Jacobs (1904) observed Golden-winged Warblers feeding their young small green worms, and on one occasion he observed a female bring a small brown butterfly to her nestlings. Jacobs (1904) also observed Golden-winged Warblers catching flying insects and the occasional spider.

The bills of *Vermivora* are straight and acute at the tip; with respect to foraging and feeding, they are suited for probing in buds and leaf clusters, spreading the vegetation apart, and grasping small insects found inside (Ficken & Ficken 1968a). In central New York, Golden-winged Warblers probed buds, leaf clusters, and to a lesser extent, flowers

84% of the time, and had a tendency to forage in the upper quarter of the vegetation in 58% of observations (Ficken & Ficken 1968a). Warblers have been described as members of a "gleaning guild"; their adaptive syndrome has been classified as "active searchers" but "passive pursuers" because they search for prey that is hard to find (must actively search for it), but attack prey that is easy to catch (passive prey) (Eckhardt 1979). Insectivorous passerines like the Golden-winged Warbler have also been classified by their type of "search modes", all of which result in the capture of different types of prey (Holmes & Recher 1986; Holmes et al. 1979a; Robinson & Holmes 1982; Holmes & Schultz 1988). "Near-surface" searching was found to be characteristic of three Parulid warblers studied in a northern hardwoods forest (Black-throated Green Warbler, *Setophaga virens*; Black-throated Blue Warbler, *S. caerulescens*; Blackburnian Warbler, *S. fusca*) (Robinson & Holmes 1982). Near-surface searching involves making many quick movements between perches while searching nearby surfaces for prey that are close enough to be obtained with a short hover; species that exhibit this behavior commonly capture small, hidden prey that is probably missed by birds searching from a farther distance (Robinson & Holmes 1982). This technique tends to be characteristic of small insectivorous birds, including warblers from the neotropics (Robinson & Holmes 1982).

Foraging Selection of Avian Insectivores

Given that the foraging ecology of Golden-winged Warblers has not been well studied, one can reference research conducted on similar insectivorous passerine species to compare methodology and significant findings. For example, MacArthur (1958) studied five species of coexisting, congeneric insectivorous warblers: Cape May *(S. tigrina)*, Myrtle *(S. coronata)*, Black-throated Green, Blackburnian, and Bay-breasted *(S.*

castanea). Since the five species were so similar in ecological preference, researchers hypothesized that any differences in environmental requirements must be very slight (MacArthur 1958). Through extensive observations, it was found that each of the five species had dissimilar feeding preferences and foraged in different 'zones' of canopy trees; therefore each species was exposed to different kinds of food, which seemed to have reduced interspecific competition (MacArthur 1958).

Foliage gleaning, insectivorous birds have been documented to preferentially forage on specific species of trees (Willson 1970; Holmes & Robinson 1981; Gabbe et al. 2002; George 2009). For instance, in a study conducted to guide floodplain forest restoration in southern Illinois, researchers determined that three tree species (kingnut hickory, *Carya laciniosa*; bitternut hickory, *C. cordiformis*; silver maple, *Acer saccharinum*) were strongly preferred by most members of the bird community while some birds specifically avoided certain trees (blue beech, *Carpinus caroliniana*; pumpkin ash, *Fraxinus profunda*; sweet gum, *Liquidambar styraciflua*) (Gabbe et al. 2002). In a northern hardwoods forest in New Hampshire, 10 avian species, including some wood warblers (e.g. Black-throated Green and Blackburnian Warblers) showed a preference for a particular tree species (yellow birch, *Betula alleghanisnsis*) and some bird species specifically avoided certain trees (American beech, *Fagus grandifolia*; sugar maple) (Holmes & Robinson 1981).

Similarly, in West Virginia, Kentucky, and Ohio, the Cerulean Warbler (*S. cerulea*) selected certain tree species as forage sites (George 2009). Researchers established tree species availability based on importance values calculated from density, frequency, and basal areas, and found that availability differed from tree species used by

Cerulean Warblers for foraging (George 2009). Cerulean Warblers were found to preferentially forage on hickory (*Carya* spp.), sugar maple, and chestnut oak (*Quercus pinus*), but strongly avoided red oak (*Q. rubra*) (George 2009).

Avian Species as a Component of the Ecosystem

Insectivorous birds have a considerable effect on the communities they inhabit, providing services that aid in the functioning of the ecosystem (Ehrlich & Mooney 1983). One of the services birds provide is the maintenance of arthropod populations (Gibb 1958). As such, research has shown that birds selectively forage from preferred tree species (Willson 1970; Holmes & Robinson 1981; Gabbe et al. 2002; George 2009), which may be related to a non-random arthropod distribution among vegetation (Holmes & Schultz 1988; Marshall & Cooper 2004).

Protective netting applied to vegetation is an effective way to study arthropod communities with and without avian predation (Holmes et al. 1979a; Mols & Visser 2002). For example, in the Netherlands, researchers examined the extent of bird foraging in an apple orchard by excluding them from apple trees with polyethylene nets (Mols & Visser 2002). Great Tits (*Parus major*) were found to reduce caterpillar damage on apple trees (13.8% to 11.2%, $P < 0.05$) and increase fruit yield from 4.7 kg to 8.8 kg apples per tree ($P < 0.05$) (Mols & Visser 2002).

Exclosures have also been utilized in a more natural environment to determine the impact foraging insectivorous birds have on caterpillar abundance (Holmes et al. 1979b, Atlegrim 1989). When crop protection netting was utilized to exclude forest birds from entire trees of striped maple (*Acer pensylvanicum*), researchers found the incidence of more sedentary Lepidoptera larvae to always be higher inside the exclosures than outside, but found no significant density differences between other, more mobile, arthropod groups (Arachnida, Coleoptera, and Hemiptera) (Holmes et al. 1979b). By visually assessing all insects found in exclosures and on untreated vegetation, it was determined that birds exhibited heavy predation on Lepidoptera larvae; using exclosures allowed researchers to evaluate caterpillar distribution with and without the influence of bird predation (Holmes et al. 1979b).

Branch clipping is a common method used to measure arthropod availability for foraging birds (e.g. Keane & Morrison 1999; Johnson 2000; Johnson & Sherry 2001). Foraging observations were incorporated into an arthropod sampling protocol to study prey availability of 3 insectivorous, foliage-gleaning migratory warblers in Jamaica: American Redstart (*S. ruticilla*), Northern Parula (*Parula americana*), and Prairie Warbler (*S. discolor*) (Johnson 2000). The principal index of food availability was defined as the density of prey in the environment as derived from branch clippings, where prey density was calculated as biomass of all trapped arthropods per gram of clipped vegetation in a sample (Johnson 2000; Johnson & Sherry 2001). Prey collected was identified, measured, and then compared among habitats, foraging attack rates and maneuvers, and use of microhabitats (Johnson 2000). Through dietary analysis, it was found that nearly all items eaten by the insectivores were captured by branch clipping, and so was determined that branch clipping was effective in measuring food availability for the warbler species studied (Johnson 2000).

Findings from these studies show the relationship between species composition, vegetation structure, prey abundance, and avian foraging ecology. Arthropod abundance varies among tree species (Holmes & Schultz 1988; Marshall & Cooper 2004), which may be linked to tree species-specific foraging preferences. Evaluating the vegetative characteristics of the Golden-winged Warbler's breeding habitat and relating these to prey abundance in a given area are key factors in understanding the foraging ecology of Golden-winged Warblers.

CHAPTER III

STUDY AREA

I examined the foraging behavior of the Golden-winged Warbler, vegetation characteristics, and caterpillar abundance at Sproul State Forest in northcentral Pennsylvania (Figure 1). Sproul State Forest is located in the Bureau of Forestry District #10 and is part of the Allegheny Highlands Forest Ecoregion (PA DCNR 2012). It lies in western Clinton and northern Centre Counties and encompasses 112,000 ha. Sproul State Forest is north of the Allegheny Front and part of the Allegheny Plateau Physiographic Province, which is characterized by high ridges and deep valleys (USGS 1986). The landscape was dominated by northern hardwood and dry oak forest. Most forest stands in Sproul State Forest were mature (80-100 years old), and thus not suitable as habitat for breeding Golden-winged Warblers. Rather, Golden-winged Warblers in this region were restricted to regenerating timber harvests, abandoned gas wells, and areas recovering from an expansive (4,000ha) wildfire that occurred in 1990 (Figure 2). Burned areas were dominated by coppicing red maples (*Acer rubrum*), sassafras (*Sassafras albidum*), sweet birch (*B. lenta*), and mountain laurel (*Kalmia latifolia*). While Sproul State forest lies in the heart of the Pennsylvania Wilds, there are some anthropogenic disturbances in the area including primitive cabins, a major gas pipeline, State Highway 144, gated and ungated access roads, and hundreds of natural gas wells.

Golden-winged Warblers inhabiting Sproul State Forest were the focus of intensive breeding-habitat research from 2008-2011. Over the past 4 years, territory density averaged 1.75 territories/10ha, ranging from 1.08 - 2.52 territories/10ha. Golden-winged Warbler breeding territories were characterized by ground cover dominated by

Rubus spp. and scattered herbaceous plants. Saplings within territories were typically comprised of black locust, black cherry, chokecherry (*Prunus virginiana*), and white pine (*Pinus strobus*), while trees generally included black cherry, black locust, white pine, pin cherry (*P. pensylvanica*), and red maple.

Sproul State Forest is important from a Golden-winged Warbler conservation perspective because Golden-wing x Blue-wing hybrids are rare and the area is devoid of Blue-winged Warblers. As such, evaluating breeding habitat characteristics, including forage substrate selection, in this portion of the Golden-winged Warbler's breeding range will help identify effective management parameters applicable throughout the expansive forested landscape of northcentral Pennsylvania.

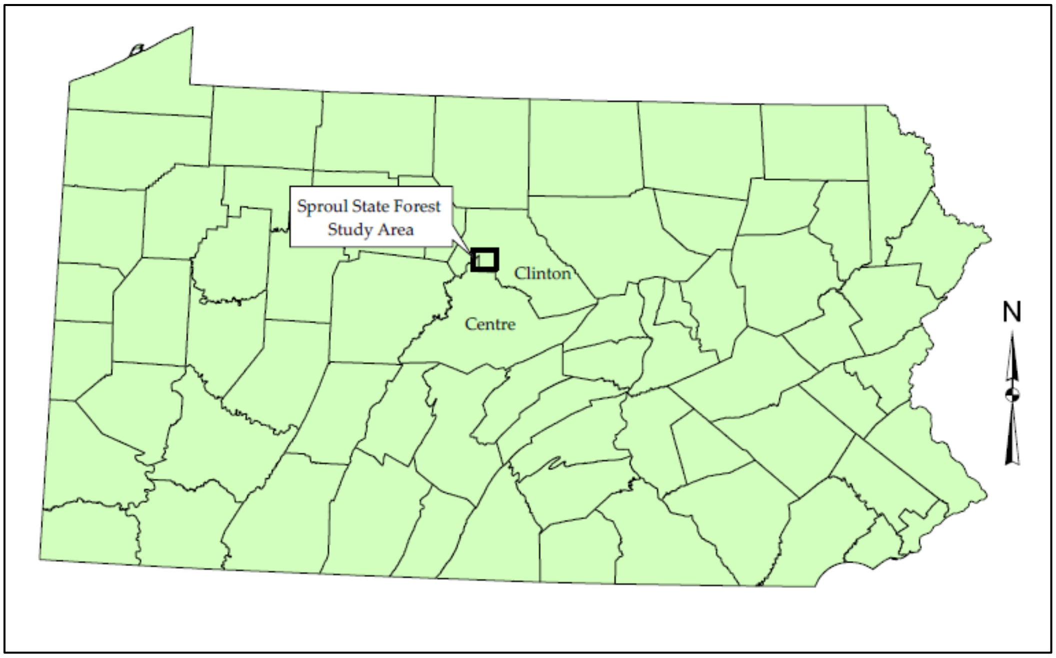

Figure 1. Golden-winged Warbler foraging observations, prey availability, and habitat characteristics were examined during the 2011 breeding season in Sproul State Forest, Pennsylvania.

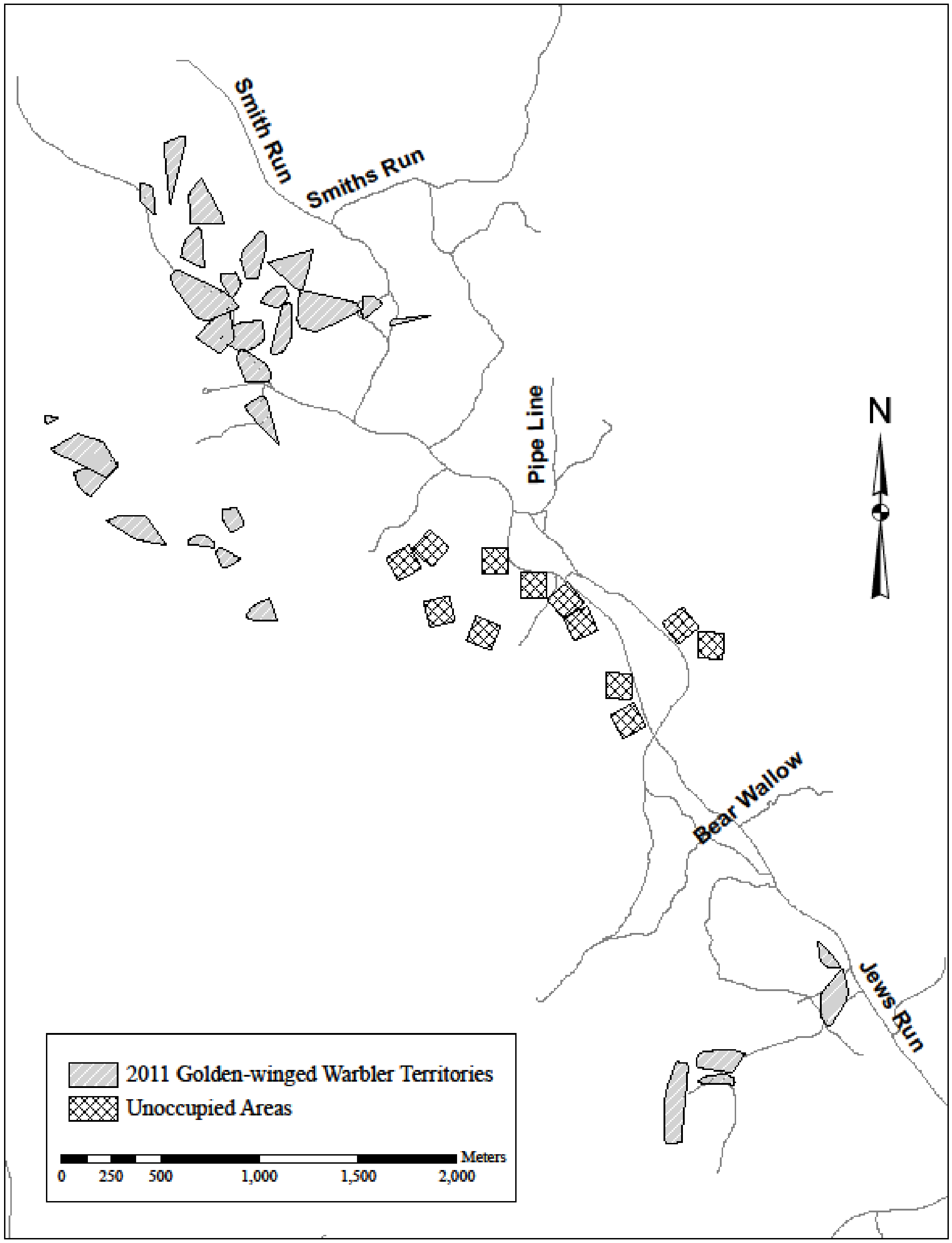

Figure 2. Golden-winged Warbler territories spot-mapped during the 2011 breeding season in Sproul State Forest, Pennsylvania.

CHAPTER IV

METHODS

Golden-winged Warbler Foraging Observations & Territory Mapping

This research was conducted between 1 May through 10 July 2011. Sproul State Forest was the focus of a larger study of Golden-winged Warbler breeding ecology beginning in 2008. As such, several males were previously banded with USGS aluminum leg bands, as well as unique combinations of colored leg bands so each individual could be visually identified from a distance (Fair et al. 2010). Unbanded territorial males were captured and fitted with leg bands using a Golden-winged Warbler type I and II song playback, a male Golden-winged Warbler decoy, and 6 m mist net.

I attempted to observe color-banded male Golden-winged Warblers for ≤30 minutes every other day between the hours of 0500 and 1800 EST. Studies have shown that first and subsequent observations in a foraging bout do not differ, thus, all observations in a foraging bout were included in the analysis (Holmes et al. 1979a; Morrison 1984; George 2009). Furthermore, Golden-winged Warblers can traverse their territories almost instantaneously so I considered movements from one tree to the next to be independent observations. The order of monitoring individuals was altered so that foraging observations were documented at varying times of day (Shields 1977). The following was recorded using field notebooks and digital voice recorders: study site, date, time of day, individual identification, individual's sex, geographic location (using a GPS), plant species, activity (singing, perching, or foraging), duration of time spent foraging, and size class of the forage site vegetation. Vegetative size class categories included: shrubs (a woody low-growing plant containing multiple stems), saplings (>0.5 m tall, 1-10 cm dbh), mid-sized trees (10 cm < dbh ≤ 19.9 cm), and large trees (≥20 cm). When prey capture was observed, observers recorded vegetation layer wherein the prey was captured (shrub layer, mid-story or canopy).

Territory mapping of male Golden-winged Warblers was conducted concurrently with foraging observations using the methods of Wakeley (1987). Territories were delineated by following males for ≥8 days; song-posts and foraging sites were marked with flagging and recorded with a handheld GPS receiver (Garmin eTrex H, North American Datum 1927). Territory mapping data and the Hawth Tools extension in ArcGIS 9.2 (ESRI 2009) were used to measure the area of each male's territory (ha) using Minimum Convex Polygons (MCPs). To construct MCPs, the Hawth Tools (Beyer 2004) extension fits the smallest possible convex polygon to geographic locations of foraging and song posts (Mohr 1947). By default, the area of each polygon was calculated; this was used to plan vegetative sampling of each male's territory.

Vegetation Sampling

Vegetative surveys were conducted at the end of the field season (late June to early July, 2011). To quantify the vegetative composition and structure within each territory, I conducted systematic random sampling along transects. A random number generator was used to determine the compass bearing, and transect starting point. Vegetation was sampled within 5m radius circular plots (Morrison 1981; Canterbury et al. 2000). In each plot, I recorded the number and species of all trees and saplings. Saplings were defined as ≥0.5 m tall and between 1.0 cm ≤ dbh < 10.0 cm and trees were defined as ≥10 cm dbh. Trees and saplings were later combined to increase power of statistical analyses. I also recorded percent herbaceous cover, percent tree seedling cover, percent bare ground, and percent cover of each shrub species. Shrubs were considered any woody, low growing plant with multiple stems.

The number of sampling plots per territory varied depending on territory size; vegetation survey plans for each territory were calculated to include 1 sampling point per one tenth of a hectare. For example, if a territory was 1.7ha, 17 vegetation plots were surveyed. This ensured that all territories were sampled proportionate to size and the patchy nature typical of Golden-winged Warbler habitat was adequately characterized (Confer et al. 2011).

Arthropod Sampling

To estimate arthropod abundance, I collected branch clippings (Holmes et al. 1986; Cooper & Whitmore 1990; Johnson 2000; Kilgo 2005). While many techniques have been employed to determine the density and distribution of arthropods, branch clipping was the most appropriate and practical method for the purpose of this study (Naef-Daenzer & Keller 1999). Branch clipping is a common method used to measure arthropod availability for foraging birds (e.g. Keane & Morrison 1999; Johnson 2000; Johnson & Sherry 2001) and dietary analyses have found that this method captures nearly all items eaten by insectivores (Johnson 2000).

Exclosure netting was applied to branches of 13 focal woody plant species present within Golden-winged Warbler territories; this allowed an evaluation of arthropod abundance without the influence of bird predation. Exclosures were constructed using 2 cm x 2 cm rolled plastic netting (1 m wide roll), cut into 2.4 m sections. Netting was folded and sewn (with cotton string) to create a bag with final exclosure dimensions of 1.2 m x 1 m.

Exclosure netting was placed on branches 10 different individuals of each target plant species: blackberry (*Rubus* spp.), black locust, blueberry (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), sweetfern (*Comptonia peregrina*), black cherry, pin cherry, chestnut oak (*Quercus prinus*), red maple, sassafras, sweet birch, white oak (*Q. alba*), and white pine. Exclosure netting was applied to branches from 22 May – 24 June 2011 throughout the study area.. Netting remained on branches for a minimum of two weeks to allow insects to recolonize vegetation (in the absence of bird predation).

To determine if bird predation had an effect on caterpillar abundances, additional branches were clipped from non-netted branches of black locust (n = 10), pin cherry (n = 5), and blackberry (n = 10), which was compared to additional, paired exclosures placed on these species. Quantification of caterpillar abundances on netted vegetation provided an opportunity to relate caterpillar abundance (in the absence of bird predation) with Golden-winged Warbler foraging observation data.

All branches were clipped from 8 June through 9 July 2011; branch collection (thus arthropod availability) was timed to coincide with Golden-winged Warbler nestling stage when the need for food resources is greatest. Branches were collected in a manner to keep arthropod loss (falling off leaves, flying away) at a minimum. I gently placed a 39 gallon, heavy duty plastic bag over the branch, the end of the bag was cinched shut, the branch was clipped, and the bag was tightly tied. Within two days of branch collection, all arthropods were counted and identified to Order using identification guides (Borror and White 1970, Knoph 1980). Because Golden-winged Warblers feed primarily on caterpillars during the breeding season, cruciform larvae were placed in screw-cap vials with 95% ethanol to prevent denaturation of proteins for genetic analyses to identify species (Gullan & Cranston 2010). Specimens were labeled with a unique identification code that corresponded to 1) the date of collection; 2) geographic location of collection site; and 3) plant species from which the larvae was collected. These specimens have been stored for future genetic analysis to determine family, genus, and species. I only preserved caterpillars because they are a major food resource for breeding insectivorous birds (Molles 2002) and it is well documented that this prey item dominates nestling provisioning by Golden-winged Warblers (Jacobs 1904; Forbush 1929; Nelson 1933; Will 1986).

Leaves from each clipping also were collected and stored in paper bags labeled with a unique code corresponding to the date of clipping, species, and whether the vegetation was netted or un-netted. Leaves in paper bags were hung to allow for air flow and to keep moisture at a minimum until they were oven dried (40°C for 48 hours) and weighed to determine dry weight (Butler & Strazanac 2000; Marshall & Cooper 2004). This data allowed arthropod captures to be expressed in relation to dry leaf weight (# caterpillars/10g dry leaf weight) (Futuyma & Gould 1979).

Statistical Analyses

Plant Species Use vs. Availability

Third-order resource selection compares used and available habitat for individual animals within their respective home range (territory) (Johnson 1980). Individual Golden-winged Warblers were considered the sampling unit which avoids problems related to independence of observations and sampling level (Aebischer et al. 1993; Manly et al. 2003). I used compositional analysis to evaluate whether Golden-winged Warblers foraged in certain tree and shrub species disproportionate to what was available within their spot-mapped territory.

I used the function `compana` (compositional analysis) in the `adehabitat` package (Calenge 2006) in Program R (R Development Core Team 2011). Use of compositional analysis relies on the relative, proportional use of resources and 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). Compositional analysis requires that any zeros in the observed use of a resource be substituted by a small, nonzero value that is an order of magnitude less than any nonzero proportion in either the used or available matrices (Aebischer et al. 1993; Cox & Afton 1998; Giese 1999). The smallest proportion of observed use for shrubs was 0.05 so a replacement value of 0.005 was used. The smallest proportion of observed use for trees was 0.004 so a replacement value of 0.0004 was used. To account for non-normality in the data, multivariate normal tests were replaced with tests based on data randomization with 10,000 repetitions (Aebischer et al. 1993). To reduce the number of resource categories within the analysis, only shrubs and trees present in > 50% of territories and utilized for foraging on at least two occasions were included. Because of these criteria, my results reflect relative preference among used species within Golden-winged Warbler territories, not avoidance. Shrub and tree species were considered to be used more than their availability when $p < 0.05$.

Caterpillar Abundance Analysis

Caterpillar abundances were highly non-normal, and thus were compared using nonparametric methods (Zar 1999). A Kruskal-Wallis rank sum test was implemented in Program R (R Development Core Team 2011) to determine if there was a significant difference in observed caterpillar abundance among woody plant species. Because tree and shrub species use by Golden-winged Warblers were analyzed independently, caterpillar abundance on trees and shrubs were also analyzed separately. If an overall difference was found, multiple comparisons were employed in Program R with the `pgirmess` package (Siegel & Castellan 1988, Giraudoux 2011) to determine species-specific differences between caterpillar abundance. Multiple comparisons ranked caterpillar abundance for each branch clipping and calculated the observed difference between abundance on two species (difference between the average sum of ranks for two species) (Siegel & Castellan 1988). The difference in caterpillar abundance between two species was considered significant when the observed difference was greater than the critical x^2 value (Siegel & Castellan 1988). An alpha level of 0.05 was used to determine significance with pairwise comparisons adjusted at $\alpha = 0.05$ (Giraudoux 2011).

Additionally, I compared caterpillar abundance among netted and un-netted branches of 3 plant species (*Rubus* spp., black locust, and pin cherry) using an independent samples t-test in SPSS version 19 (SPSS Inc., Chicago, IL). Caterpillar abundance on blackberry was marginally non-normal and so it was log(x+1) transformed prior to analysis (Zar 1999).

Analysis of Occupied vs. Unoccupied Areas

Vegetative structure of territories occupied by Golden-winged Warblers was compared to adjacent, similarly aged, yet unoccupied, areas using independent samples t-test (Zar 1999) in SPSS version 19 (SPSS Inc., Chicago, IL). Specifically, I compared percent cover of shrubs and herbaceous cover, number of saplings, and number of trees between territories and unoccupied areas. Both tree and sapling counts were non-normal, and were log-transformed to fit the normal distribution [x'=log(x+1), Zar 1999]. Structure of occupied and unoccupied areas was determined to be significantly different when $p < 0.05$.

Due to non-normality of data, a Mann-Whitney U test and SPSS version 19 (SPSS Inc., Chicago, IL) was used to compare compositional differences in ground cover between Golden-winged Warbler territories and adjacent unoccupied areas (Zar 1999). Ground cover variables included percent cover of bare ground, tree seedlings, herbaceous cover, and percent cover of each shrub species (mountain laurel, blueberry, sweet fern, and *Rubus* spp.). I also conducted an indicator species analysis (Dufrêne & Legendre 1997) in PC-ORD 6.0 (McCune & Mefford 2011) to determine tree species indicative of Golden-winged Warbler territories or unoccupied areas (Patton et al. 2010). This method, a form of cluster analysis, combines data on the concentration of species abundance in a particular group and faithfulness of species occurrence in a particular group (Dufrêne & Legendre 1997). These two components are combined to produce indicator values (IV), which are then tested for statistical significance by Monte Carlo randomizations (Dufrêne & Legendre 1997). A significant result indicated that the plant species was characteristic to either territories or unoccupied areas and was present in the majority of the plots belonging to an area (Dufrêne & Legendre 1997). Species were considered to be indicators of a particular area when $p < 0.05$.

CHAPTER V

RESULTS

Plant Species Use vs. Availability

I observed fourteen male Golden-winged Warblers foraging on trees and shrubs for 15194 s and 3062 s, respectively. On average, each individual was observed foraging on trees for 1058 s and shrubs for 278 s (Table 1). Average time spent foraging in one location was 124 s (maximum: 1140 s). Golden-winged Warbler males were observed foraging for an average of 7 days (minimum = 4 d; maximum = 12 d) with an average of 9 foraging bouts/individual (minimum = 4; maximum = 24 d) (Table 1). For the purpose of summarizing foraging observations, a foraging bout was considered foraging observations collected within a short amount of time (i.e. observations collected within <5 minutes of each other).

A total of 25 tree species were recorded within Golden-winged Warbler territories (Table 2). Of the 25, 7 tree species met my criteria for inclusion in the compositional analysis. In other words, only 7 tree species were present in at least half of territories and foraged on at least two times. Tree species included in the analysis were black cherry, black locust, pin cherry, sweet birch, red maple, sassafras, and white oak. It should be noted that although white pine and red pine were present in relatively high quantities within territories (Table 2), they were not used for foraging and thus were not included in the compositional analysis. Golden-winged Warbler use of these 7 tree species differed from random ($\Lambda = 0.052$, $p = 0.010$). Black locust and pin cherry were both foraged in more than black cherry while white oak was foraged on more than sassafras and sweet birch (Table 3).

Two of the 14 Golden-winged Warblers were not observed foraging on shrubs, thus, they were excluded from the shrub selection analysis. Four shrub species were recorded within territories: *Rubus* spp., blueberry, mountain laurel, and sweet fern. Mountain laurel and *Rubus* spp. were the only shrub species on which birds were observed foraging; therefore, these two species were the only shrubs included in the analysis. Foraging use of the two shrub species differed significantly from random ($\Lambda = 0.067$, $p = 0.016$). *Rubus* spp. was selectively foraged on, compared to the use of mountain laurel (Table 3).

Table 1. Individual male Golden-winged Warbler foraging observations collected during the 2011 breeding season at Sproul State Forest, Pennsylvania.

Individual ID	Time Observed Foraging on Trees (s)	Time Observed Foraging on Shrubs (s)	Total Time Observed Foraging (s)	# Foraging Bouts	# Days**
CHG*	823	0	823	5	4
GREB*	1106	0	1106	10	7
JBH	138	440	578	18	12
JBZ	4559	1239	5798	24	12
JUA*	936	0	936	8	7
LPK	1184	7	1191	5	4
NEWT	1200	32	1232	6	5
ORD	413	28	441	8	7
ORG1	1112	15	1127	7	6
ORJB	890	40	930	6	5
SLGW	1591	72	1663	7	6
SM1	55	705	760	4	4
T01	884	389	1273	8	6
YWSL	303	95	398	9	7
Total	15194	3062	18256	125	92
Average	1085	278	1304	9	7

*Not included in the shrub analysis
** Number of days an individual was observed foraging

Table 2. Tree species recorded within Golden-winged Warbler territories (n = 14) during the 2011 breeding season in Sproul State Forest, Pennsylvania.

Species	Total Abundance[a]	% Territories[b]	% of Total Species[c]	Foraged On?
Red Maple*	1587	92.9	41.49	Y
Black Locust*	1023	85.7	26.75	Y
Pin Cherry*	213	78.6	5.57	Y
Black Cherry*	184	64.3	4.81	Y
Chokecherry	97	71.4	2.54	Y
Sweet Birch*	74	85.7	1.93	Y
Sassafras*	41	50.0	1.07	Y
White Oak*	22	50.0	0.58	Y
Black Gum *(Nyssa sylvatica)*	18	14.3	0.47	Y
Red Oak	8	14.3	0.21	Y
Paper Birch *(Betula papyrifera)*	4	28.6	0.10	Y
Chestnut Oak	2	14.3	0.05	Y
White Pine	359	50.0	9.39	N
Red Pine *(Pinus resinosa)*	129	35.7	3.37	N
Norway Spruce *(Picea abies)*	21	7.1	0.55	N
Staghorn Sumac *(Rhus typhina)*	11	14.3	0.29	N
Abies spp.	10	7.1	0.26	N
Striped Maple	10	7.1	0.26	N
Fraxinus spp.	3	7.1	0.08	N
Yellow Birch	3	14.3	0.08	N
Yellow Poplar (*Liriodendron tulipifera*)	2	14.3	0.05	N
Bigtooth Aspen (*Populus grandidentata*)	1	7.1	0.03	N
Malus spp.	1	7.1	0.03	N
Grey Birch (*Betula populifolia*)	1	7.1	0.03	N
Quaking Aspen (*P. tremuloides*)	1	7.1	0.03	N

a. Total abundance of tree species in all Golden-winged Warbler territories
b. Percent of territories tree species occurred in
c. Percent of total tree species sampled in all Golden-winged Warbler territories
* Included in compositional analysis

Table 3. Simplified ranking matrix from compositional analysis for Golden-winged Warblers based on proportional tree/shrub species use (foraging) and proportional tree/shrub species availability. Foraging observations were collected from Sproul State Forest in northcentral Pennsylvania during the 2011 breeding season. Tree species use ($\Lambda = 0.052$, $p = 0.010$ by randomization) and shrub species use ($\Lambda = 0.067$, $p = 0.016$ by randomization) differed from random. Each mean element (cell) in the matrix represents the difference in used and available log ratios (calculated from proportions), averaged over 14 (tree species use) and 11 (shrub species use) Golden-winged Warblers.

	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

	Rubus spp.	Mountain Laurel	Rank
Rubus spp.			1
Mountain Laurel	$p < 0.05$		2

Note: Ranks represent the importance of each habitat in ascending order from most important (1) to least important (7). Significant p values indicate an actual difference between the ranks of two species, where the ranking indicates the direction of the difference.

Structure and Composition of Territories vs. Unoccupied Areas

My analysis revealed differences in vegetative structure between areas occupied (n = 14) and unoccupied (n = 12) by territorial male Golden-winged Warblers (Table 4). Occupied areas had more herbaceous cover ($t = -2.586$, $p = 0.016$), fewer saplings ($t = 5.421$, $p < 0.001$), and more trees ($t = -3.536$, $p = 0.002$) compared to unoccupied areas. Shrub cover did not differ between occupied and unoccupied areas. Ground cover vegetation differed between areas occupied and unoccupied by Golden-winged Warbler territories (Table 5). Unoccupied areas had a higher percent cover of tree seedlings ($U = 40.0$, $p = 0.024$), blueberry ($U = 13.0$, $p < 0.001$), and mountain laurel ($U = 7.0$, $p < 0.001$) and a lower percent cover of *Rubus* spp. ($U = 0.0$, $p < 0.001$) and herbaceous material ($U = 33.0$, $p = 0.009$).

Indicator species analysis identified many floristic differences between areas occupied and unoccupied by Golden-winged Warbler territories (Table 6). Six tree species were found to be indicators of occupied 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%, $p = 0.041$) were all indicators of occupied territories. Sassafras (IV = 99.6%, $p = < 0.001$), chestnut oak (IV = 90.6%, $p = < 0.001$), and red oak (IV = 44.0%, $p = 0.044$) were indicators of unoccupied areas (Table 6).

Table 4. Structural differences in vegetation between areas occupied and unoccupied by Golden-winged Warbler territories during the 2011 breeding season in Sproul State Forest, Pennsylvania. Structural differences were considered significant at $p < 0.05$ (in bold text).

Structural Variable		Mean	SD	*t*	*p*
% Herbaceous Cover	Occupied	30.75	10.98	-2.586	**0.016**
	Unoccupied	16.77	16.42		
% Shrub Cover	Occupied	62.26	14.87	0.282	0.781
	Unoccupied	64.23	20.76		
# Saplings[a]	Occupied	14.09	6.95	5.421	**< 0.001**
	Unoccupied	58.50	53.25		
# Trees[a]	Occupied	2.30	1.23	-3.536	**0.002**
	Unoccupied	0.94	0.80		

a. # of saplings and trees were log10 transformed for analyses; means and standard deviations (SD) are shown for untransformed variables.

Figure 3. Structural differences in vegetation between areas occupied and unoccupied by Golden-winged Warbler territories during the 2011 breeding season in Sproul State Forest, Pennsylvania. Means for the same variable with the same letters are not statistically different.

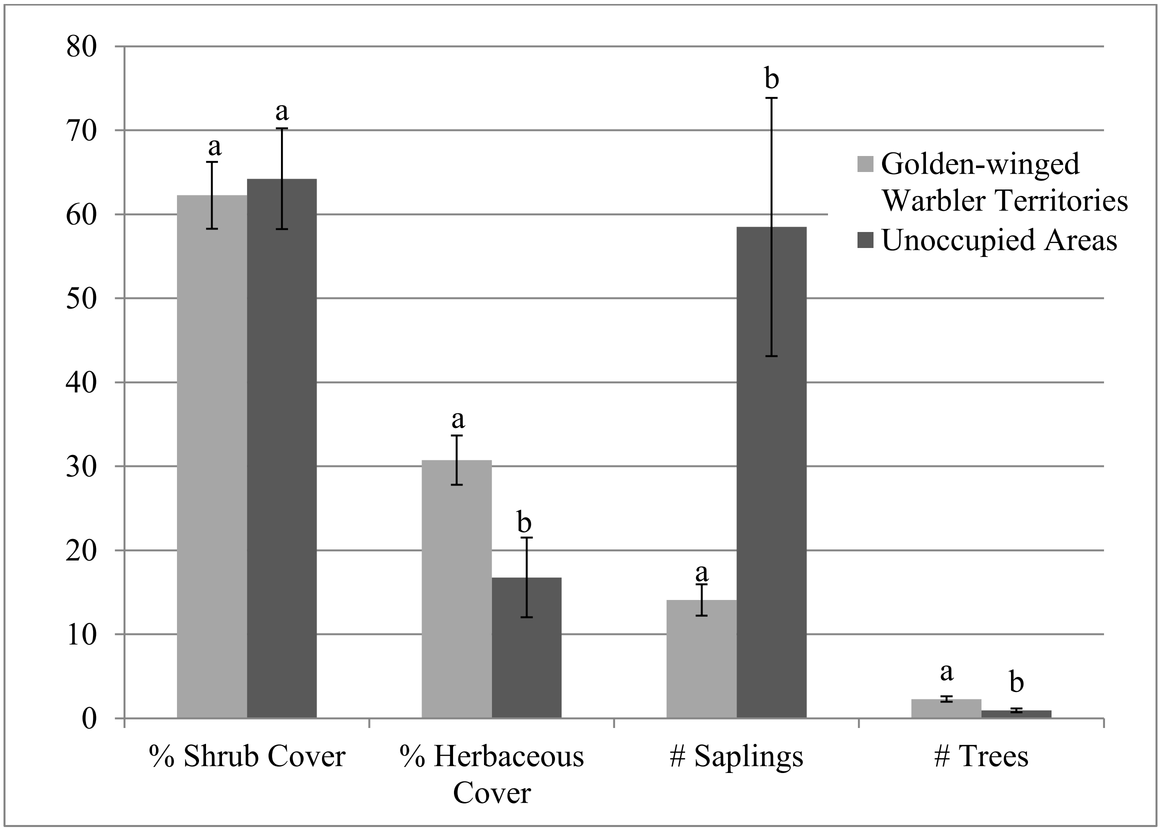

Table 5. Differences in ground cover composition between areas occupied and unoccupied by Golden-winged Warbler territories during the 2011 breeding season in Sproul State Forest, Pennsylvania. Significant differences ($p < 0.05$) are highlighted in bold text.

Ground Cover		Mean	SD	Mann-Whitney U	*p*
% Bare Ground	Occupied	4.31	4.79	61.0	0.235
	Unoccupied	8.93	9.34		
% Tree Seedlings	Occupied	2.67	2.74	40.0	**0.024**
	Unoccupied	10.07	12.10		
% Herbaceous Cover	Occupied	30.75	10.98	33.0	**0.009**
	Unoccupied	16.77	16.42		
% *Rubus* spp.	Occupied	43.49	20.96	0.0	**< 0.001**
	Unoccupied	0.11	0.23		
% Mountain Laurel	Occupied	4.70	7.07	7.0	**< 0.001**
	Unoccupied	30.54	18.61		
% Blueberry	Occupied	10.10	9.53	13.0	**< 0.001**
	Unoccupied	30.33	10.82		
% Sweetfern	Occupied	3.97	3.09	71.5	0.520
	Unoccupied	3.25	3.06		

Table 6. Indicator species analysis of floristic differences between areas occupied and unoccupied by Golden-winged Warbler territories during the 2011 breeding season in Sproul State Forest, Pennsylvania. Significance was determined at $p < 0.05$ (bold text).

Common Name	Scientific Name	Max. Group[a]	Observed IV[b]	IV from Randomized Groups: Mean	IV from Randomized Groups: Standard Deviation	*p*
Sassafras	*Sassafras albidum*	0	99.6	50.5	10.11	**< 0.001**
Chestnut Oak	*Quercus pinus*	0	90.6	35.1	8.32	**< 0.001**
Black Locust	*Robinia pseudoacacia*	1	85.7	32.8	7.91	**< 0.001**
Sweet Birch	*Betula lenta*	0	79.3	67.2	10.56	0.149
Chokecherry	*Prunus virginiana*	1	70.6	34.3	9.50	**0.001**
Pin Cherry	*P. pensylvanica*	1	64.5	45.4	9.98	**0.048**
Black Cherry	*P. serotina*	1	63.9	29.7	8.87	**0.002**
Witch Hazel	*Hamamelis virginiana*	0	63.8	41.2	9.42	**0.019**
Red Maple	*Acer rubrum*	0	60.7	55.5	5.62	0.179
White Pine	*Pinus strobus*	1	50.0	24.0	8.98	**0.005**
Red Oak	*Q. rubra*	0	44.0	26.9	8.06	**0.044**
White Oak	*Q. alba*	1	37.9	28.8	7.81	0.134
Red Pine	*P. resinosa*	1	35.7	18.8	8.01	**0.041**
Black Oak	*Q. velutina*	0	25.0	13.1	5.73	0.083
Paper Birch	*B. papyrifera*	1	22.1	17.7	6.59	0.329
Pitch Pine	*P. rigida*	0	16.7	10.1	5.15	0.208
Staghorn Sumac	*Rhus typhina*	1	14.3	10.1	5.26	0.495
Yellow Birch	*B. alleghanisnsis*	1	14.3	10.0	5.15	0.476
Tulip Poplar	*Liriodendron tulipifera*	1	9.0	12.9	5.34	1.000
Virginia Pine	*P. virginiana*	0	8.3	7.7	0.60	0.465
Black Gum	*Nyssa sylvatica*	1	8.0	13.0	6.16	0.743
Bigtooth Aspen	*Populus grandidentata*	1	7.1	7.7	0.60	1.000
Apple *spp.*	*Malus spp.*	1	7.1	7.7	0.60	1.000
Spruce *spp.*	*Abies spp.*	1	7.1	7.7	0.60	1.000
Grey Birch	*B. populifolia*	1	7.1	7.7	0.60	1.000
Norway Spruce	*Picea abies*	1	7.1	7.7	0.60	1.000
Quaking Aspen	*P. tremuloides*	1	7.1	7.7	0.60	1.000
Striped Maple	*A. pensylvanicum*	1	7.1	7.7	0.60	1.000
Ash *spp.*	*Fraxinus spp.*	1	4.0	9.8	5.38	1.000

a. Max. group refers to type of location the species indicates best, occupied (1) or unoccupied (0)
b. Observed indicator values (IV) show % of perfect indication based on combining values for relative abundance and relative frequency for the max. group

Caterpillar Abundance on Woody Plant Species

Caterpillar abundance differed among netted tree species (Kruskal-Wallis χ^2 = 54.366, df = 8, $p < 0.001$). Black locust, pin cherry, and black cherry had the highest caterpillar abundances among netted tree species, and sassafras, sweet birch, and white pine had the lowest (Table 7; Figure 4). Multiple comparisons revealed that black locust had more caterpillars than chestnut oak, sassafras, sweet birch, white pine, and white oak (Table 8). Pin cherry had more caterpillars than sassafras, sweet birch, and white pine, while black cherry had more caterpillars than sweet birch and white pine. Caterpillar abundance also differed among shrub species (Kruskal-Wallis χ^2 = 17.407, df = 3, $p < 0.001$). *Rubus* spp. had more caterpillars compared to mountain laurel, while sweetfern had more caterpillars than both mountain laurel and blueberry (Table 9; Figure 5). Caterpillar abundance was not different between netted and un-netted branches of black locust, blackberry, or pin cherry (Table 10; Figure 6). In the case of black locust, the difference between netted and unnetted branches approached significance (t = 1.731, p = 0.097) (Table 10). While no statistical analyses were conducted, the abundances of all insect orders were documented and can be found in Table 11.

Table 7. Average number of caterpillars/10g dry leaf weight on netted woody plant species. Branches were collected during the 2011 Golden-winged Warbler breeding season from Sproul State Forest, Pennsylvania.

Species	# Branch Clippings (n)	Mean # Caterpillars/10g Dry Leaf Weight	SD
Black Locust	15	5.155	3.163
Pin Cherry	10	3.420	1.967
Sweetfern	10	2.789	1.180
Rubus spp.	15	2.690	2.217
Black Cherry	10	1.517	0.707
Red Maple	10	0.862	0.812
Blueberry	10	0.831	0.765
Mountain Laurel	10	0.586	0.717
White Oak	10	0.439	0.372
Chestnut Oak	10	0.432	0.288
Sassafras	10	0.383	0.332
Sweet Birch	10	0.306	0.431
White Pine	10	0.178	0.190

Table 8. Multiple comparisons of average # caterpillars/10g dry leaf weight among netted tree species collected at Sproul State Forest, Pennsylvania during the 2011 Golden-winged Warbler breeding season. Observed difference (O, difference between the average sum of ranks for two species) were considered significant when greater than the χ^2 critical value (C). Significant differences between species are highlighted in bold text (Kruskal-Wallis χ^2 = 54.366, df = 8, p < 0.001).

Species		Black Cherry	Black Locust	Chestnut Oak	Pin Cherry	Red Maple	Sassafras	Sweet Birch	White Oak	White Pine
Black Cherry	O	-	13.88	29.20	7.45	20.65	32.95	**39.50**	30.65	**43.00**
	C	-	35.98	39.41	39.41	39.41	39.41	39.41	39.41	39.41
Black Locust	O	13.88	-	**43.08**	6.43	34.53	**46.83**	**53.83**	**44.53**	**56.88**
	C	35.98	-	35.98	35.98	35.98	35.98	35.98	35.98	35.98
Chestnut Oak	O	29.20	**43.08**	-	36.65	8.55	3.75	10.30	1.45	13.80
	C	39.41	35.98	-	39.41	39.41	39.41	39.41	39.41	39.41
Pin Cherry	O	7.45	6.43	36.65	-	28.10	**40.40**	**46.95**	38.10	**50.45**
	C	39.41	35.98	39.41	-	39.41	39.41	39.41	39.41	39.41
Red Maple	O	20.65	34.53	8.55	28.10	-	12.30	18.85	10.00	23.35
	C	39.41	35.98	39.41	39.41	-	39.41	39.41	39.41	39.41
Sassafras	O	32.95	**46.83**	3.75	**40.40**	12.30	-	6.55	2.30	10.05
	C	39.41	35.98	39.41	39.41	39.41	-	39.41	39.41	39.41
Sweet Birch	O	**39.50**	**53.83**	10.30	**46.95**	18.85	6.55	-	8.85	3.50
	C	39.41	35.98	39.41	39.41	39.41	39.41	-	39.41	39.41
White Oak	O	30.65	**44.53**	1.45	38.10	10.00	2.30	8.85	-	12.35
	C	39.41	35.98	39.41	39.41	39.41	39.41	39.41	-	39.41
White Pine	O	**43.00**	**56.88**	13.80	**50.45**	23.35	10.05	3.50	12.35	-
	C	39.41	35.98	39.41	39.41	39.41	39.41	39.41	39.41	-

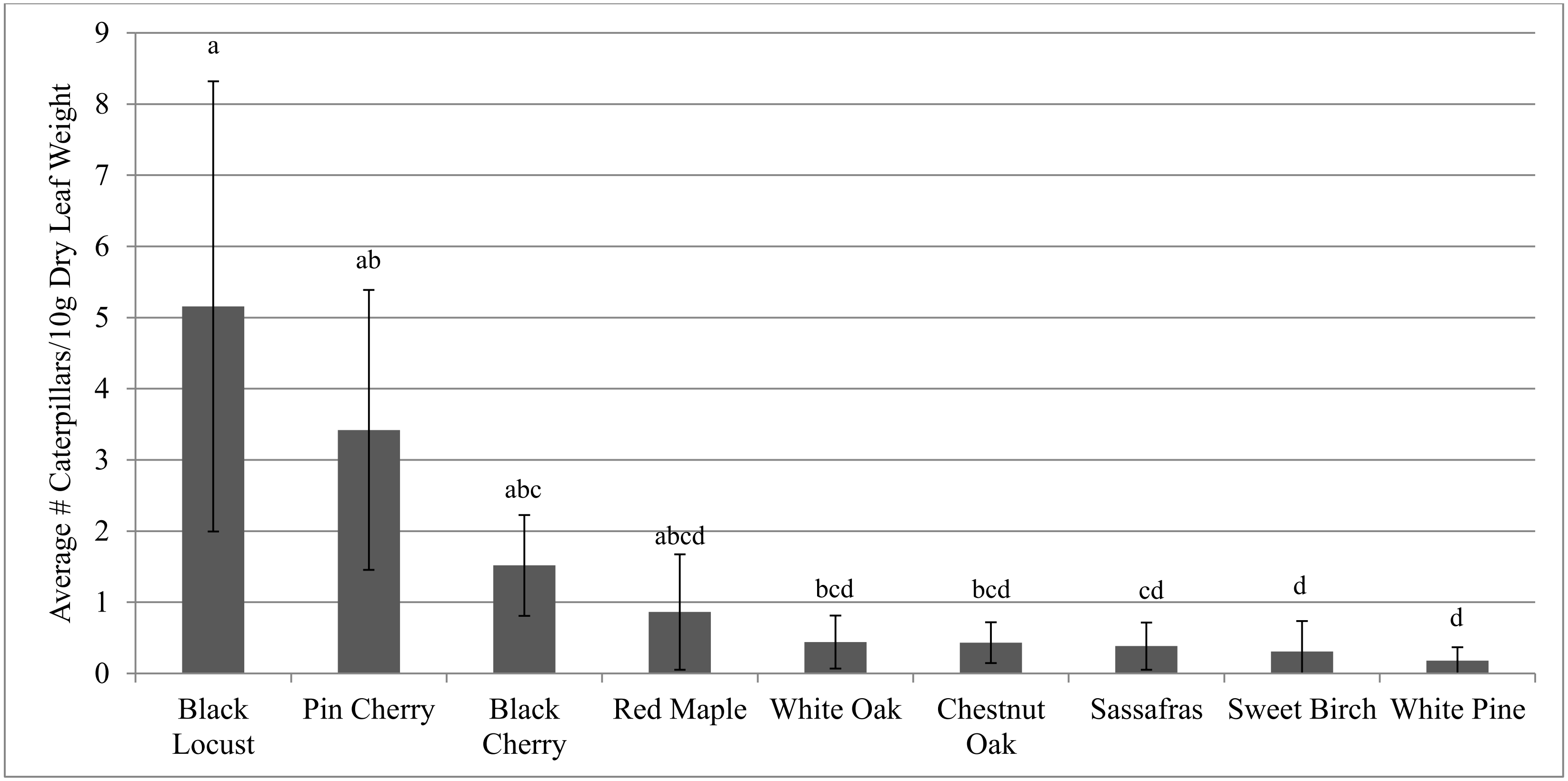

Figure 4. Average # caterpillars/10g dry leaf weight on netted tree species collected at Sproul State Forest, Pennsylvania during the 2011 Golden-winged Warbler breeding season. Means for species with the same letters are not statistically different. Error bars are +/- 1 standard deviation.

Table 9. Multiple comparisons of average # caterpillars/10g dry leaf weight among netted shrub species collected at Sproul state Forest, Pennsylvania during the 2011 Golden-winged Warbler breeding season (Kruskal-Wallis $\chi^2 = 17.407$, df = 3, $p < 0.001$). Observed difference (O, difference between the average sum of ranks for two species) were considered significant when greater than the χ^2 critical value (C). Significant differences between species are highlighted in bold text.

Species		*Rubus* spp.	Blueberry	Mountain Laurel	Sweetfern
Rubus spp.	O	-	12.65	**15.45**	4.70
	C	-	14.15	14.15	14.15
Blueberry	O	12.65	-	2.80	**17.35**
	C	14.15	-	15.50	15.50
Mountain Laurel	O	**15.45**	2.80	-	**20.16**
	C	14.15	15.50	-	15.50
Sweetfern	O	4.70	**17.35**	**20.16**	-
	C	14.15	15.50	15.50	-

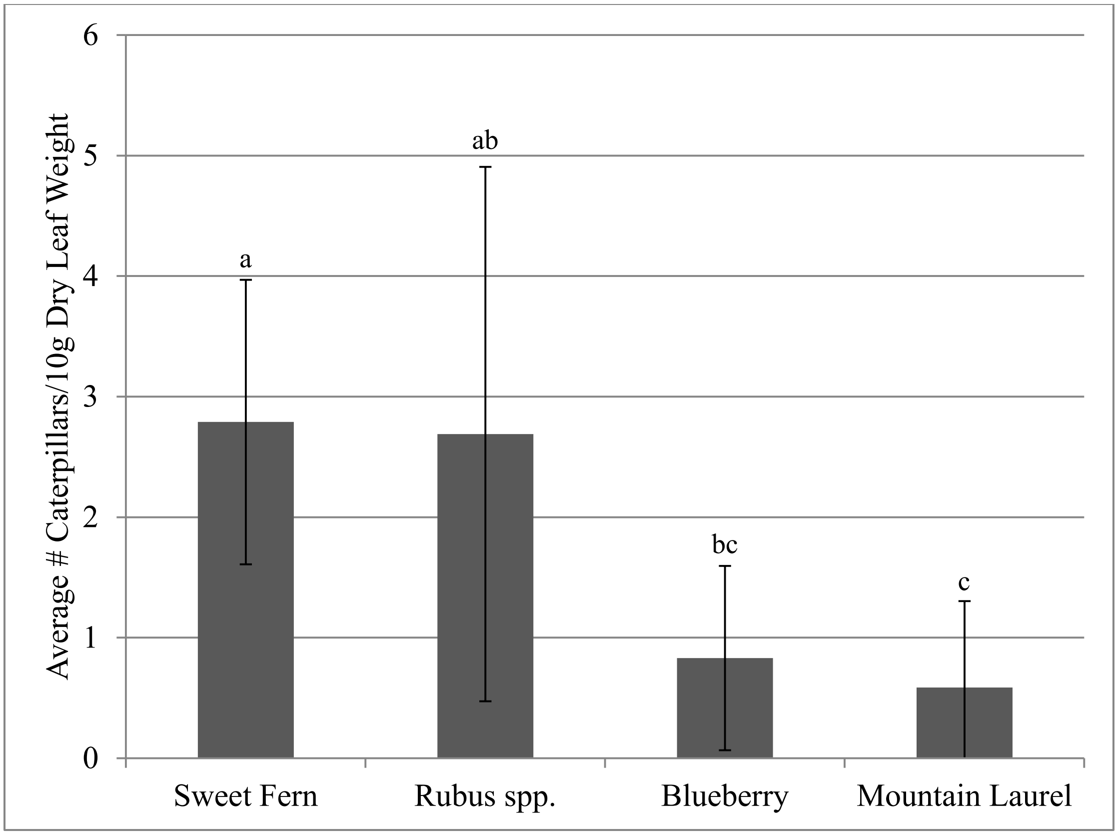

Figure 5. Average # caterpillars/10g dry leaf weight on netted shrub species collected at Sproul State Forest, Pennsylvania during the 2011 Golden-winged Warbler breeding season. Means for species with the same letters are not statistically different. Error bars are +/- 1 standard deviation.

Table 10. Average number of caterpillars/10g dry leaf weight on netted and un-netted woody plant species collected at Sproul State Forest, Pennsylvania during the 2011 Golden-winged Warbler breeding season.

Species		# Branch Clippings (n)	Mean # Caterpillars/10g Dry Biomass	SD	SE	*t*	*p*
Black Locust	Netted	15	5.155	3.16	0.82	1.731	0.097
	Unnetted	10	3.085	2.52	0.80		
Pin Cherry	Netted	10	3.420	1.97	0.62	1.353	0.199
	Unnetted	5	1.997	1.81	0.81		
Rubus spp.	Netted	15	2.690	2.22	0.57	0.185	0.855
	Unnetted	10	2.502	2.08	0.66		

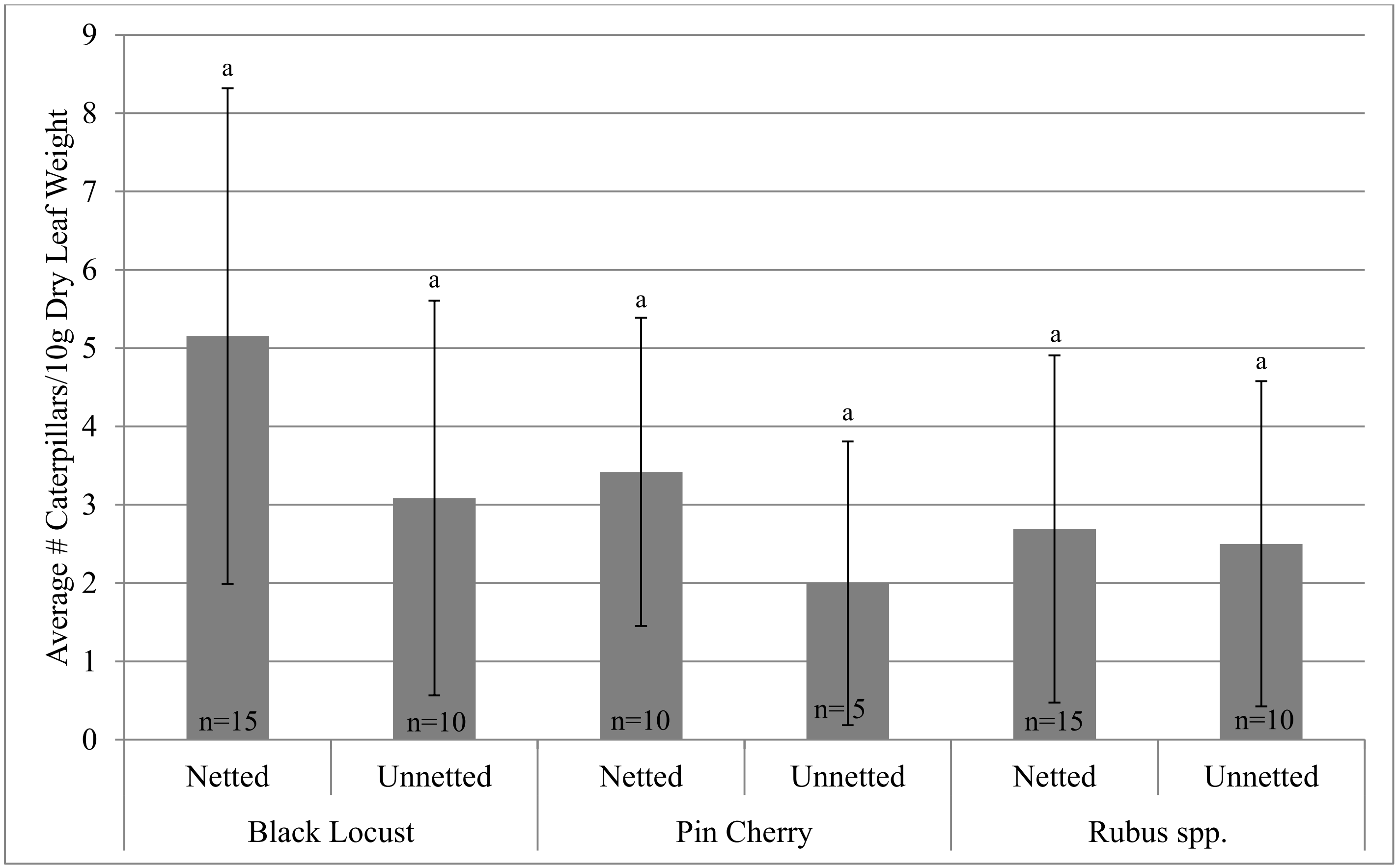

Figure 6. Average number of caterpillars/10g dry leaf weight on netted vs. unnetted woody plant species collected at Sproul State Forest during the 2011 Golden-winged Warbler breeding season. Error bars are +/- 1 standard deviation. Means for the same species with the same letters are not statistically different.

Table 11. Average abundance for each insect Order/10g dry leaf weight collected from netted woody plant species. Branches were collected during the 2011 Golden-winged Warbler breeding season at Sproul State Forest, Pennsylvania. Standard errors are reported in parentheses.

Order	*Rubus* spp.	Blue-berry	Black Cherry	Black Locust	Chestnut Oak	Mtn. Laurel	Pin Cherry	Red Maple	Sassafras	Sweet Birch	Sweet-fern	White Oak	White Pine
Caterpillars	2.690 (0.572)	0.831 (0.242)	1.517 (0.224)	5.155 (0.817)	0.432 (0.091)	0.586 (0.227)	3.420 (0.622)	0.862 (0.257)	0.383 (0.105)	0.306 (0.136)	2.789 (0.373)	0.439 (0.118)	0.178 (0.060)
Lepidoptera (Adult)	0.213 (0.102)	0.000 (0)	0.071 (0.037)	0.022 (0.022)	0.168 (0.054)	0.000 (0)	0.039 (0.039)	0.034 (0.034)	0.000 (0)	0.207 (0.182)	0.037 (0.037)	0.312 (0.113)	0.024 (0.024)
Hymenoptera	0.046 (0.034)	0.326 (0.221)	0.302 (0.111)	1.387 (0.591)	0.698 (0.163)	1.029 (0.534)	0.372 (0.196)	0.438 (0.108)	0.188 (0.076)	1.079 (0.595)	0.414 (0.180)	3.529 (2.900)	0.136 (0.070)
Diptera	0.653 (0.267)	0.278 (0.107)	0.328 (0.108)	0.265 (0.239)	0.071 (0.036)	1.112 (0.230)	0.163 (0.126)	2.271 (1.263)	0.084 (0.066)	5.074 (3.658)	2.474 (1.372)	0.350 (0.140)	0.034 (0.024)
Homoptera	1.062 (0.337)	0.918 (0.406)	1.695 (0.555)	2.294 (0.847)	2.808 (0.680)	1.322 (0.354)	12.219 (4.240)	3.865 (2.513)	0.117 (0.062)	33.530 (11.770)	8.780 (2.149)	8.288 (4.620)	0.236 (0.119)
Coleoptera	0.265 (0.086)	0.037 (0.037)	1.039 (0.264)	1.718 (0.784)	0.463 (0.079)	0.389 (0.156)	0.628 (0.178)	0.530 (0.228)	0.290 (0.109)	0.947 (0.362)	0.216 (0.152)	1.170 (0.559)	0.185 (0.081)
Hemiptera	1.247 (0.541)	0.250 (0.250)	10.131 (4.975)	1.306 (0.391)	1.135 (0.498)	1.145 (0.419)	0.186 (0.124)	0.170 (0.919)	0.044 (0.029)	0.495 (0.495)	0.278 (0.164)	1.031 (0.433)	0.142 (0.059)
Orthoptera	0.211 (0.099)	0.000 (0)	0.000 (0)	0.719 (0.719)	0.142 (0.070)	0.023 (0.023)	0.146 (0.077)	1.012 (0.919)	0.000 (0)	0.036 (0.036)	0.230 (0.135)	0.060 (0.045)	0.010 (0.010)

Table 11. Continued

Order	*Rubus* spp.	Blue-berry	Black Cherry	Black Locust	Chestnut Oak	Mtn. Laurel	Pin Cherry	Red Maple	Sassafras	Sweet Birch	Sweet-fern	White Oak	White Pine
Psocoptera	0.000 (0)	0.000 (0)	0.170 (0.075)	0.005 (0.005)	0.096 (0.067)	0.069 (0.056)	0.286 (0.124)	0.023 (0.023)	0.063 (0.044)	0.000 (0)	0.169 (0.114)	0.618 (0.448)	0.000 (0)
Neuroptera	0.062 (0.062)	0.000 (0)	0.000 (0)	0.027 (0.022)	0.049 (0.049)	0.000 (0)	0.123 (0.082)	0.000 (0)	0.018 (0.018)	0.000 (0)	0.000 (0)	0.069 (0.046)	0.000 (0)
Trichoptera	0.000 (0)	0.000 (0)	0.181 (0.121)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.024 (0.024)	0.000 (0)	0.037 (0.037)	0.000 (0)
Thysanoptera	0.433 (0.291)	0.000 (0)	0.919 (0.548)	0.590 (0.215)	0.933 (0.428)	0.000 (0)	0.714 (0.411)	0.000 (0)	6.423 (1.622)	1.950 (1.366)	0.105 (0.105)	1.920 (1.243)	0.013 (0.013)
Collembola	0.000 (0)	0.089 (0.089)	0.057 (0.057)	0.000 (0)	0.037 (0.037)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.010 (0.010)
Isoptera	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
Dermaptera	0.085 (0.085)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
Zoraptera	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.010 (0.010)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
Araneae	0.587 (0.183)	0.678 (0.183)	0.501 (0.116)	0.774 (0.220)	0.686 (0.252)	0.203 (0.082)	0.535 (0.195)	0.627 (0.219)	0.631 (0.312)	0.698 (0.346)	0.405 (0.142)	1.408 (0.428)	0.331 (0.176)
Unidentifiable Pupae	2.668 (1.272)	0.000 (0)	0.028 (0.028)	0.043 (0.034)	0.051 (0.041)	0.184 (0.118)	0.111 (0.059)	0.034 (0.034)	0.023 (0.023)	0.038 (0.038)	0.230 (0.114)	0.045 (0.031)	0.063 (0.063)
Unidentifiable	0.146 (0.075)	0.049 (0.033)	0.217 (0.049)	0.378 (0.239)	0.000 (0)	0.556 (0.092)	0.613 (0.063)	0.749 (0.532)	0.068 (0.046)	0.293 (0.156)	0.180 (0.109)	0.306 (0.146)	0.145 (0.081)

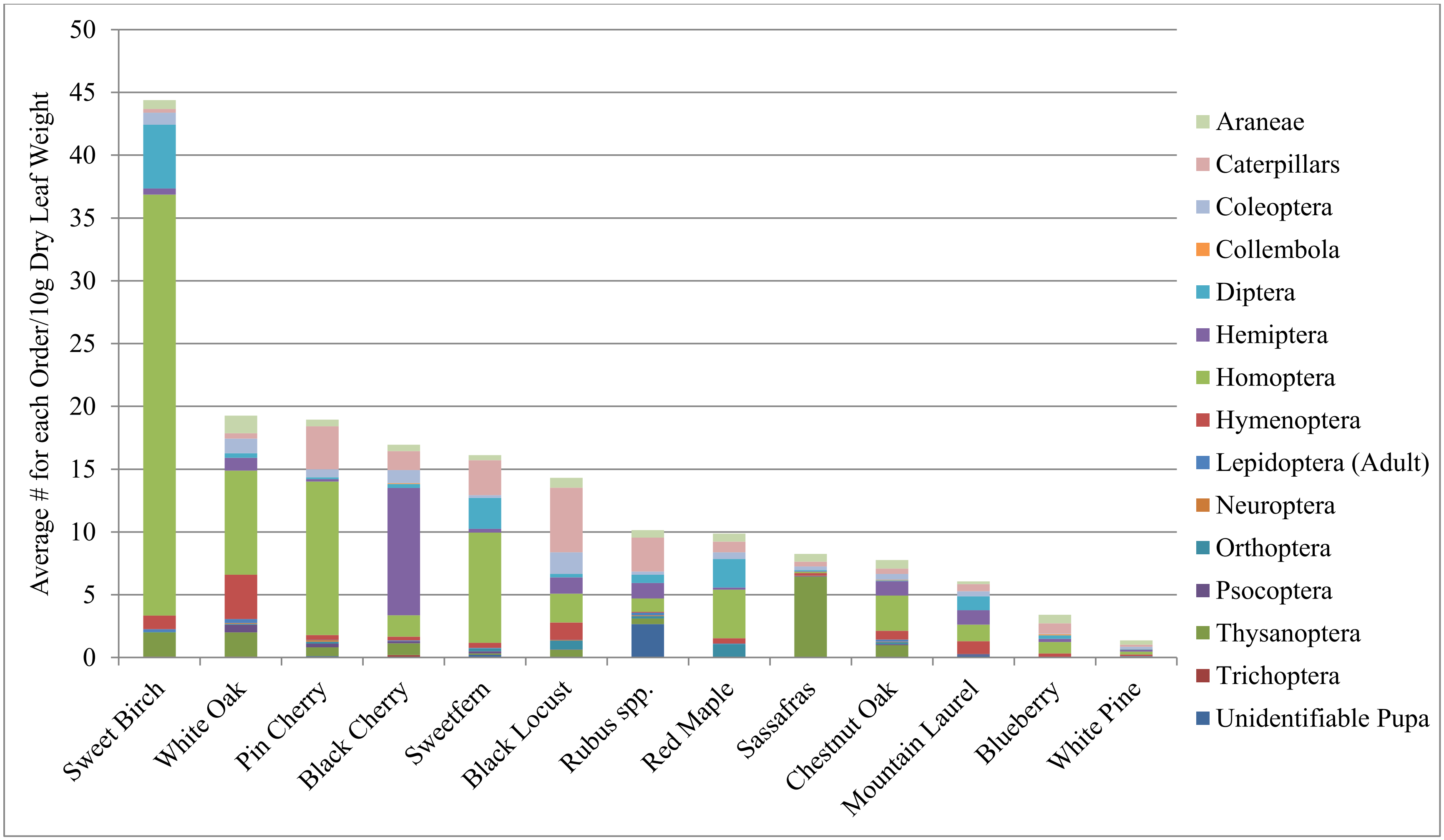

Figure 7. Average abundance for each insect Order/10g dry leaf weight collected from netted woody plant species. Branches were collected during the 2011 Golden-winged Warbler breeding season at Sproul State Forest, Pennsylvania.

CHAPTER VI

DISCUSSION

Composition of woody plant species appears to be an important aspect of Golden-winged Warbler foraging ecology. My research found that Golden-winged Warblers selectively foraged on several woody plant species within their territories. This finding was positively linked to species-specific prey abundance, which was unequal among woody plant species sampled. Additionally, Golden-winged Warbler territories were compositionally and structurally different from adjacent, similarly aged, unoccupied areas. Golden-winged Warblers selective use of woody plant species and floristic differences between territories and unoccupied areas warrants consideration of woody species composition and structure when managing breeding habitat for this insectivorous song bird.

Golden-winged Warblers monitored during my study foraged on pin cherry and black locust more than black cherry, relative to their availabilities. These results do not indicate that black cherry was 'avoided', but that it was used as a forage substrate less than its availability compared to black locust and pin cherry. Black locust and pin cherry had the highest abundance of cruciform larvae (i.e. caterpillars), which is a major food source for many breeding insectivorous birds including the Golden-winged Warbler (Molles 2002; Confer et al. 2011). Food availability is a major factor affecting reproductive success in breeding passerines; thus, selection of a breeding territory that provides food resources necessary for rearing young has important consequences for an individual's fitness (Simons & Martin 1990; Rodenhouse & Holmes 1992; Verhulst 1994).

Black locust was an indicator of Golden-winged Warbler territories on reclaimed surface mines in Kentucky and males were often observed gleaning insects from the leaves of this tree species (Patton et al. 2010). The importance of black locust to passerine foraging ecology has been reported for other songbirds whereby four of eight species in Illinois preferred black locust as a foraging substrate (Hartung & Brawn 2005). Nonetheless, neither of these studies quantified prey abundance, and thus could not provide a mechanistic explanation for the observed use of black locust by breeding songbirds. Results from my study provide empirical evidence that support the findings of Patton et al. (2010) regarding the close relationship between black locust and Golden-winged Warbler breeding habitat. In my study, black locust was not only an indicator of Golden-winged Warbler territories, it was also selectively foraged on by breeding Golden-winged Warblers. My finding that black locust had the highest abundance of caterpillars among the woody species sampled provides the first empirically-based explanation of the Golden-winged Warbler's close association with this early successional tree species.

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 weight) (Day & Monk 1977; Bassam 1998). Nitrogen content of food is an important determinant of larval Lepidoptera (i.e. caterpillar) growth, survival and reproductive rates (Mattson 1980; Schowalter & Crossley 1988). Indeed, herbivorous insects selectively feed on nitrogen-rich foliage (Athey & Connor 1989; Marquis & Lill 2010) and grow larger and produce more fecund adults when raised on higher nitrogen diets (Scriber & Slansky 1981). As such, it is reasonable to suggest that Golden-winged Warblers in my study may have established territories in areas with more black locust, and preferentially foraged on this species to access more abundant and better quality caterpillar prey (Schoener 1971).

Pin cherry and black cherry were also indicators of Golden-winged Warbler territories in my study area. While caterpillar abundance did not differ between these two species (Figure 3), Golden-winged Warblers selectively foraged on pin cherry, relative to the use of black cherry. Furthermore, caterpillar abundance on pin cherry was more than two times the abundance found on black cherry (Table 6). Both black and pin cherry are chemically defended against herbivory via alkaloids, sterols, triterpenes, and benzenoids (Ricklefs 2008), but the former mounts a higher defense (Burns & Hankala 1990; Eisner & Siegler 2005). Some Lepidoptera species have evolved to overcome this defense and preferentially feed on black cherry (Eastern tent caterpillar, *Malacosoma americanum*), however prey consuming a chemically defended plant may be less palatable to birds (Eisner & Siegler 2005). Although black cherry supported the 4th highest caterpillar abundance of 13 woody plant species sampled, Golden-winged Warblers may have foraged on the species less than its availability because of the presence of unpalatable prey. Pin cherry, on the other hand, is less chemically defended (Burns & Hankala 1990; Eisner & Siegler 2005) so caterpillars may be more abundant. The combined effects of caterpillar abundance and palatability are likely the driving force behind selective foraging of pin cherry over black cherry by foraging Golden-winged Warblers.

Golden-winged Warblers in my study also selectively foraged on white oak, compared to sassafras and sweet birch. In West Virginia, two foliage gleaning songbirds

(Red-eyed Vireos, *Vireo olivaceus* & Scarlet Tanagers, *Piranga olivacea*) also consistently foraged on oaks more than sweet birch in both young and mature forests (Maurer & Whitmore 1981). Although I found that white oak only had a marginally higher abundance of caterpillars than sassafras and sweet birch, the latter two exhibited some of the lowest abundances of caterpillars among woody species sampled. Sassafras was an indicator of areas unoccupied by Golden-winged Warblers, although white oak and sweet birch were not indicative of either occupied or unoccupied areas. Oils extracted from sassafras leaves contain the monoterpene geraniol (Gant & Clebsch 1975). Various monoterpenes are toxic to insects and serve as a feeding deterrent (Barnard & Xue 2004; Gershenzon & Dudareva 2007).

In a concurrent study on Golden-winged Warblers in Sproul State Forest, Pennsylvania, white oak was found to be an indicator of areas used by radio-tracked Golden-winged Warblers outside their traditional spot mapped territories (Frantz 2012). The fact that Golden-winged Warblers selectively foraged on white oak in my study, coupled with results from Frantz's (2012) study, suggests the importance of white oak to breeding Golden-winged Warblers.

The selection of white oak by foraging Golden-winged Warblers was somewhat surprising because white oak exhibited a relatively low abundance of caterpillars compared to other species examined (Figure 3). Nonetheless, Golden-winged Warblers may have been foraging in white oak for alternate prey types. For example, white oak supported the greatest abundance of Hymenoptera (3.53 Hymenoptera/10g dry leaf weight, SE = 2.90) and spiders (1.41 spiders/10g dry leaf weight, SE = 0.43) of all woody plant species sampled (Table 11, Figure 7). White oak exhibited approximately two times the abundance of both arthropod groups compared to black locust, which had the second highest abundance of both Hymenoptera and spiders (Table 11). Indeed, Golden-winged Warblers have been documented to consume other arthropods, including spiders (Jacobs 1904; Forbush 1929). It is therefore possible that males were foraging on white oak greater than its availability because of a high abundance of arthropods other than caterpillars. I hypothesize that males may have opportunistically foraged on white oak to obtain prey for themselves due to high abundances of spiders and Hymenoptera.

Another possible explanation for the seemingly contradictory finding of low caterpillar abundance and selective foraging on white oak is a temporal disconnect between foraging observations, branch clippings, and nutritional quality of leaves. In England, several species of Lepidoptera larvae abruptly stopped feeding on oak (*Q. robur* L.) leaves in June to feed on other trees (Feeny 1970). It was hypothesized that this was partially due to increasing "toughness" of the oak leaves and a sharp increase in leaf tannins, which may have reduced the availability of nitrogen and possibly made leaves less palatable (Feeny 1970). As the growing season progresses into summer, tannins in white oak leaves increase and nitrogen content of leaves declines (Wold & Marquis 1997), making white oak a less nutritious species for caterpillars to feed on later in the summer.

With respect to shrub use, Golden-winged Warblers selectively foraged on *Rubus* spp. relative to the use of mountain laurel and the former had a greater abundance of caterpillars. Mountain laurel comprised almost seven times the ground cover of unoccupied areas compared to Golden-winged Warbler territories (Table 5). Furthermore, there was considerably more *Rubus* spp. within Golden-winged Warbler territories compared to unoccupied areas (Table 5). These results are in agreement with Golden-winged Warbler Best Management Practices, which states that *Rubus* spp. provides an important nesting substrate and cover for nesting birds (Bakermans et al. 2011).

Sweetfern, which is not actually a fern but a low-growing shrub, supported a high number of caterpillars, similar to *Rubus* spp. However, Golden-winged Warblers did not selectively forage on this species. In fact, we never observed Golden-winged Warblers foraging on this species. The high number of caterpillars I found on sweetfern is not surprising given this species' nitrogen fixing properties (Schemnitz 1973). Indeed, nitrogen content of food is an important determinant of caterpillar growth, survival and reproductive rates (Mattson 1980; Schowalter & Crossley 1988) and herbivorous insects have been found to selectively feed on nitrogen-rich foliage (Athey & Connor 1989; Marquis & Lill 2010). This begs the question: if caterpillars are such an important component of a Golden-winged Warbler's diet during the breeding season, why didn't we observe them foraging on a species with such a high abundance of caterpillars?

I propose that a possible answer lies in the fact that only *male* Golden-winged Warblers were monitored during my study. Passerines, however, have been shown to exhibit sexual differences in foraging patterns, especially foraging height (Morse 1968; Williamson 1971; Holmes 1986). These differences are thought to exist because males and females forage near their centers of activity. Holmes (1986) reported that female Black-throated Blue Warblers foraged lower, around the height of their nest, while males foraged higher, near the height of their song posts (Holmes 1986). Additionally, males of 4 species of wood warblers in Maine were found to forage near the height of their song posts, while females foraged near the height of their nests (Morse 1968). If Golden-winged Warblers exhibit similar sex-biased foraging patterns, then the center of activity for female Golden-winged Warblers would be low to the ground because Golden-winged Warblers are ground nesters (Confer et al. 2011). Thus, it is possible that females foraged on the caterpillar rich, low growing (≤ 0.5m) sweetfern, while males did not. This possibly highlights the importance of female observations in passerine foraging studies, and suggests the need for further research to elucidate the feeding habits of female Golden-winged Warblers.

Golden-winged Warblers may also not have been observed foraging on sweet fern due to observer bias (Bradley 1985). Sweet fern is a very low growing shrub (~ 0.5 m in height) and Golden-winged Warbler territories were often so dense at this level that is possible that males did in fact forage on sweet fern but were just not observed doing so.

Another unexpected finding was that white pine was an indicator of Golden-winged Warbler territories. Recently developed habitat management guidelines for Golden-winged Warblers state that no more than 27% of the recorded number of residual trees/acre should be coniferous (Roth et al. 2012). Golden-winged Warblers do not nest in areas with high coniferous components (Roth et al. 2012), although pines were documented to be one of the most common sapling and tree species present around Golden-winged Warbler nest sites on reclaimed mine lands in southeastern Kentucky (Patton 2009).

While white pine was an indicator of Golden-winged Warbler breeding habitat, it does not appear to provide foraging opportunities. I never observed male Golden-winged

Warblers foraging on white pine and this species had the lowest abundance of caterpillars of all woody plant species sampled. White pines might have been an indicator of Golden-winged Warbler territories because conifers provide protection from weather (Johnson et al. 1991) and are a natural component of the forest type in my study area. Thus, I stress that habitat management guidelines should incorporate the various habitat needs of breeding passerines, including ample space, cover, and foraging opportunities.

Management Implications

Avian ecologists have long emphasized the importance of vegetation density and foliage structure of passerine habitat, and often dismiss of the significance of floristic composition (e.g. MacArthur & MacArthur 1961; Rotenberry & Weins 1980; Vale et al. 1982; Diaz et al. 2005). However, not all plants are equally nutritious for insects (Reader & Southwood 1981), which may cause an uneven distribution of insects among woody plant species. This likely explains selective foraging by Golden-winged Warblers in my study and insectivorous breeding birds elsewhere (Willson 1970; Holmes & Robinson 1981; Gabbe et al. 2002; George 2009). Selective foraging by male Golden-winged Warblers, along with high insect abundances, indicate that black locust, pin cherry, white oak, and *Rubus* spp. are important components of Golden-winged Warbler breeding habitat in northcentral Pennsylvania. Other species that may also provide foraging habitat for Golden-winged Warblers but require further research include sweetfern, black cherry, and white oak. While vegetative structure is undoubtedly an important factor that influences habitat selection of breeding Golden-winged Warblers, plant species composition appears to be equally important.

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