GAUGING THE SUCCESS OF TIMBER HARVESTS MANAGED FOR

GOLDEN-WINGED WARBLERS (*Vermivora chrysoptera*): CHARACTERISTICS

AND TERRITORY DENSITY WITHIN A WETLAND REFERENCE SYSTEM

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Title: Gauging the Success of Timber Harvests Managed for Golden-winged Warblers (*Vermivora chrysoptera*): Characteristics and Territory Density within a Wetland Reference System

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The Golden-winged Warbler (*Vermivora chrysoptera*) is an imperiled songbird that breeds in early-successional plant communities of eastern North America. Conservation efforts on the breeding grounds have become a priority because population declines are understood to be driven chiefly by the loss/degradation of breeding habitat. Although the species is known to use a variety of upland and wetland habitat types, most previous research on the species has been conducted solely in uplands. I studied Golden-winged Warbler use and habitat characteristics in the Poconos region of Pennsylvania. Density estimates suggest that both timber harvests and wetlands support similar densities of Golden-winged Warblers. Microhabitat occupancy models revealed that those wetlands I surveyed with high densities of 1-2 m tall shrubs (>2x as many shrubs) supported fewer Golden-winged Warblers whereas wetlands with more saplings (>2x as many saplings) and sedge cover (~1.3x as many sedge observations) supported more warblers. Finally, I found that macro-scale habitat variables that I quantified did not predict species occupancy of wetlands, likely due to the homogeneous nature of the study area. My study suggests that both wetlands and timber harvests have similar capacity to support Golden-winged Warblers. Further, wetlands in the Poconos should be evaluated at the microhabitat-scale for vegetative attributes that meet Golden-winged Warbler habitat requirements, rather than at the macro-habitat scale.

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CHAPTER I

INTRODUCTION

The Golden-winged Warbler is a neotropical migratory songbird that breeds in early successional habitats in eastern North America (Confer et al, 2011). While many populations of North American songbirds are declining, the Golden-winged Warbler has experienced the steepest rate of decline –as high as 7.1% per year in Pennsylvania (Sauer et al, 2012). Other factors contributing to these declines are hybridization and competition with the closely-related Blue-winged Warbler (*V. cyanoptera*) (Confer et al, 2011) and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Both Blue-winged Warblers and Brown-headed Cowbirds are known to reduce Golden-winged Warbler reproductive success (Confer et al, 2003; Confer et al, 2010). The negative impacts of Blue-winged Warbler and Brown-headed Cowbirds on Golden-winged Warbler populations can be minimized through the availability of high-quality habitat at both landscape and patch scales (Brittingham & Temple, 1983; Confer et al, 2010). Researchers largely agree that the primary driver of Golden-winged Warbler population declines is the loss of breeding habitat (Roth et al, 2012).

It has been postulated that Golden-winged Warblers historically bred in early-successional forests following wildfires, beaver flooding, and other disturbances (i.e., wind events). Natural large-scale disturbance events produced great amounts of open forest which subsequently became Golden-winged Warbler breeding habitat (Klaus & Buehler, 2001). Today, due to wildfire suppression, reduced beaver flooding activity, and reforestation of previously abandoned farmland, early-successional communities suitable as Golden-winged Warbler breeding habitat have become uncommon. Habitat

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management strategies for Golden-winged Warblers vary across the species' range and include timber harvests, controlled livestock grazing, periodic mowing of managed shrublands, and prescribe fire. In Pennsylvania, timber harvest prescriptions that result in appropriate amounts and distribution of grasses, shrubs, and residual trees is one of the most common methods used for creating Golden-winged Warbler breeding habitat (Bakermans et al, 2011).

A breeding range-wide study was conducted from 2008-2011 to generate habitat management guidelines for the Golden-winged Warbler. One result of this extensive effort was the, *Forestland Best Management Practices for the Golden-winged Warbler*, which provides guidance for the use of forestry practices to create Golden-winged Warbler breeding habitat (Bakermans et al, 2011). These guidelines are currently being implemented on public lands managed by several state agencies. Additionally, an incentive program called Working Lands for Wildlife (WLFW) was initiated in 2012 by USDA-NRCS and U.S. Fish and Wildlife Service to promote the creation of Golden-winged Warblers habitat on private lands. Forestry-based conservation practices are most commonly used to create breeding habitat on private lands enrolled in the WLFW program (E. Bellush, pers. com.).

While timber harvest remain one of the most prominent methods used to create Golden-winged Warbler nesting habitat in Pennsylvania, the species is also known to nest in other early successional habitats (Confer, 1992). For example, naturally-occurring wetlands may provide the critically-important habitat structure required for the species and are thusly known to be important for breeding Golden-winged Warblers (Gill & Murray, 1972; Confer et al, 2010; Rossell et al, 2003). Although Golden-winged Warbler

use of wetlands for nesting is well-documented, the rates of use and habitat requirements in these wetlands have received less study compared to upland habitats where researchers may more easily study the species' ecology. Confer et al (2010) found that Golden-winged Warbler nesting success in New York was higher in wetlands than in adjacent upland habitats (i.e., power line right-of-ways and managed shrublands). Confer et al (2010) provided important insight about the potential differences between upland and wetland communities for providing Golden-winged Warbler breeding habitat. However, no studies have compared the densities of Golden-winged Warbler breeding territories between managed uplands and nearby natural wetlands. Moreover, my study is the first to empirically describe the characteristics of naturally-occurring shrub-wetlands used by nesting Golden-winged Warblers. Evaluation of Golden-winged Warbler use of wetland habitat in northeastern Pennsylvania where timber harvests and wetlands occur in close proximity to each other will elucidate the relative value of timber harvests and wetlands for providing quality Golden-winged Warbler breeding habitat in the region. Further, quantification of habitat characteristics in wetlands and avian densities within both timber harvests and adjacent wetlands will assist biologists in discerning the relative contribution that these two early-successional communities provide toward meeting Golden-winged Warbler habitat and population goals.

Objectives

1. Estimate and compare densities of Golden-winged Warbler breeding territories in upland timber harvests and natural shrub wetlands across the Poconos Region

2. Describe the microhabitat characteristics most important to supporting breeding Golden-winged Warblers within shrub wetlands of the Poconos Region

3. Describe the macro-scale habitat attributes most important to predicting the presence

of breeding Golden-winged Warblers within shrub wetlands of the Poconos Region

CHAPTER II

LITERATURE REVIEW

Golden-winged Warbler: Physical Description

First described in 1760, the Golden-winged Warbler is a migratory songbird that

breeds throughout eastern North America (Gill, 2004; Confer et al, 2011). The Golden-

winged Warbler, like many other members of family *Parulidae*, is a relatively small bird,

weighing about 9 g and measuring approximately 13 cm in length (Confer et al, 2011).

Although short-lived like many passerines, band-recapture data demonstrate that Golden-

winged Warblers may live as long as 7-9 years (Lutmerding & Love, 2013). While, under

certain circumstances, identification of hybrids between Golden-winged Warblers and the

closely-related Blue-winged Warbler (*V. cyanoptera*) can prove challenging,

phenotypically pure Golden-winged Warblers are visually distinct (Bent, 1953; Parkes,

1951). Male Golden-winged Warblers have a black facial pattern in which the throat,

lores, and auriculars are black, while the malar and supercillium are bright white (Pyle,

1997; Confer et al, 2011). This bird's "chickadee-like" appearance is further emphasized

by its overall gray plumage with wings, nape, back, and rectrices a medium gray tone

(Confer et al, 2011). Interestingly, it has been suggested that the plumage similarities

between the Golden-winged Warbler and the Black-capped Chickadee (*Parus

atricapillus*) are not coincidental, but rather the result of direct selection via mimicry of

the latter by the former (Ficken & Ficken, 1974).

Although somewhat chickadee-like, easily the most striking features of the

Golden-winged Warbler, true to the bird's namesake, are the brilliant yellow wing and

crown-patches (Bent, 1953; Confer et al, 2011). Brighter in the male, it is believed that

the bright crown of the Golden-winged Warbler may be important for mate-attraction and courting females (Ficken & Ficken, 1968a). Indeed, the male regularly erects his yellow crown when displaying for females. The female Golden-winged Warbler is visually very similar to the male, however, her facial markings are dusky grey rather than black and the crown is a more muted, olive yellow than that of the male (Pyle, 1997).

Breeding Range and Habitat

The breeding distribution of the Golden-winged Warbler spans throughout much of Eastern North America (Confer et al, 2011; Sauer et al, 2012). This range extends from its southern extreme in Georgia, north to Massachusetts in the east and extends west through the Great Lakes (Buehler et al, 2007). The northern extent of the breeding range occurs in parts of Minnesota and southern Manitoba, Canada (Buehler et al, 2007; Sauer et al, 2012). Within the past century, the Golden-winged Warbler has experienced a range-shift that appears to be moving northward (Confer & Knapp, 1981; Buehler et al, 2007). Gill (1980) describes the expansion of the Golden-winged Warbler at the forefront of its range in Connecticut where, in 1843, the species was seen only as a migratory vagrant. By 1875, the first confirmed breeding record was made in Connecticut and by 1893 the bird was found breeding in small numbers throughout the state. By the year 1902, the Golden-winged Warbler was described as a "common summer resident" of the state of Connecticut (Gill, 1980). Today, while the Golden-winged Warbler continues to expand its range north, the species is seeing significant declines in the eastern and southern portions of this range (Sauer et al, 2012).

Despite northward expansion over the past century, the breeding range of the Golden-winged Warbler is still limited (Confer et al, 2011; Sauer et al, 2012). Within

this restricted geographic range, the Golden-winged Warbler is further limited by its specialized habitat requirements (Confer & Knapp 1981; Bakermans et al, 2011). The Golden-winged Warbler is a forest-dwelling species, requiring a landscape where forest is the dominant cover-type (Bakermans et al, 2011). Indeed, the *Golden-winged Warbler Best Management Practices for Maryland and Pennsylvania* suggest that ideal habitat for Golden-winged Warblers are those landscapes comprised of ≥70% forest (Bakermans et al, 2011).

Within predominantly forested landscapes, the Golden-winged Warbler specializes further on early-successional habitat with appropriate vegetative structure (Cooke, 1904; Confer et al, 2011). Historically, these young communities were the result of large-scale forest disturbance and subsequent forest regeneration (Hunter et al, 2001). These disturbance events included a host of occurrences such as wildfire, abandoned beaver (*Castor canadensis*) meadows, grazing by native ungulates (e.g., elk: *Cervus elaphus),* and extreme wind events (Hunter et al, 2001). In addition to natural disturbances, wide-scale forest-clearing by the timber and agricultural industries were commonplace prior to the 1900s (Williams, 1992). Such anthropogenic forest disturbances likely helped many early successional bird species increase in overall population size (Hunter et al, 2001). Because of this extreme historic trend of forest-removal in eastern North America, we now see the preservation of mature forest as nearly synonymous with forest conservation (Askins, 2001). Presently, Golden-winged Warblers are now associated strongly with anthropogenically-altered habitats (e.g., timber harvests, power line rights-of-ways) that mimic historic natural disturbances (Hunter et al, 2001; Klaus & Buehler, 2001; Confer et al, 2011).

Although Golden-winged Warblers prefer nesting within large patches of early-successional habitat, individual breeding territories are small, generally <1-3 hectares in size (Murray & Gill, 1976; Confer & Knapp, 1981). Golden-winged Warblers, therefore, frequently nest in a loose colony-like aggregation with many territories concentrated within large disturbed patches but are scarce elsewhere (Confer & Knapp, 1981). Within these early-successional habitat patches, Golden-winged Warblers show a high affinity for forest ecotones (Klaus & Buehler, 2001; Confer et al, 2003; Patton et al, 2010). Confer et al (2003) reported that most Golden-winged Warblers in New York incorporated a forest edge as a component of their territories. Likewise, in the southern portion of its breeding range, Patton et al (2010) found that Golden-winged Warbler territories tended to be within 28-45 m of mature forest edge.

In addition to utilizing the edge of disturbed patches of forest, Golden-winged Warblers also require patches of herbaceous vegetation and low shrubs in which to nest (Confer et al, 2003; Rossell et al, 2003; Klaus & Buehler, 2001; Confer & Knapp, 1981). Klaus and Buehler (2001) reported that most of the Golden-winged Warbler nests located in timber harvests (n=23) were along edges where disturbance promoted the growth of herbaceous cover. Indeed, it is believed herbaceous patches play a critical role in the occupancy of early-successional areas by Golden-winged Warblers as timber harvests lacking herbaceous patches also seem to lack nesting Golden-winged Warblers (Klaus & Buehler, 2001).

In addition to using edges and the herbaceous patches for nesting, Golden-winged Warblers utilize a more open disturbed area than do other *Vermivora* (i.e., Blue-winged Warblers; Confer et al, 2003). Confer and Knapp (1981) observed that Golden-

winged Warblers preferred to nest in areas that were considerably younger than their Blue-winged congeners; Golden-winged Warblers used areas where secondary succession was in its earlier stages while Blue-winged Warblers more frequently used more mature areas with higher tree density. Supporting this idea, Confer et al, (2003) found that Golden-winged Warblers nested in areas that had tree densities about 20% lower than did Blue-winged Warblers. The combination of reduced canopy cover and subsequent herbaceous areas ultimately results in especially open patches within a patch of disturbed forest –a common component of Golden-winged Warbler territories (Frech & Confer, 1987). These herbaceous areas, important for Golden-winged Warbler nesting, frequently host grasses (e.g., *Andropogon* spp.), sedges (e.g., *Carex* spp.), goldenrods (*Solidago* spp.), asters (*Aster* spp.), and blackberry (*Rubus* spp.) as the most abundant plant genera (Klaus & Buehler, 2001). Wetland communities, although supporting different plant species assemblages than upland communities, still maintain the primary structural components required by breeding Golden-winged Warbler (Rossell et al, 2003; Confer et al, 2010).

Golden-winged Warbler Decline

In 1966 the North American Breeding Bird Survey (BBS) was initiated by the USGS Patuxent Wildlife Research Center in response to the devastating effects of the pesticide DDT (dichlorodiphenyltrichloroethane) on bird populations (Sauer et al, 2012). Since its beginning, the BBS has relied upon trained volunteers to identify birds along specific routes as a method to monitor many North American bird populations (Link & Sauer, 1998). The results of the BBS have highlighted the declines of numerous bird species, particularly neotropical migrants (Peterjohn et al, 1995; Sauer et al, 2012).

Perhaps one of the most marked declines seen as a result of BBS observations is that of the Golden-winged Warbler (Buehler et al, 2007, Sauer et al, 2012). Eastern North America has seen some of the steepest declines across this warbler's range with the Appalachian Mountains hosting losses of -7.1%/yr. since 1966. Conversely, some locations have seen rapid increases in Golden-winged Warblers populations, even as high as +33.4%/yr. as observed in Manitoba. Despite these localized increases, the overall trend for the species is a significant decrease of -2.6%, annually (Sauer et al, 2012). Although many species of early-successional birds are declining, the startling rates of population loss seen by the Golden-winged Warbler are nearly five times faster than most others (Sauer et al, 2012). The species' dramatic population declines led to a petition for the Golden-winged Warbler's listing under the US Endangered Species Act in 2010 (Will, 2009).

There are numerous considerations that must be made with regards to the management of neotropical migratory birds (Finch, 1991). One consideration, unique to migratory species, loss of quality wintering habitat, is believed to be partially responsible for the decline of neotropical migratory Parulids (Rappole & McDonald, 1994). Indeed, it is believed that deforestation in Central/South America is a contributing factor behind the loss of Golden-winged Warbler populations (Buehler et al, 2007). While the degradation of wintering habitat is no doubt a contributing factor behind Golden-winged Warbler population declines, it is believed to be a secondary cause (Confer & Larkin, 1998). Golden-winged Warbler declines began more than a century ago (Gill, 1980; Confer & Larkin, 1998) while extensive deforestation in Central/South America has proliferated more recently (Geist & Lambin, 2001). Moreover, Golden-winged Warblers are

increasing in abundance at the northern extremes of their range, further suggesting that loss of quality wintering ground habitat is not solely responsible for this bird's population decline (Sauer et al, 2012; Confer & Larkin 1998; Confer & Knapp, 1981).

In addition to wintering ground degradation contributing to the decline of Golden-winged Warbler populations, several other factors appear to be negatively influencing this species' persistence (Buehler et al, 2007; Bakermans et al, 2011). Prolonged interaction with Blue-winged Warblers on the breeding grounds is understood to be detrimental to Golden-winged Warblers (Gill, 1980; Confer et al, 2003; Confer et al, 2010). As such, Golden-winged Warbler habitat management is directed to areas where Blue-winged Warblers are less likely to occur (e.g., areas of higher elevation and high % forest cover; Golden-winged Warbler Working Group, 2013). The dynamics of these two congeners are discussed below (see "Interaction with Blue-winged Warblers").

The Brown-headed Cowbird (*Molothrus ater*) is a prairie songbird that, prior to the 1800s, was found primarily in the Western US (Brittingham & Temple, 1983). Following European settlement and subsequent clearing of forest, this grassland species infiltrated many portions of eastern North America where it was once rare or absent (Lowther, 1993). Today, the Brown-headed Cowbird ranges throughout almost the entirety of the US, extending as far East as Maine and New Brunswick, Canada (Sauer et al, 2012). Because the Brown-headed Cowbirds prefer landscapes within limited forest cover, protection of large expanses of forest will thus minimize the negative pressure of cowbird parasitism on Golden-winged Warblers and other forest-breeding passerines (Brittingham & Temple, 1983).

While the range expansions of other bird species (e.g., European Starling *Sternus vulgaris,* an alien cavity-nester) have had little impact on Golden-winged Warblers, the cowbird is an obligate brood parasite that exploits the Golden-winged Warbler (among other species) as a host (Coker & Confer, 1990). Female Brown-headed Cowbirds reduce the fecundity of their host by removing one of the host bird's eggs from the host nest and replacing it with one of her own (Lowther, 1993). Upon hatching, the parasitic cowbird nestling generally outcompetes its brood-mates through larger hatch-size and more vigorous begging behavior (Lichtenstein & Sealy, 1998). Golden-winged Warblers, poorly adapted to presence of brood parasites, are thus negatively affected by nest parasitism by cowbirds (Confer et al, 2003).

Although the aforementioned ecological pressures are believed to contribute to the decline of the Golden-winged Warbler, loss/degradation of high-quality breeding habitat has been cited as the most important mechanism behind population losses (Roth et al, 2012). Historically, Golden-winged Warblers have enjoyed range-expansion facilitated by the abandonment of farmland throughout the eastern US (Confer & Knapp, 1981). Unfortunately, many of these formerly-abandoned farmlands have undergone succession and are now closed-canopied forests that lack the structure needed by breeding Golden-winged Warblers (Confer & Knapp, 1981; Confer et al, 2011). This loss of habitat on the breeding grounds, seems to account for most of the decline of both Golden-winged Warblers and Blue-winged Warblers that we see today (Gill, 1980; Trani et al, 2001).

Territorial Behavior and Courtship

In spring, male Golden-winged Warblers migrate from their wintering grounds and arrive on the breeding grounds in late April-May (Confer et al, 2011; Ficken & Ficken, 1967; 1968a; 1968c). Upon arrival, males are very conspicuous not only because of their colorful plumage, but because of their constant singing (Ficken & Ficken 1967; Confer et al, 2003). Avian song, like most animal vocalization, is a specialized mode of communication (Kroodsma & Byers, 1991). While the motivation behind passerine singing behavior seems to be highly context-specific, two major functions of the Golden-winged Warbler song are clear: territorial defense and mate attraction (Gill & Lanyon, 1964; Murray & Gill, 1976; Ficken & Ficken, 1967; 1968a). Male Golden-winged Warblers sing constantly upon arrival to breeding habitat and use song as a method of claiming ownership of a breeding territory. Subsequently, females arrive on the breeding grounds and it is believed that they select males, at least in part, based on song characteristics (Ficken & Ficken, 1968a). The avian song has been demonstrated to be an "honest signal" of male quality in many bird species such as the Black-capped Chickadee, (Otter et al, 1997), Eurasian Blackcap (*Sylvia atricappila*; Hoi-Leitner et al, 1995), and Song Sparrows (*Melospiza melodia*; Reid et al, 2004). It is thus unsurprising that male Golden-winged Warblers sing so frequently and conspicuously during the initiation of the breeding season.

The primary song of the Golden-winged Warbler is a two-parted, buzzy trill. The song begins with a high-pitched introductory note followed by several (0-5) lower-pitched notes ("Zee Bee-Bee-Bee") (Ficken & Ficken, 1967). Though the number of "Bee" notes varies among individuals, Ficken and Ficken (1967) found that males

reduced the number of "Bees" from 3.7 to 2.4 "Bees"/song upon obtaining a mate. Furthermore, they also found that as the nesting season progresses, the amount of singing activity begins to decline until fledging, at which time males cease singing almost entirely (Confer et al, 2003).

Though the song is critically important to Golden-winged Warblers for effective communication, plumage characteristics are also believed to play a major role in territorial overlap and sexual recognition. In particular, Ficken and Ficken (1968b) found that one of the most important factors influencing the identification of an individual by other *Vermivora* was facial pattern. In fact, Ficken and Ficken (1968c) found that male Golden-winged Warblers do not treat males with differing facial patterns as conspecifics. Golden-winged Warblers also seem to rely heavily on plumage for attracting mates. Furthermore, Ficken and Ficken (1968c) found that Golden-winged Warblers that sang "Blue-winged" songs still attracted females twice as quickly as birds showing the "Brewster's" phenotype, despite their vocal abnormalities. Indeed, numerous studies have demonstrated that plumage characteristics of the Golden-winged Warbler, particularly facial pattern, act as an important communication mechanism (Leichty & Grier 2006; Murray & Gill, 1976). Leichty and Grier (2006) experimentally bleached the throat and auriculars of male Golden-winged Warblers in Minnesota resulting in birds with "Brewster's" hybrid facial phenotypes. A greater proportion of these pseudo-hybrids lost their original breeding territories than did un-bleached controls.

Female Golden-winged Warblers arrive on the breeding grounds several days after males have established territories (Ficken & Ficken, 1968a). Most phenotypically "pure" Golden-winged Warblers appear to obtain mates within a week or so following

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their arrival on the breeding grounds (Ficken & Ficken, 1968c). Upon arrival, females are believed to establish pair bonds with territorial males almost immediately. Courtship, lasting one-three days, consists of a variety of different behaviors that are exhibited by both sexes (Murray & Gill, 1976). During early courtship, the female frequently produces buzzy "Tzip" call-notes that are thought to inform the male of her whereabouts and to further cement their pair bond (Murray & Gill, 1976; Ficken & Ficken, 1968a). During courtship, males approach their females often, using a variety of displays including chasing, aggression, bill-dueling, and tail-spreading (Ficken & Ficken, 1968a). Ultimately, many of the male's advances are met with solicitation by the female, and the pair copulates. Copulation, though common during early courtship, appears to be infrequent following the early stages of nest-building (Ficken & Ficken, 1968a).

Nesting and Brood-rearing

Following several days of courtship, female Golden-winged Warblers build their nests within dense herbaceous vegetation contained within their males' territories (Klaus & Buehler, 2001; Bulluck & Buehler, 2008; Confer et al, 2011). Used solely for the rearing of young, females build a single nest, though she may abandon her nest and re-build elsewhere if disturbed during early nesting (i.e., nest-construction, egg-laying) or if the nest is predated (Confer et al, 2011). The loose, open-cup nest is built directly on the ground, though the nest can sometimes be elevated slightly by leaf litter substrate (Bent, 1953). The nest is generally supported by rigid plant stems such as goldenrod, fern fronds, or the stems of woody shrubs/saplings (Bent, 1953). Beginning with the outer, most coarse materials, the female begins nest construction with a cup of dead leaves showing a preference for leaves that retain their shape after drying such as Oak (*Quercus*

spp.) and American Beech (*Fagus grandifolia)* to form the "outer shell" of the nest (Chapman, 1907). Nest-building continues with the female adding finer material such as the bark from wild grape (*Vitis* spp.) or Viburnum (*Viburnum* spp.; Confer et al, 2011). The completion of the nest is marked by the female adding a lining of grasses, fine bark, and sometimes hair (Bent, 1953; Confer et al, 2011). Although the nest of the Golden-winged Warbler is placed within the direct reach of many terrestrial predators, it is usually well-concealed within the local vegetation (Confer et al, 2011). The process of constructing a nest takes from one to four days for the female to complete (Ficken & Ficken, 1967; Baicich & Harrison, 1997).

Normally, a single day elapses between the completion of the nest and the laying of the first egg (Ficken & Ficken, 1967). Like many birds, the female Golden-winged Warbler lays her eggs on consecutive days with a single egg being laid each day (Bent 1953). The female lays eggs in this pattern until a full clutch has been laid which varies from 3-7 eggs, though 5 is more typical (Confer et al, 2011). Clutches laid later in the season frequently have fewer eggs (Confer et al, 2003). Upon the completion of her clutch, the female incubates the eggs while her mate continues to defend his territory and seek food for the brooding female (Chapman, 1907). The female incubates the clutch for 10-11 days at which point the eggs hatch approximately synchronously (Confer et al, 2001; 2003).

Hatchling Golden-winged Warblers are similar to many other passerines in that they are developmentally precocial at the time of emergence from the egg (Confer et al, 2001). As such, they rely on their parents for all forms of care such as thermoregulation, sanitation, and nutrition (Gill, 1990). Female Golden-winged Warblers incubate the

brood as a method of maintaining the body temperature of the nestlings (Gill, 1990;

Confer et al, 2001). During the nestling-period, both adults hunt insects, particularly

caterpillars (order: Lepidoptera), to feed to the developing young (Confer et al, 2001;

Bellush, 2013). Although most passeriformes have equal rates of provisioning between

sexes, Reed et al, (2007) found that male Golden-winged Warblers, feed the young more

frequently than the female during the latter portion of the nestling life-phase. The

developing nestlings, nourished and tended by their parents, spend approximately 8-10

days (9 is average) in the nest prior to fledging (Confer et al, 2001; 2003).

  Like other songbirds, Golden-winged Warbler fledglings are far from independent

immediately following departure from their nest (Gill, 1990). These fledglings are fed by

their parents for several weeks and may not be fully independent for up to 31 days

(Confer et al, 2011). Golden-winged Warblers are a split-brooded species, that is, the

nestling brood is divided and a single parent cares for each of the two groups (Confer et

al, 2011). For the first few days, most fledglings remain relatively close to the nest,

however, these independent families soon part ways and most travel outside the natal

territory within five days post-fledging (Streby & Andersen, 2013). While with their

parents, fledglings beg for food constantly with a cricket-like "Tzzzz" (Faxon in Bent,

1953). Adults respond to begging calls by feeding their fledglings until they are fully able

to feed themselves at which time they separate from their parents (Bent, 1953; Confer et

al, 2011). Golden-winged Warblers are not known to produce multiple broods throughout

the course of a single breeding season (Confer et al, 2011).

Factors That Influence Songbird Nesting Success

Nesting success is generally thought of as the proportion of nests built that produce fledglings as well as the proportion of eggs within each nest that hatch and subsequently become fledglings (Mayfield, 1961). Understanding animal productivity and recruitment is critical for evaluation of habitat quality as the density of animals therein may prove to be a misleading metric of habitat value (Van Horne, 1983), but see Boves et al, (2013) for an alternate view. There are numerous mechanisms behind nest failure during both the incubation and nestling stages of the nesting cycle (Ricklefs, 1969). Some of the most common causes of nest failure for songbirds are brood parasitism, intraspecific competition, adverse weather events, adult death, nest abandonment, and predation of nest contents (i.e., eggs or young; Ricklefs, 1969; Etterson et al, 2007). Golden-winged Warbler nest success (the proportion of observed nests that successfully produce fledglings) appears to be variable with some studies reporting rates of success as low as 33% and other studies observing rates of >58% (Hanski et al, 1996; Bulluck & Buehler, 2008). While the proportion of nests that fledge young (nest success) is important to consider, passerine annual fecundity (arguably a more important statistic, from a management standpoint) is generally defined as a function of clutch size, nest success, number of nesting attempts, and number of broods per season (Thompson, 2007).

Predation is generally regarded to be the primary cause of nest failure for passerine birds (Ricklefs, 1969; Martin, 1988). Moreover, several of the other mechanisms behind nest failure (e.g., adult death, nest abandonment) are often the result of predation (Thompson, 2007). One major influencing factor that affects depredation

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rate of nests (i.e., nest failure) is detectability of the nest itself (Cresswell, 1996). Indeed, individuals that conceal their nests within dense vegetation seem to enjoy higher rates of nesting success than birds nesting in more exposed locations (Martin, 1992). Weidinger (2002) found that Yellowhammers (*Emberiza citronella*) and, to a lesser extent, Eurasian Blackcaps (*Sylvia atricapilla*) had a positive relationship between nest concealment and nest success. While this pattern has been absent from some studies (e.g., Filliater et al, 1994; Howlett & Stutchbury, 1996), complex edges with dense, concealing vegetation has been shown to produce much higher nesting success in Indigo Buntings (*Passerina cyanea*) and other songbird species when compared to more open habitats, more conducive to predator nest-searching (Suarez et al, 1997). This phenomenon is also seen in Golden-winged Warblers as clutch size has been shown to be positively correlated with herbaceous cover (Confer et al, 2003). Indeed, it appears that herbaceous, concealing vegetation is an important component of high-quality Golden-winged Warbler nesting habitat as it allows nests to be well-hidden from predators (Klaus & Buehler, 2001).

In addition to the conspicuity of the nest itself, nest predation (and thus nesting success) is affected by the density of predators within close proximity of the nest (Ricklefs, 1969). Because Golden-winged Warblers usually nest along forest-edge ecotones, this principle is especially important to the species' ecology as predation risk is understood to be greater along edges (Yahner, 1988; Peak et al, 2004). It is no surprise that many common nest predators (e.g., eastern chipmunks; *Tamias striatus*, northern raccoon; *Procyon lotor*, coyote; *Canis latrans*) preferentially use edge communities for foraging, explaining much of the "edge effect" sometimes seen within these ecotone

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areas (Ozaga & Harger 1966; Forsyth & Smith, 1973; Pedlar et al, 1997). Moreover, ephemeral communities with natural successional processes are understood to be different from permanent early-successional habitats (e.g., wildlife openings; Smetzer et al, 2014), even supporting lower rates of nest predation (Suarez et al, 1997). Still, as a disturbance-dependent species, the Golden-winged Warbler is well-adapted to nesting within forest ecotones as it provides dense cover and thick, predator-deterring vegetation that other potential nest sites fail to provide (Suarez et al, 1997; Confer et al, 2003; Rossell et al, 2003).

While Golden-winged Warblers occur within disturbed areas of forest, this disturbance is not synonymous with fragmentation of the forest itself (Lord & Norton, 1990). Indeed, disturbed forest may well still be in-tact forest (in a state of early succession) whereas fragmented forest typically becomes a compromised ecosystem (Hunter et al, 2001; Primack, 2010). Prior to European settlement, North America's forest remained largely in-tact with periodic natural disturbance (Hunter et al, 2001). Today, however, we now see extensive forest fragmentation across the northeastern US which appears to be an important driver behind many bird population declines (Robinson et al, 1995). While many birds have seen declines correlated with fragmentation of North America's forest, one species, the Brown-headed Cowbird, has experienced range-expansion and inflated population size as a direct result of forest loss and fragmentation (Lowther, 1993).

As an obligate brood parasite, the expansion of the Brown-headed Cowbird appears to coincide with the decline of many Neotropical migratory songbirds such as the Golden-winged Warbler (Brittingham & Temple, 1983). Some host species, found

across the cowbird's native range (e.g., Yellow Warbler; *Setophaga petechia*), have evolved strategies to thwart cowbird parasitism, however, hosts such as the Golden-winged Warbler have had limited historic selection pressure from cowbirds and thus developed no such defenses (Clark & Robertson, 1981; Coker & Confer, 1990). Golden-winged Warblers often fail to abandon their nest when parasitized by Brown-headed Cowbirds and simply accept the cowbird egg as their own (Coker & Confer, 1990). Presence of a cowbird egg in the nest is detrimental to individual fecundity; Confer et al (2003) found that the number of fledglings/nest produced is reduced from 2.3 to 1.0 when the nest becomes parasitized by Brown-headed Cowbirds. Cowbird parasitism ranges in frequency for Golden-winged Warblers with some studies reporting 0% of nests parasitized (Klaus & Buehler, 2001) to 30% of nests parasitized (Confer et al, 2003). To further reduce the effects of cowbirds on Golden-winged Warblers, areas with minimal agricultural influence should be the highest priority for habitat management as these areas attract cowbird activity (Buehler et al, 2007). Ultimately, increased landscape-scale forest cover is known to reduce the pressure of Brown-headed cowbird parasitism on forest passerines (Brittingham & Temple 1983; Coker & Confer 1990; Confer et al, 2003; Buehler et al, 2007).

Interaction with Blue-winged Warblers

Historically, the Golden-winged Warbler existed primarily in allopatry with its congener, the Blue-winged Warbler (Confer et al, 2011; Gill, 1980). Prior to the last century, the Blue-winged Warbler's range existed primarily south of Southern Michigan and west of the Appalachian Mountains. The Golden-wing, conversely, bred primarily within the northern portion of the Midwest and the Appalachian Mountains (Cooke,

1904). Within the past century, the Blue-winged Warbler has expanded its range

Northward and Eastward -largely into sympatry with the Golden-winged Warbler (Gill et

al, 2001). Following this recent range-expansion, breeding Blue-winged Warblers now

occur throughout the lower-elevation areas of Appalachia as well as most of New

England and the Midwest: the former stronghold for breeding Golden-winged Warblers

(Sauer et al, 2012). In Connecticut, the Blue-winged Warbler was believed to be absent in

1843, "uncommon" in 1877 and by 1890, Blue-winged Warblers were considered

"abundant" (Gill, 1980). This range expansion is attributed to, in part, the abandonment

of small farms throughout New England in response to the opening of the Erie Canal and

the prevalence of more industrialized agriculture (Kingsley, 1974; Gill, 1980). These

abandoned farms subsequently underwent the process of succession and thus became

habitat for Blue-winged Warblers, thus facilitating the spread of the species (Gill, 1980).

The Golden-winged and Blue-winged Warblers, though apparently separate

species, are believed to be at a critical point in their evolutionary histories (Ficken &

Ficken, 1968b; Gill, 1980). In the past, ornithologists have debated the species status of

the Golden-winged and Blue-winged Warblers, some suggesting that they are more likely

"semi-species" (Short, 1969). Ultimately, based on the current rate of hybridization

between these species and the reinforcement of reproductive isolating mechanisms (e.g.,

sexual selection against hybrids), these two birds are given the taxonomic status of

independent species (Short, 1969; Ficken & Ficken, 1968b). Following a recent

taxonomic change, the Golden and Blue-winged Warblers are now also the sole extant

members of the genus *Vermivora* (Chesser et al, 2011). This taxonomic classification

reflects the close relationship between these species as Gill (1997) found that the

nucleotide composition of the mitochondrial DNA (mtDNA) between the species differs by only 3.0-3.2%. Indeed, the two species are believed have diverged within the past several million years (Gill, 1997; Vallender et al, 2007; Confer et al, 2011). Vallender et al (2007) also found that nuclear DNA, a region of the genome that shows a relatively rapid rate of mutation, was almost identical for Golden-winged and Blue-winged Warblers, further highlighting their very recent speciation.

Hybrids of Golden-winged and Blue-winged Warblers are understood to be, like their parents, completely fertile (Faxon, 1911; Parkes, 1951; Ficken & Ficken 1967; Confer et al, 2011). The first generation F1 hybrid, resulting from a "pure" Golden-winged and Blue-winged Warbler pair, is commonly known as a "Brewster's Warbler". Prior to 1911, the Brewster's Warbler and other *Vermivora* hybrids (i.e., "Lawrence's Warbler") were considered to be a separate species (e.g., Brewster's Warbler: "*Helminthophila leucobronchialis*"; Faxon, 1911). Though not truly a separate warbler species, the Brewster's Warbler's plumage shows traits of both parent species (Parkes, 1951); this F1 hybrid has light grey underparts, slate gray back, rump and head (like a Golden-winged Warbler) with a facial pattern and white wing-bars similar to a Blue-winged Warbler (see Ficken & Ficken, 1967, Fig. 1). To complicate matters further, when Brewster's Warblers backcross to either Golden-winged Warblers or Blue-winged Warblers, the resulting F2 generation may have the phenotypes of a Brewster's Warbler, Golden-winged Warbler, Blue-winged Warbler, or a mix of characters exhibited by any of these birds (Faxon, 1911; Parkes, 1951; Ficken & Ficken, 1967). One such backcross, the Lawrence's Warbler, shows the facial pattern of a Golden-winged Warbler and the overall wing and contour plumage similar to a Blue-winged Warbler (Parkes, 1951).

Though the variability in hybrid phenotype is extensive, a simple Mendelian genetic model explains most of the patterns seen in *Vermivora* hybrid plumage inheritance (Parkes, 1951).

Despite their fertility, hybrids of Golden-and Blue-winged Warblers are less fit than their phenotypically "pure" parents. Ficken & Ficken (1968a) found that territorial Brewster's Warbler males attracted females approximately one week later than phenotypically-normal Golden-winged Warblers. These males are apparently "passed-up" by the earliest-arriving females (Ficken & Ficken, 1968a). Additionally, male Golden-winged Warblers who had their facial patterns experimentally altered to match that of a Brewster's hybrid also failed to obtain mates as effectively as unaltered males (Leichty & Grier, 2006). One potential explanation for this phenomenon is that male Brewster's Warblers exhibit far less aggressive behavior toward females than do parental-type warblers (Ficken & Ficken, 1968b). This aggression, important for the solicitation of copulation, appears to be critical for reproduction in Golden-winged Warblers and thus its suppression would greatly reduce the efficiency of the courtship process (Ficken & Ficken, 1968a).

While the recent range-expansion of the Blue-winged Warbler is understood to have negative effects on Golden-winged Warbler populations, the exact mechanism responsible for these declines remains somewhat unclear (Gill & Murray, 1972, Will, 1986; Gill, 1997; Confer & Larkin, 1998; Shapiro et al, 2004; Vallender et al, 2009). It has been reported that Blue-winged Warblers are socially and behaviorally dominant over Golden-winged Warblers and thus serve as competition for resources (Will, 1986). Golden-winged Warblers also appear to have smaller clutch-sizes when their territories

are within close proximity of a Blue-winged Warbler's territory (Confer et al, 2003). Interestingly, others have found that territorial males of these two species largely ignore each other and that territories between the two species overlap widely (Ficken & Ficken, 1968b; Gill & Murray, 1972; Confer & Larkin, 1998). Confer and Larkin (1998) also found that, when aggressive encounters did occur between the two species, Golden-winged Warblers were usually dominant over Blue-winged Warblers. In addition to serving as potential competition, Gill (1997) reported that the mitochondrial DNA (mtDNA) of the Blue-winged Warbler in Pennsylvania was rapidly and asymmetrically becoming introgressed into that of the Golden-winged Warbler. Gill (1997) thus suggested that perhaps female hybrids would preferentially backcross with Golden-winged Warbler males which could explain the asymmetrical introgression seen in that study. In contrast to Gill's 1997 work, Shapiro et al, (2004) found that Golden-and Blue-winged Warblers in Michigan and West Virginia had nearly equal levels of genetic introgression with 15% of Golden-winged Warblers showing Blue-winged Warbler introgression and 12% of Blue-winged Warblers showing Golden-winged Warbler introgression.

Perhaps the most alarming finding regarding the interaction between Golden-winged Warbler and Blue-winged Warbler populations is that reported by Gill (1980). Gill (1980) described how Golden-winged Warblers are predictably extirpated by Blue-winged Warblers within 50 years of their arrival. These changes in avian community composition are characterized by the initial colonization by Blue-winged Warblers followed by a subsequent increase in the number of Brewster's hybrids and, ultimately, the local extirpation of the Golden-winged phenotype (Gill, 2004; Gill, 1980). This

concern is supported by findings that suggest that many phenotypically "pure" Golden-winged Warblers have Blue-winged Warbler mtDNA incorporated into their DNA (Vallender et al, 2009). In some parts of the Golden-wing's range, rates as high as 17% of birds which indicates that Blue-winged Warbler mtDNA introgression has occurred (Vallender et al, 2009). Although it is unclear why Blue-winged Warblers replace Golden-winged Warblers in areas of sympatry, it remains obvious that prolonged hybridization between these two species is to the genetic detriment of both (Gill, 1980; 1997; Will, 1986; Vallender et al, 2007; 2009).

Habitat Management

Many species of early-successional birds across North America are declining at an alarming rate (Sauer et al, 2012). These losses, most pronounced in the northeast, correlate with the loss of disturbance-mediated habitat such as shrubland and young forest in which these species breed (Askins et al, 2001; King & Schlossberg, 2014). If these populations are to be restored, generation of high-quality breeding habitat is a critical first step to offset historic population losses (Brawn et al, 2001). One major challenge that land managers face is that early-successional areas are seemingly undesirable as they were historically created by forest disturbance events (e.g., fire) that could threaten components of human society such as buildings, roads, etc. (Askins et al, 2001). Furthermore, many forested areas occur on private land where management is nearly absent and landowners often choose to leave mature forest as such (Trani et al, 2001). Even when timber harvests do occur on private lands, they are often diameter limit cuts that do not facilitate the regeneration stands into young forest (Heiligmann et al, 1993). It is now understood that these disturbance-driven young forests are surprisingly

valuable to species of management interest such as American Woodcock (*Scalopax minor*), Ruffed Grouse (*Bonasa umbellus*), bobcat (*Lynx rufous*), black bear (*Ursus americana*) and New England cottontail (*Sylvilagus transitionalis*), to name a few (Dessecker & McAuley, 2001; Litvaitis, 2001; Capel et al, 2008).

There are numerous ways to create habitat for early-successional wildlife (Thompson & DeGraaf, 2001). Silvicultural practices such as timber harvest that employ over-story removal emulate natural forest disturbances by removing most large trees from a forest and thusly creating early-successional areas in which young trees regenerate (Kimmins, 2004). Timber harvest can be conducted using either even-aged or uneven-aged prescriptions to produce different forest growth dynamics/stand characteristics (Brawn et al, 2001). Historically, natural fires strongly influenced the ecology of North America's forest but fire has become much less common today (Attiwill, 1994; Nowacki & Abrams, 2008). Prescribed burning also mimics natural disturbance but, rather than manually removing trees using heavy equipment, trees and understory vegetation are burned by a human-made fire (Mannan et al, 1994). There are numerous additional techniques which promote early-successional upland habitat (e.g., prescribed grazing by livestock) that serve as options for land managers seeking to support disturbance-adapted bird species (Bock et al, 1993; Roth et al, 2012).

Although many early-successional bird species are declining, the Golden-winged Warbler has experienced accelerated rates, exceeding 5 times faster than most early-successional birds (Bakermans et al, 2011; Sauer et al, 2012). In response to these staggering losses, a group of scientists assembled in 2005 to form the *Golden-winged Warbler Working Group* (GWWG) with a mission statement of "ensuring the

conservation of Golden-winged Warbler populations through sound science, education, and management" (Roth et al, 2012). Shortly following the group's establishment, in 2008 the GWWG was awarded several years of funding from the US Fish and Wildlife Service, the National Fish and Wildlife Foundation and several state agencies with which to conduct a breeding range-wide study to develop region-specific management strategies to support Golden-winged Warblers (Roth et al, 2012). The result of this study was the *Golden-winged Warbler Status Review and Conservation Plan*, intended to guide and direct management activities for the species (Roth et al, 2012).

With a 2010 population estimate of 418,000 pairs, the GWWG aims to increase the number to 472,000 pairs of Golden-winged Warblers by 2020 and to 638,000 by 2050 (Roth et al, 2012). In order to meet these goals, the GWWG describes a series of habitat management strategies citing techniques such as timber harvest, prescribed burning, reforestation of surface mines, and prescribed grazing (Roth et al, 2012). The Golden-winged Warbler breeding range can be divided into two population segments: the Great Lakes and the Appalachian (Roth et al, 2011; Bakermans et al, 2011). These two population-regions are further divided by the GWWG into sub-regions within which management activity may be focused (Golden-winged Warbler Working Group, 2013). Because of the prevalence of forest across Pennsylvania, timber harvest serves as the primary tool for Golden-winged Warbler habitat creation (McCaskill et al, 2009; Bakermans et al, 2011).

Wetland Communities

Although the use of wetlands by Golden-winged Warblers is a well-documented phenomenon, little is known about their wetland breeding ecology in comparison to use

of upland habitat (Rossell et al, 2003; Confer et al, 2010). It is believed that the Golden-winged Warbler's very specialized habitat preferences likely arose because the species evolved with very distinct patterns of vegetation structure (Frech & Confer, 1987; Klaus & Buehler, 2001). Although upland ecosystems such as forest provide such structure following disturbance events, wetlands also provide the vegetative characteristics required by the species (Rossell et al, 2003). In fact, it is believed that wetlands historically played a very important role in the creation of new Golden-winged Warbler habitat as succession occurred within abandoned beaver ponds forming wet meadows (Askins, 2001; Confer et al, 2011). Moreover, wetlands are also believed to be one of the last remaining habitats used by Golden-winged Warblers that are not of anthropogenic origin (Confer et al, 2010).

Rossell et al, (2003) found that, although water was not a requisite for Golden-winged Warbler territories, the presence of flooded areas seemed to provide the open, herbaceous patches required for nesting by the species. Rossell (2001) found that Golden-winged Warblers preferred song perches to be close to water, when possible. Furthermore, Confer et al, (2010) found that Golden-winged Warblers in New York had higher nesting success in wetland habitats than those that nested in nearby upland habitats. Interestingly, although Golden-winged Warblers seem to use wetland habitats readily, Blue-winged Warblers do not show the same pattern (Will, 1986; Confer et al, 2010). Both Blue-winged Warblers and hybrids appear to be less common in wetlands when compared to their Golden-winged congeners (Confer et al, 2010). The result is a lowered prevalence of hybridization between Golden- and Blue-winged Warblers within wetland habitats (Confer et al, 2010). This difference in habitat preference may

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be a factor that helps to segregate these two species in areas of prolonged sympatry (Confer et al, 2003).

Study Area

This study was conducted in northeastern Pennsylvania. I surveyed avian communities and vegetation at 64 sites (32 wetlands and 32 timber harvests) distributed across Delaware State Forest (DSF; n=59) and Promised Land State Park (PLSP; n=5). DSF consists of >32,000 hectares of public land scattered throughout two counties and comprises the entirety of Pennsylvania's 19th forest district (PA DCNR, 2014). PLSP was approximately 1,200 hectares and embedded within DSF. DSF and PLSP are positioned within the heart of the Pocono Mountains of Pike and Monroe counties (Cuff, 1989). The Poconos Mountains, though often designated as the *Pocono Plateau*, fall within the Appalachian Glaciated Low Plateau (Shultz, 1999). This area is characterized by rounded hills and valleys, ultimately making the area one of the most rugged within Pennsylvania (White & Chance, 1882). Because the Poconos were historically glaciated, the soils in the region are chiefly un-weathered inceptisols -the direct product of glacial till and thus of little use to agriculture (White & Chance 1882; Cuff, 1989). As a result, Pike and Monroe counties remain almost completely forested with minimal agricultural influence (McCaskill et al, 2009). This forested landscape is dominated by mature forest ecosystems (80-100 years post-harvest) with wetlands, suburban, and urban areas scattered throughout (McCaskill et al, 2009).

The upland forest-types within DSF and PLSP vary widely with scrub oak, dry-oak heath, northern hardwood forests constituting the majority. The dominant tree species within the area include chestnut oak (*Quercus prinus*), white oak (*Q. alba*), northern red

oak (*Q. rubra*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*) and sweet birch (*Betula lenta*). The most common shrub species within the study area included the mountain laurel (*Kalmia latifolia*), scrub oak (*Q. ilicifolia*), witch-hazel (*Hamamelis virginiana*), blueberry (*Vaccinium* spp.), raspberry (*Rubus* spp.) and sweet fern (*Camptonia peregrine*). The understory community consisted of a diverse array of forb species (e.g. *Solidago* spp., ferns) intermixed with various sedges (e.g., *Carex pennsylvanica*) and grasses (Wherry et al, 1979). Shade-tolerant forbs such as wild sarsaparilla (*Aralia nudicaulis*), northern bracken fern (*Pteridium aquilinum*), hay-scented fern (*Dennstaedtia punctilobula*), and whorled loosestrife (*Lysimachia quadrifolia*) were also common within upland areas of high canopy cover (Wherry et al, 1979).

A diverse array of wetlands also occurred within DSF and PLSP boundaries with hardwood swamps, coniferous bogs, sedge marshes and alder swamps among the most common. In fact, this region of Pennsylvania hosts more wetlands/sq. km than any other portion of the state (Majumdar et al, 1989). Many of these wetlands, while hosting significantly different plant communities than uplands, still maintained the vegetative structure required by breeding Golden-winged Warblers. Although the species composition of DSF/PLSP wetlands varied by wetland type, some of the most dominant overstory species were red maple, red spruce (*Picea rubens*), and eastern white pine (*Pinus strobus*). The most common plants comprising the mid-story shrub layer of DSF wetlands were Ericaceous species such as highbush blueberry (*V. angustifolium*), meadowsweet (*Spirea* spp.), and swamp azalea (*Rhododendron viscosum*). The most abundant understory plants within many of these wetlands tend to be sedges (e.g., *Carex*

stricta, C. urticulata), various ferns (e.g., *Osmundastrum cinnamomeum, Onoclea sensibilis*) and mosses (e.g., *Sphagnum* spp.) among others (Majumdar et al, 1989).

CHAPTER III

METHODS

Site Selection

All timber harvests selected for point count surveys were those that had been

recently harvested (3-11 years post-harvest) and conformed to the habitat guidelines set

into place by the Golden-winged Warbler Working Group (Bakermans et al, 2011). All

timber harvests included in my study had to meet the criteria of having a residual basal

area of 10-40 ft^2/acre with mature, healthy standing trees scattered throughout the

regenerating stand. The stands that I surveyed included the majority of the recent timber

harvests meeting these requirements in the area. Because these harvests are conducted in

a manner that supports the long-term sustainability of healthy forests, the subsequent

regeneration of the plant community occurs gradually and often in a patchy, irregular

pattern –characteristics required by the Golden-winged Warbler for breeding habitat

(Golden-winged Warbler Working Group, 2013). Moreover, many of the timber harvests

in this study were also within close proximity (<4km) to other timber harvests or natural

wetlands that potentially support breeding aggregations of Golden-winged Warblers. This

proximity to neighboring pairs of Golden-winged Warblers may be important for the

species due to its propensity to nest in loose colonies (Confer & Knapp, 1981).

To select early-successional palustrine wetlands, I used the geographic

information system ArcGIS version 10.2 (Environmental Systems Research Institute

2011) incorporating a combination of data (i.e., 2013 National Agriculture Imagery

Program; US Dep't of Agriculture, 2008; and the National Wetlands Inventory 2009

shapefile of Pennsylvania wetlands; US Fish & Wildlife Service, 2009) to delineate

wetland boundaries. Wetlands were selected as candidate locations for surveying if they were any of the following wetland types: 1. freshwater emergent wetland or 2. shrub-wetland (Cowardin et al, 1979). Shallow, palustrine-type wetlands were considered for surveying if they appeared (based upon visual examination of areal imagery) to be plant communities which were relatively open and dominated by shrubs while also supporting interspersed trees (i.e., potential Golden-winged Warbler habitat, Rossell et al, 2003). Most of the wetlands surveyed were characterized by hydric soils along the low banks of slow-moving streams or lowland areas with saturated soil conditions. I selected all wetlands that met these defined criteria and were located within the Delaware State Forest or Promised Land State Park property boundaries. From this list of sites, I selected the largest wetlands for inclusion in this study (n=32 wetlands). These wetlands ranged in size from 2.5 – 61.4 ha.

Avian Point Count Surveys and Point Locations

In order for me to survey the maximum number of potential habitat locations (both upland and wetland), it was critical to employ a structured, time-efficient sampling method that maintains high Golden-winged Warbler detectability. Point count surveys (or point transect surveys) are a standard sampling technique for terrestrial landbirds (e.g., passerines) that fit this description (Ralph & Scott 1981; Bibby et al, 2000). In fact, the point count survey may be the single most common technique for sampling avian community composition (including single-species occurrence) and is undoubtedly one of the least expensive (in comparison to methods such as spot mapping, mist-netting, etc.; Ralph et al, 1995; Frantz et al, 2014). Although wetland size constrained point placement somewhat, I attempted to place wetland surveys such that points were both randomly-

located as well as ≥80 m from edge. For wetlands too small to allow such placement of points, the survey was conducted in the center of the wetland. Wetland centers were generated in ArcMap using the calculate centroid function of the "calculate geometry" tool.

Point counts are also convenient because they provide an index of species abundance and avian community composition without requiring the surveyor to physically handle birds. This *in situ* observation approach makes the method easy to employ and is subject to fewer legal and political restrictions because the study subjects are essentially unaffected by the sampling event. The survey protocol that I selected for my study are based on those recommended by the *Golden-winged Warbler Conservation Plan* (Roth et al, 2012).

I conducted point counts at 64 locations to compare Golden-winged Warbler occurrence in upland timber harvests (n=32) and natural wetlands (n=32) across the Poconos region. Point count surveys were conducted from 10 May- 15 June 2014 and began 15 minutes post-sunrise and continued until four hours post-sunrise. Each point count location was surveyed twice and surveys were conducted approximately 14 days apart. This survey window encompassed most of the Golden-winged Warbler breeding season while including minimal overlap with migration/post-breeding dispersal periods (Highsmith, 1989). Although all bird species were recorded during these surveys, special attention was given to Golden-winged Warblers as the species was the focus of this project. Weather conditions were also recorded prior to each point count, though little variation was ultimately observed in weather as I did not conduct point count surveys during adverse weather conditions (e.g., high wind, precipitation, etc.).

Each morning, I visited a group of points to sample and proceeded to conduct as many surveys as possible within the morning before four hours post-sunrise. Wetland and timber harvest groups of point count surveys were conducted on alternating days, ensuring that they were conducted within the same temporal range. Upon arriving at each point, I first remained quiet and inconspicuous for about one minute to allow birds to resume normal, undisturbed activity before beginning the point count. Each point count lasted a total of 10 minutes and consisted of me passively observing and recording all avian life within the area. During the point survey, I recorded all individual birds that were detected by either sight or sound. Each bird's species, detection-type (visual, vocal, etc.), sex (if possible) and distance (m) from observer was recorded (using a hand-held rangefinder). In addition to recording bird presence during the point count, I also divided each 10-minute survey into a series of smaller, two-minute sub-surveys (McNeil et al, 2014). This allowed me to generate a series of detection histories for each point for the greater 10-minute survey (which facilitated occupancy modeling analyses; see below). During each two-minute survey, I recorded whether a Golden-winged Warbler was detected or not which ultimately generated five detection occasions for each point visit and point replicates yielded a total of ten detection history entries (across two separate dates). For example, detection histories for three sites (site visits separated by a comma) may appear as:

Site A: 00000,00000
Site B: 01101,00010
Site C: 00000,11111

Where 1 represents a detection of a Golden-winged Warbler and a 0 represents a non-detection for the species. For Site A, the species was never detected. For Site B, the

species was detected on the 2nd, 3rd, and 5th sub-count during the first visit, and on the 4th

sub-count of the second visit. Site C had no Golden-winged Warblers detected during the

first visit, but the species was detected in every sub-count of the second visit. Sub-count

specific detection data were only used for occupancy modeling whereas the point count

survey was viewed as a single, 10-minute survey for Golden-winged Warbler density

estimation in program DISTANCE.

Microhabitat Quantification

The objective for vegetation sampling was to quantify the floristic characteristics

at a microhabitat scale relevant to Golden-winged Warbler breeding ecology. Ultimately,

when coupled with the landscape-level analysis (see "Landscape-scale habitat

quantification" below), these habitat characteristics encompass the majority of habitat

scales used by Golden-winged Warblers when selecting breeding localities. To study

vegetation at the microhabitat scale, I used a nested sampling design (Fig. 1) with the

coarsest sampling being done at an 11.3m radius and the finest conducted at a 5 m radius

from point center. The sampling protocol is designed to characterize vegetation across

strata (broadleaf herbaceous/sedges, shrub/sapling, trees) that are known to be important

to Golden-winged Warblers. Because many of the habitat features that I desired to sample

were too fine to effectively quantify with most remotely-sensed data (e.g., individual

herbaceous plants and sedges), microhabitat data had to be collected directly in the field.

At the finest scale (5 m), I did a complete census of all saplings and shrubs that

meet my definitions of each category (as well as identified each individual sapling/shrub

to the species level). I defined shrubs and saplings by a combination of criteria

considering both life history and general growth pattern. *Shrubs* were defined as woody
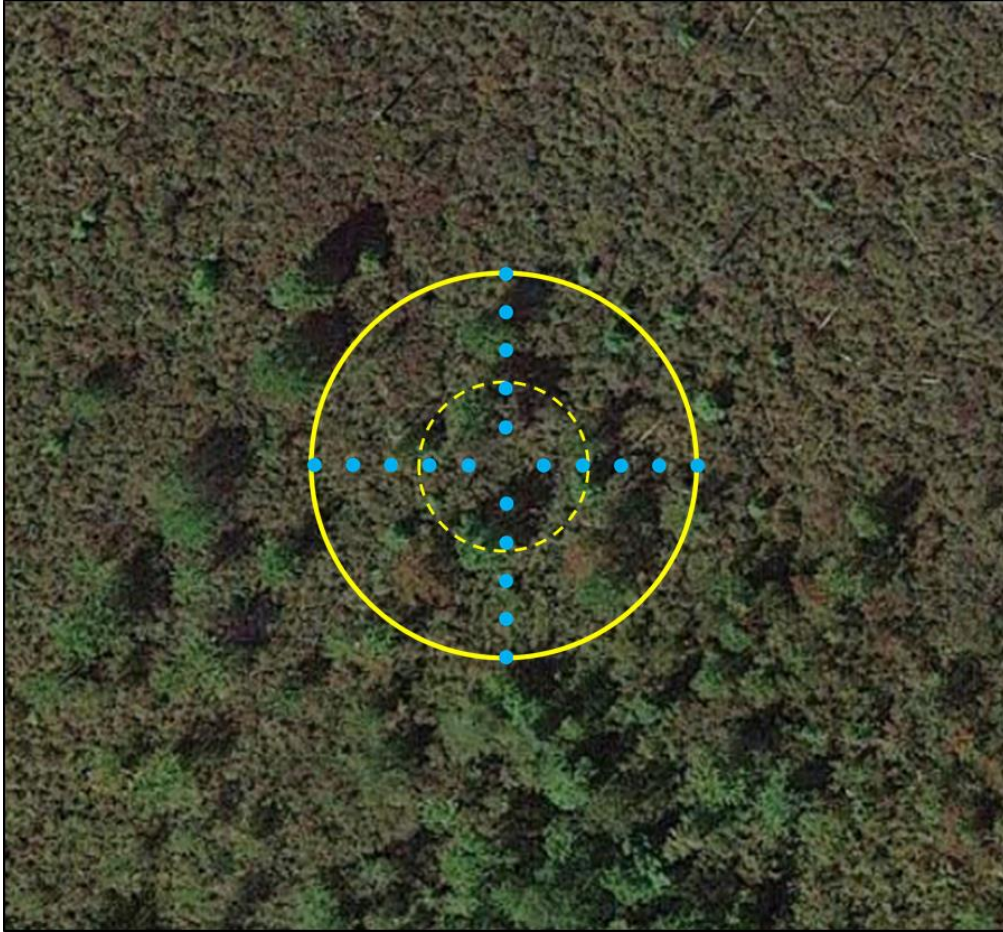
Figure 1. Aerial photo of a typical wetland site with the microhabitat vegetation sampling scheme for point count locations. Total snag count, tree count, basal area, and average shrub and sapling heights were quantified at the 11.3 m (larger, solid circle) radius. All 1-2m shrub, >2m shrub, and sapling stem counts, and woody stem diversity were quantified at the 5 m (smaller, dashed circle) radius. Percent cover was quantified for sedge, herb, shrub, and sapling at five points along each of four radial transects in each cardinal direction (represented by blue dots).

plants that tend to remain relatively small (<10 m in height, usually) and are characterized by multiple stems branching from the root. Shrubs were divided into multiple categories: 1-2 m tall shrubs and >2 m tall shrubs were quantified using formal counts (see below), whereas all shrubs (including those growing <1 m in height) were. *Saplings* were defined as woody plants that, although small, had the capacity to grow large, usually represented in other areas (i.e., uplands) by full-sized trees. Additionally, saplings were characterized by a growth structure of a single main stem rising from the root. Saplings were counted only when their stems were <10 cm in diameter and $\geq$1 m in height. For each category of woody stem (1-2 m shrub, >2 m shrub, and sapling), I generated estimates of species diversity at each point. For each point count location, I combined all three woody stem categories into a single metric of "woody stem diversity" using the standardized Shannon-Weiner diversity index ($e^{H'}$; $H'=-\sum_{i=1}^{R} p_i \ln p_i$, where H' represents the diversity index, R is the site's species richness, and p_i symbolizes the proportion of individuals belonging to the ith species).

Erect, singular woody plants with stems (appearing like large saplings) $\geq$10 cm in diameter were classified as "trees". Trees were quantified at the 11.3 m radius scale by counting all live trees and recoding their species and *diameter at breast-height* (DBH). If a tree's main trunk was branched below breast-height, it was treated as two separate trunks, rather than measuring the diameter of the entire trunk-bundle as a single, large stem. I used the area generated from the DBH measurements of trees within each 11.3 m plot to calculate "basal area" (SBA$=\frac{\sum_{i=1}^{n} BA_i}{A}$, where SBA represents the *stand basal area* [m^2/ha], BA$_i$ is the basal area of all trees i [m^2], and A is area [in hectares] of the 11.3 m radius plot) for each point location. In addition to quantifying the abundance of live trees,

I also recorded the total number of snags (defined as dead, standing timber ≥2 m in height and ≥10 cm DBH) within the 11.3 m radius plot. Further, I also estimated the average height (to the closest 0.1 m) of all shrubs (both 1-2 m and >2 m shrubs combined) and all saplings within 11.3 m of the point center. These estimates gave me a general metric of quantifying the shrub and sapling layers, respectively about the point count area.

In addition to the shrub/sapling and tree quantification metrics within the 11.3 m radius plot, I also quantified percent cover for vegetation strata along four radial transects using an ocular-tube transect (modified from James and Shugart, 1970; Thomas et al, 1996) extending in each cardinal direction for a length of 11.3 m (strata observed every 1.9 m; five readings in each direction). The goal of the ocular-tube transects was to quantify the various microhabitat strata at each point to describe the strata present and provide an abundance index for those strata. At each of the five ocular tube readings, I recorded all vegetation strata present (through the crosshairs of an ocular tube) within the following four categories: sedge, herbaceous broadleaf plants, shrubs, and saplings (Fig. 2). The same criteria were used to classify shrubs, saplings, etc. for the ocular-tube transects as was used for the total counts in the 5m and 11.3m plots. Although the category "sedge" was used for all narrow-leaved monocots on surveys (e.g., sedges, grasses, etc.), the majority of "sedge" recorded on ocular tube transects were truly sedges (i.e., *Carex* spp.). Each point also had its distance (m) to nearest forest edge measured using a hand-held rangefinder and confirmed using ArcMap version 10.2, later. Microhabitat sampling resulted in a total of 13 site-specific microhabitat variables for each point count location: 1) total number of 1-2 m shrubs within 5 m; 2) total number of >2 m shrubs within 5 m; 3) total number of saplings within 5 m; 4)

40
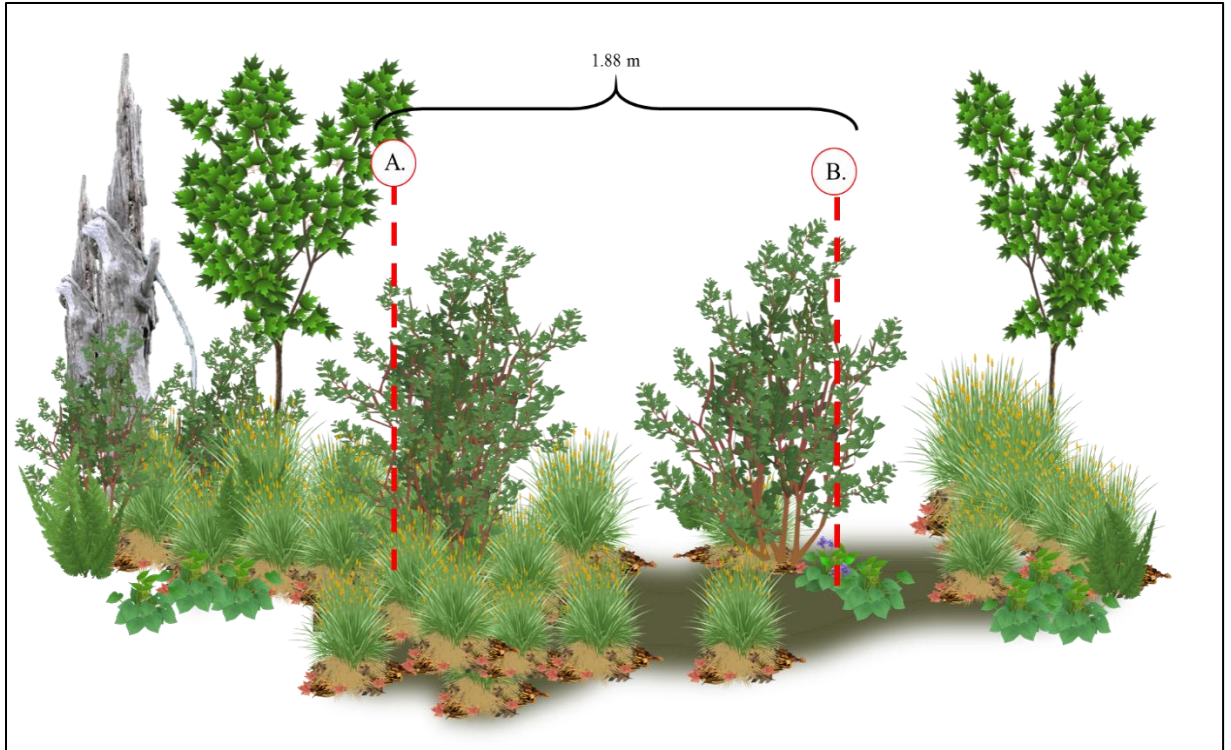
Figure 2. A diagram showing an example of how vegetative strata were sampled along ocular tube transects. Each point count location had five 11.3 m transects along which five ocular tube readings were conducted. The first reading occurred 1.88 m from point center and consecutive reading was 1.88 m further until the last (5th) occurred 11.3 m from the point center. The ocular tube vertical transect A. would capture 1. sedge, 2. shrub, and 3. sapling whereas ocular tube transect B. would only capture 1. forb and 2. shrub.

standardized Shannon-Weiner diversity for woody stems ($e^{H'}$) within 5 m; 5) average shrub height within 11.3 m; 6) average sapling height within 11.3 m; 7) point distance to nearest forest edge; 8) total number of snags within 11.3 m; 9) SBA within 11.3m; 10) percent cover sedge; 11) percent cover herbaceous; 12) percent cover shrub; and 13) percent cover sapling.

Macro-scale Habitat Quantification

Although micro-scale habitat features are an important factor that predicts the occurrence of many animal species (including birds; Weakland & Wood, 2005), birds are not restricted to small, microhabitat-scale features. Indeed, larger scales have been shown to also predict the occurrence of many bird guilds and even many individual species (Hunter et al, 2001; Bakermans et al, 2005). Further, several studies have shown that Golden-winged Warblers in particular require relatively large spatial extents for certain parts of their breeding-season behaviors (Streby et al, 2015; Frantz, 2013). To complement my aforementioned microhabitat scale data, I used remote-sensed data to quantify Golden-winged Warbler habitat at three spatial scales relevant to Golden-winged Warbler life history and ecology: 100, 250, and 500 m radius. The 100 m radius was chosen as it approximately resembles the minimum scale at which a Golden-winged Warbler male establishes a territory (Aldinger et al, 2014). The intermediate, 250 m scale was chosen to represent the territory + immediate surrounding area, mimicking the proposed habitat needs for male home-ranges by Frantz (2013). Finally, I chose the 500 m as my largest spatial extent because several other studies have suggested that Golden-winged Warblers use habitat at this scale (Streby et al, 2012; Streby et al, 2015)

especially during the post-fledging period. I quantified two metrics at all three spatial extents; land cover composition and structural heterogeneity.

In order to quantify the *land cover composition* at a macro-habitat scale within the three buffer zones (100, 250, and 500 m radius) around each point, I used the freely-available 2011 National Land Cover Data set (NLCD; Fry et al, 2011). The NLCD provides a raster data file for the entire continental United States with a 30-meter resolution, released to the public in 2013 (Homer et al, 2012). The NLCD classifies the entire US (independently by each 30 m cell) as one of 16 different land cover types, though not all of them were represented within my buffer zones or even within my study area. I used ArcGIS v. 10.2 to convert the raster NLCD file (clipped to my study area) to a vector-based file for further analyses. I used the NLCD vector file, and ArcMap's "clip" and "calculate geometry" tools to estimate the area of each land cover type within each buffer zone extent. Using the areas generated in ArcGIS, I calculated the proportion of each land cover type within each extent by dividing the area of each land cover type by the total area of each scale. At the 100 m extent, only three land cover types were found within >50% of plots and thusly appropriate for inclusion in analysis: deciduous forest, emergent wetland, and woody wetland. The 250 m included the same three cover types as the 100 m radii, however, it also included mixed forest. The 500 m extent naturally included the same land cover types as the 100 and 250 m extents but also included shrub/scrub. Other land cover types (i.e., coniferous forest, open water, grassland, and developed areas) were also found within at least some of the extents, however, these land cover types were never common enough to be included in further analyses, that is, the proportion of each cover type was = 0 for most sites. The result of the NLCD data

extraction was a series of percent cover type variables for 1) deciduous forest 2) mixed

forest 3) shrub/scrub 4) woody wetland and 5) emergent wetland (see Fig. 3).

I also quantified the *structural heterogeneity* within each of the three spatial

extents. Structural heterogeneity has long been recognized as an important component of

Golden-winged Warbler breeding habitat (Confer, 1992), however, this feature can be

somewhat difficult to measure with remotely-sensed data. One method that has been

employed to quantify structural heterogeneity is remote calculation of image texture (St-

Louis et al, 2006). I used raster format aerial photography from the freely-available

National Agriculture Imagery Program (NAIP) ortho 2013 raster for Pike Co.,

Pennsylvania as a base with which to calculate the macro-scale texture (St-Louis et al,

2006, Fig. 4). To calculate the macro-scale horizontal heterogeneity (hereafter, texture) at

the three spatial scales, I used the "focal statistics" tool in ArcGIS to calculate attributes

of the NAIP image raster values. By doing this for a neighborhood of 5x5 cells (1 m

resolution), ArcGIS was able to smooth squares of pixels to estimate the raster value

mean and standard deviation for each location. Using these values, I calculated the

average coefficient of variation for the entire 100, 250, and 500m spatial extent for each

point. This coefficient provided a metric as to how much horizontal heterogeneity

occurred around each point. I incorporated texture values into macro-scale habitat

models.

I assessed the extent to which my macro-scale habitat variables were independent

(within and among spatial extents) using a Spearman rank correlation matrix. I found that

the adjacent scales (100 + 250 m and 250 + 500 m radii) tended to have correlated

variables for both the NLCD habitat variables and the image textures. Because several of
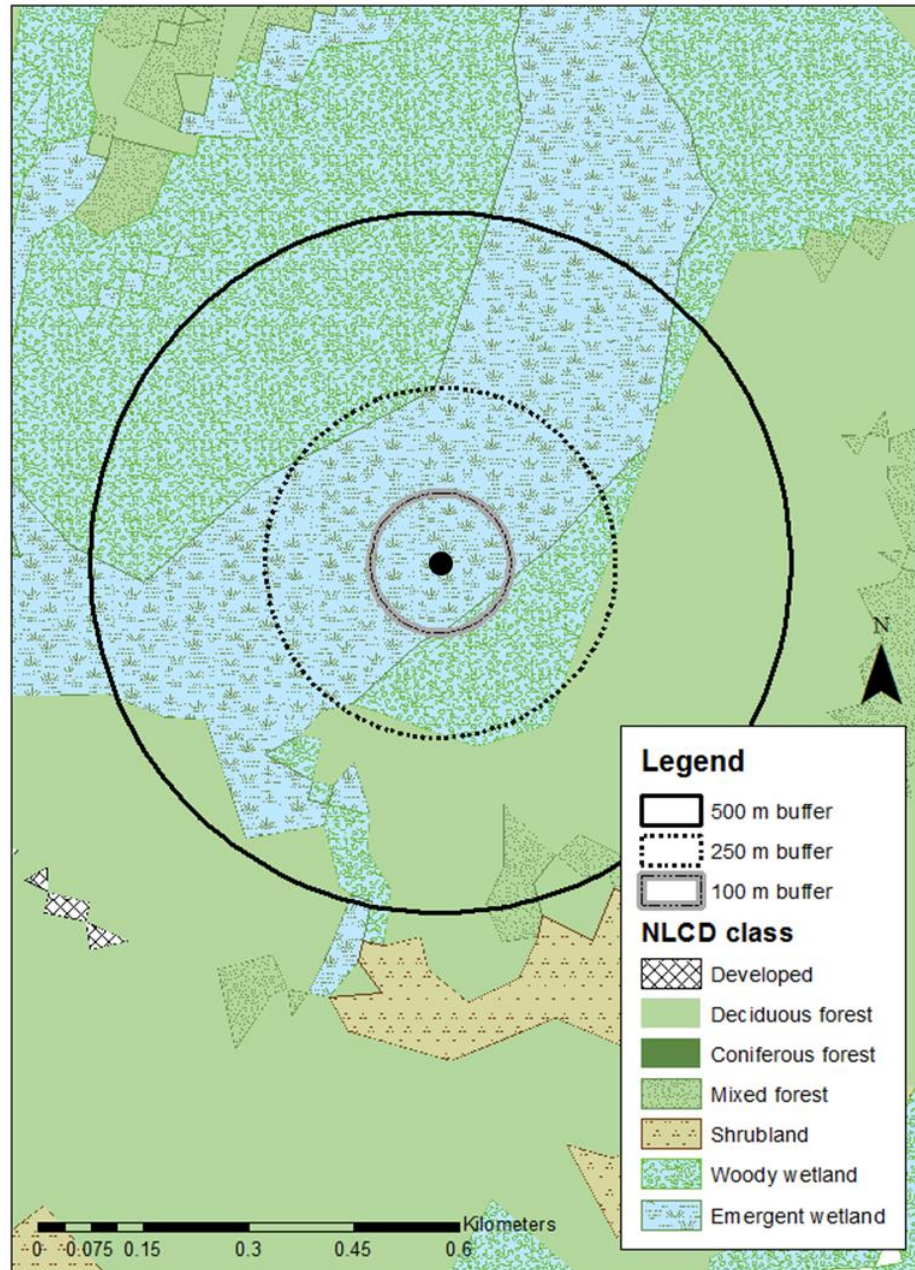
Figure 3. An example of macro-scale habitat-level sampling scheme for a wetland in northeastern Pennsylvania that was surveyed for Golden-winged Warblers. Land cover types are vector-format transformations of the National Land Cover Database (NLCD). The point count location is represented by a black dot. The circles represent the 100 m, 250 m, and 500 m radial spatial extents within which landcover composition and image texture were calculated.
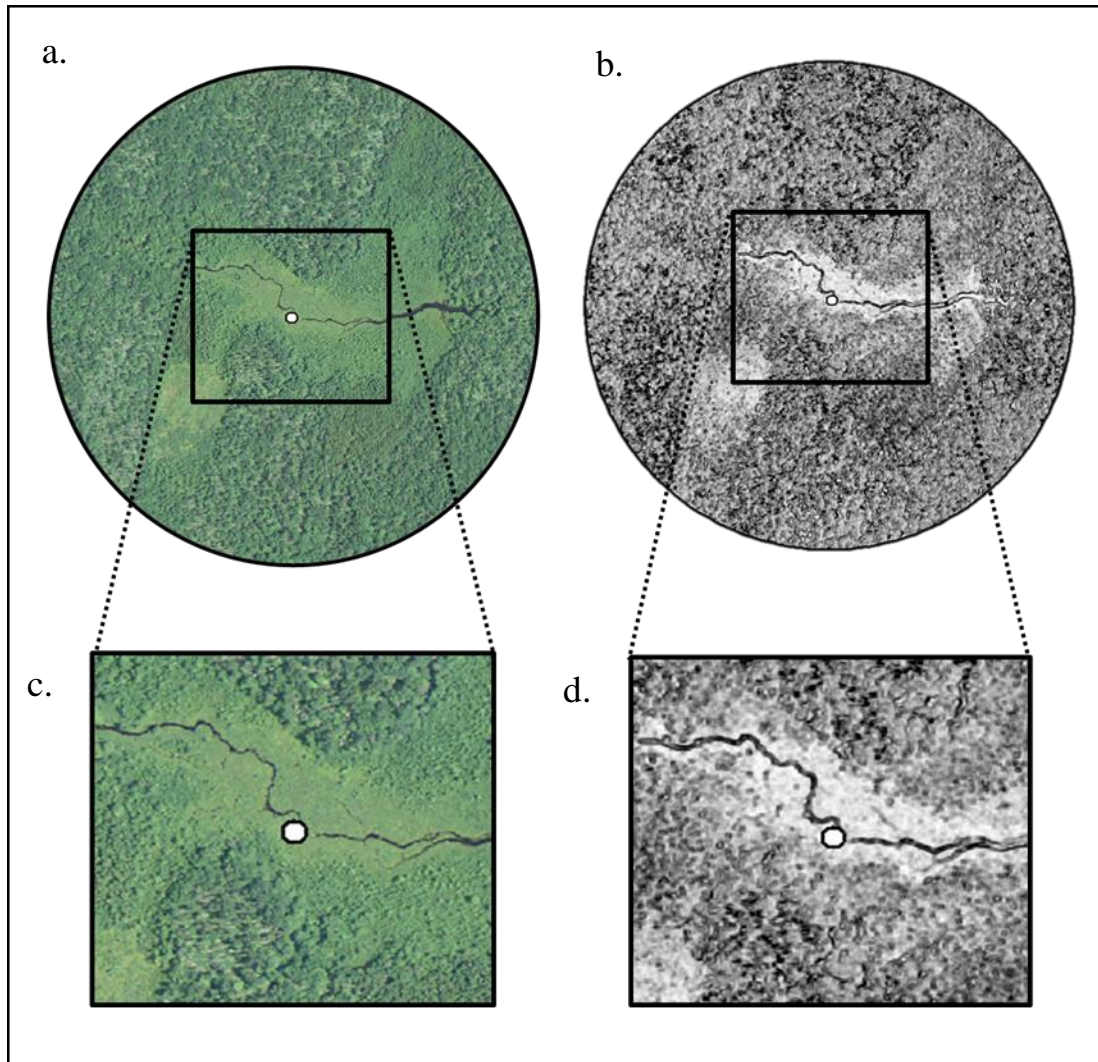
Figure 4. An example of macro-scale image texture (500 m radius) for a wetland point count location in northeastern Pennsylvania. The image texture analysis began using a NAIP ortho raster (a) which was converted to an image "texture" (b). Although superficially the image texture looks like a black-and-white conversion of the original NAIP raster, closer inspection reveals that the NAIP image shows broad cover characteristics (c), the image texture characterizes the structural complexity (d).

these variables were correlated (using a threshold value of r_s=0.70 as the cutoff for value

correlation), we ran the three spatial extents separately which alleviated the issue of

correlated variables. Macro-scale habitat sampling resulted in a total of 4, 5, and 6 site-

specific macro-scale habitat variables for each point count location at 100, 250, and 500

m radius, respectively; all spatial extents included texture, emergent wetland, woody

wetland, and deciduous forest while mixed forest was only included in 250 and 500 m

radii and shrub/scrub was restricted to the 500m radius.

Statistical Analyses

Comparison of Golden-winged Warbler Density in Timber Harvests and Wetlands

To examine potential differences in Golden-winged Warbler density between

timber harvests and naturally-occurring wetlands throughout Delaware State Forest and

Promised Land State Park, I generated density estimates for Golden-winged Warblers

using program DISTANCE version 6.2 (Thomas et al, 2010). DISTANCE uses object

(usually animals) observation data in the form of distances (linear distances from a line-

transect or radial distances from a point-transect) to generate density estimates (#

animals/unit area) across a given level of resolution (region, study area, site, etc.;

Marques et al, 2011; Thomas et al, 2002). DISTANCE models a detection function for

the dataset to generate density estimates based on the distances at which animals were

observed from the survey location (Thomas et al, 2010). One critical component of

distance sampling for density estimation is the modeling of a detection function to fit the

data (Thomas et al, 2010, Buckland et al, 2003). Prior to the final analysis of this dataset,

I ran a set of models in program DISTANCE using appropriate combinations of key

function and series expansion and ultimately selected the model with the lowest Akaike's

Information Criterion (AIC) value (Buckland et al, 2003). The model with the lowest AIC for my dataset was a detection function with a hazard rate key function (all three series expansions –*cosine, simple-polynomial* and *hermite polynomial* yielded equal AIC values), and was thus selected for the data analysis (Buckland et al, 2003).

Only male Golden-winged Warblers were considered in my DISTANCE sampling analysis because nearly all Golden-winged Warbler detections were initiated by song –an exclusively male behavior. Prior to the analysis of data in program DISTANCE, I truncated the dataset based on observation distances. Buckland et al, (2003) recommended that the outer 10% of observations be truncated from most analyses. Following distance-observation truncation, there were n=100 Golden-winged Warbler observations used in the analysis (62 in timber harvests and 38 in wetlands). For these remaining observations, I ran a model with stratum (i.e., site) –level resolution estimates for both *density* and *encounter rate* but a global (equal across all sites) –level *detection function*. The global detection function allowed me to treat detection probability equally across all sites in Delaware State Forest and Promised Land State Park.)

Modeling Golden-winged Warbler Detection Probability (p) in Wetlands

A primary goal of my study was to model which habitat features of shrub-wetlands in the Poconos region discern between sites where Golden-winged Warblers were and were not detected during point counts. Because my study relies on data derived from point count surveys, it is important to consider the mechanisms responsible for generating the data that I collected during my point counts. According to Burnham and Anderson (2002), there are two main factors governing the ability to detect any species on a survey: occupancy and detection probability. The first factor, "occupancy"

(generally depicted as ψ), is the actual state of the site with respect to species existence at a location (sites are either truly occupied or truly unoccupied). Unless the observer misidentifies the species of interest, a "1" recorded at a location confirms the occupancy of a site. Though 1's recorded for a site can confirm occupancy, 0's are more complicated as this failure to observe the species of interest can be driven by two mechanisms: true absence (i.e., the species was not occupying the site) or detection failure (i.e., the species was present at the site, but the observer failed to detect it). This failure to detect a species is driven by the product of two detection components: availability (the probability that the species was available for sampling [e.g., a bird vocalizes], p_a) and perceptibility (the probability that the species is detected by the observer when available, p_d). The probability that a species will be detected at a site, given that the site is truly occupied is known as a species' "detection probability" (generally depicted as p). Although occupancy is the primary metric of interest to this and many other animal habitat studies, it is important to account for detection probability as very few wildlife species can ever be truly surveyed with $p=1.0$ (MacKenzie et al, 2002).

Imperfect detection probability, generally regarded as a nuisance parameter, is frequently modeled to allow detection probability to vary as a function of survey-specific covariates (Johnson, 2008). An animal's perceptibility is a direct function of the observers' detection skills, species distance from the observer, species cue production rate, conspicuity of cues (e.g., volume of songs, duration of breeding displays, etc.), types of cues (e.g., songs vs. "chip" calls), etc. These factors are affected by survey-specific factors such as date (Spear et al, 1999), time (e.g., Ralf et al, 1995), and weather (e.g., Conway, 2011).

I modeled Golden-winged Warbler detection probability as a function of two survey-specific covariates: Julian date and minutes-since-sunrise (i.e., time). I ran a series of single-season occupancy models in Program R v.2.14.1 (R Development Core Team, Vienna, Austria; 2011) using the package "*unmarked*" and ranked them using the package "*AICcmodavg*". I ran a series of occupancy models which allowed occupancy ψ to remain constant while modeling binary detection histories as a function of either one or both of the survey-specific detection covariates. Models selection was done using AIC, particularly AIC corrected for small sample size (AICc). I evaluated models using the all possible subsets method of model construction and models were ranked according to descending AICc values with the lowest AICc considered as the best combination of variables (Burnham & Anderson, 2002). For occupancy models within the candidate set, I applied the generalized rule of models with $\Delta AIC_c < 2.0$ of the top model qualifying models as "competing" (Burnham & Anderson, 2002). Because the top detection model represented a model with the covariates most important in explaining variation in detection probability, I included those detection covariates as part of all models to explain variation in occupancy. This allowed me to model how occupancy varied as a function of habitat covariates while accounting for the detection covariates that would otherwise confound habitat modeling. Detection covariates were standardized prior to incorporation in detection models so that all had a mean of 0 and a standard deviation of 1.0.

Modeling Golden-winged Warbler Occupancy (ψ) in Wetlands

In order to describe how Golden-winged Warbler occupancy is impacted by both microhabitat and macro-scale habitat features in early-successional wetlands of the Poconos region, I used an information-theoretic approach to develop several sets of

single-season occupancy models. These models allowed me to consider Golden-winged Warbler occupancy as a function of habitat covariates (at various scales) while accounting for imperfect detection during surveys. The mathematical framework behind occupancy modeling exercises are very similar to logistic regression (Burnham & Anderson, 2002). The key assumptions of such occupancy modeling according to MacKenzie et al (2002) are: 1) Sites are closed to changes in occupancy during the "season" (i.e., occupied and unoccupied sites remain as such, respectively during the 10-minute point count sampling period) 2) The species is never incorrectly "detected" at sites where it is truly absent 3) Detections are independent (i.e., a detection at one site does not influence the probability of detection at other sites) 4) There is no un-modeled heterogeneity in detection probability.

To model occupancy, I used the *all-subsets* method of model selection using up to 1-3 covariates per model. All habitat covariates, like the detection covariates, were standardized prior to analysis (Marquardt, 1980). All habitat covariates were subjected to a Pearson's correlation analysis prior to inclusion to ensure that collinear variables were removed from the model set. Using a value of r=0.80 as a threshold, we found that none of our habitat variables were correlated and thus all were included in modeling. I limited the number of covariates within each model to a maximum of three to prevent the over-parameterization of models. My final candidate model set as the result of my model-building exercise for wetland microhabitat (including a null model) was n=470 models. Total number of candidate models for the three wetland spatial extents were n=15, n=26, and n=42 models for 100, 250, and 500 m radii, respectively. To rank models in each candidate set, I estimated the likelihood value for each model which can be interpreted as

the likelihood of the model given my dataset. Using the likelihood estimates, I generated

AIC values for each model corrected to account for small sample size (AIC$_c$). Although

AIC$_c$ values on their own are relatively meaningless, their rankings with respect to the top

model in each candidate set (the model with the lowest AIC$_c$ value) depict how well each

model explains the variation in the data. Although I considered the generalized rule of

models with ΔAIC$_c$ < 2.0 of the top model qualifying models as "competing" (Burnham

& Anderson, 2002), model averaging allowed me to explore occupancy relationships

while ameliorating the effects of uninformative parameters (Arnold, 2010). In addition to

AIC$_c$, I also estimated AIC$_c$ weights (ω) for each model (Burnham & Anderson, 2002). I

used the cumulative ω for models containing each given variable to rank each habitat

covariate according to its relative importance (Arnold, 2010). I used model-averaging to

estimate regression coefficients and standard error for each habitat variable, (Burnham &

Anderson, 2002). Finally, I evaluated the significance of each habitat variable by the

85% confidence intervals with intervals overlapping with zero being interpreted as

little/no relationship (Arnold, 2010).

I tested for model overdispersion by calculating the variance inflation factor ($\hat{c}$;

residual deviance over the residual degrees of freedom) of the most parameterized models

in the candidate model set. I looked for values of $\hat{c}$ that were greater than a value of 1.0

which suggest overdispersion. Overdispersion would be the result of variance levels

exceeding those expected under the assumptions of a binomial distribution (MacKenzie

et al, 2006). I also calculated the area-under-the-curve values (AUC) for each model to

evaluate their predictive abilities using the package "*pROC*" in program R; AUC=1.0

would suggest a model that perfectly predicts the occurrence of Golden-winged Warblers

whereas an AUC value of 0.5 would suggest a model that performed as effectively as randomly guessing the occupancy state of a site (Fielding & Bell, 1997).

CHAPTER IV

RESULTS

Timber Harvest – Wetland Density Comparison

Based on the raw point count data, the naïve rate of occupancy for upland timber

harvests managed for Golden-winged Warblers across the Poconos was 1.0 (32/32) while

the wetlands, in contrast, had a naïve occupancy of 0.58 (18/32; see Appendix A). I

observed a total of 117 Golden-winged Warblers during the course of my study. When

the data are examined from a distance observation perspective, it is clear that

observations at distances greater than 150 m become much less consistent, despite there

being more potential area at such radii within which warblers could potentially occur (see

Fig. 5). I truncated the distance at 150 m which removed slightly more than the 10%

minimum recommended by Buckland et al, (2003) (n=17 detections removed; 14.5%).

The range of distances removed as a result of truncation were 152-250 m. Two wetland

sites (Hay Road North and Little Bushkill Creek; see appendix A) had their only Golden-

winged Warbler observations occurring outside the truncation zone of 150 m and thus the

site density was =0, despite the target species' presence on point count surveys. In timber

harvests and natural wetlands, I recorded 67 and 50 independent observations of Golden-

winged Warblers (during 10-minute surveys), respectively. The average number of

Golden-winged Warblers observed per 10-minute survey was 1.05 males/timber harvest

survey and 0.78 males/wetland survey. When only sites where Golden-winged Warblers

were detected are considered, the average number of males detected/ 10-minute survey

increases in wetlands to 1.32 male/survey. Of the 117 total males observed in this study,

most (79%) were first detected as a result of either a Type I or, to a lesser extent, Type II
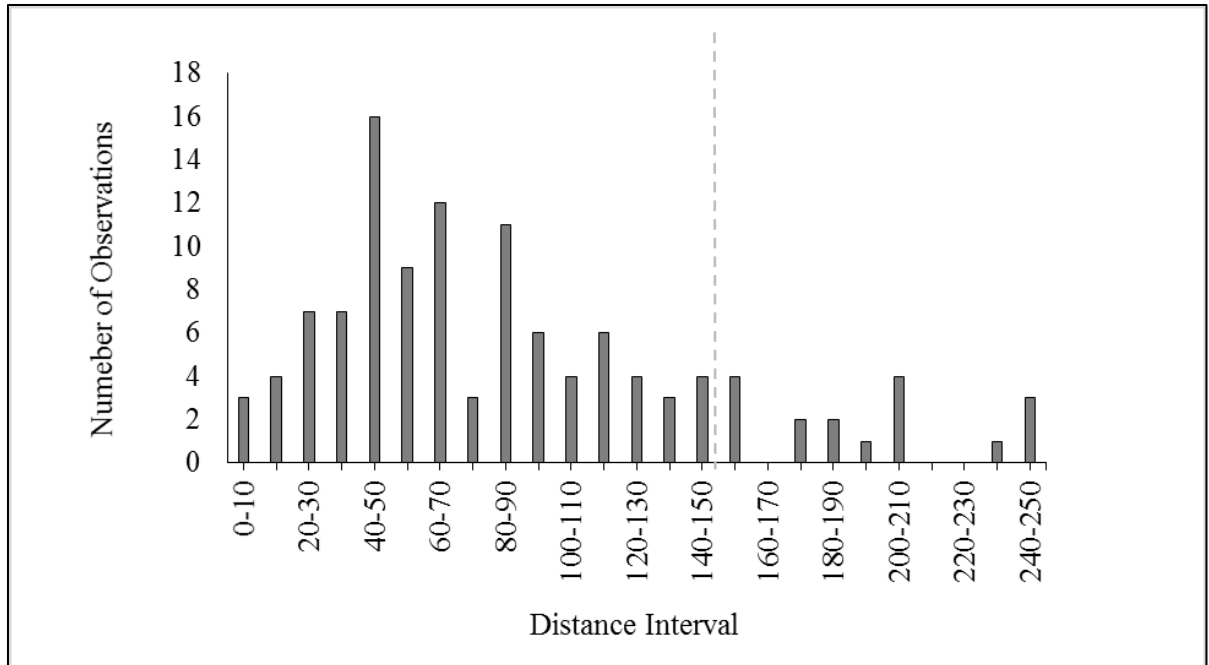
Figure 5. The distribution of distances at which Golden-winged Warbler observations were made at point count locations in natural wetlands and timber harvests of northeastern Pennsylvania, May-June 2014. The distance intervals represent the distance bin within which each observation was made. The dashed line represents the point of truncation for the DISTANCE analysis.

songs as an initial cue. The rest of the males that I observed were either initially detected visually (18%) or while producing non-song vocalizations (i.e., "chip" calls; 3%). The average distance-to-observer for Golden-winged Warbler males during surveys was 87 m although observations ranged from 6 m to as far as 250 m from my survey location (Fig. 5). Male Golden-winged Warblers were also generally detected early in the survey as the average time to first detection was ~3 minutes into the survey and 70% were detected within the first two minutes of the point count. Female Golden-winged Warblers (or females of most species, for that matter) were rare on my point count surveys. Non-Golden-winged *Vermivora* comprised a total of seven observations during all surveys (approx. 5%). I observed three individual hybrid males during wetland surveys (two "Brewster's" and one "Lawrence's" Warbler) and two Brewster's hybrids during surveys in timber harvests and one male Blue-winged in a timber harvest (Fig. 6). Although limited sample size precludes me from conducting a DISTANCE analysis using the non-Golden-winged Warbler *Vermivora* observations, raw point data suggests that Blue-winged Warblers and hybrids were rarer than the Golden-winged Warbler, regardless of habitat type.

Using the 100 Golden-winged Warbler observations (truncated from 117 points by eliminating 17 points that were >150m from the observer), I estimated site-level density across all timber harvest and wetland sites. The estimate for density across all sites (timber harvests + wetlands) was 3.30 (±0.90) males/10 hectares. Density estimates across all surveyed locations were 4.80 (±1.4) males/10 ha for managed upland timber harvests and 2.8 (±1.2) males/10 ha for wetlands (Fig. 7a.). When only considering sites

Figure 6. Digitized field sketches of the *Vermivora* spp. observed during 2014 point count surveys in northeastern Pennsylvania, USA. Golden-winged Warbler (*V. chrysoptera*, upper left, n=117 observations) was found in wetlands and timber harvests. Blue-winged Warbler (*V. cyanoptera*, upper right, n=1 observation) was only observed in a single timber harvest. "Lawrence's" phenotype hybrids (*V. chrysoptera* x *V. cyanoptera*, lower left, n=1 observation) was observed exclusively in a single wetland. The "Brewster's" phenotype hybrids (*V. chrysoptera* x *V. cyanoptera*, lower right, n=7 observations) was observed within both wetlands and timber harvests.
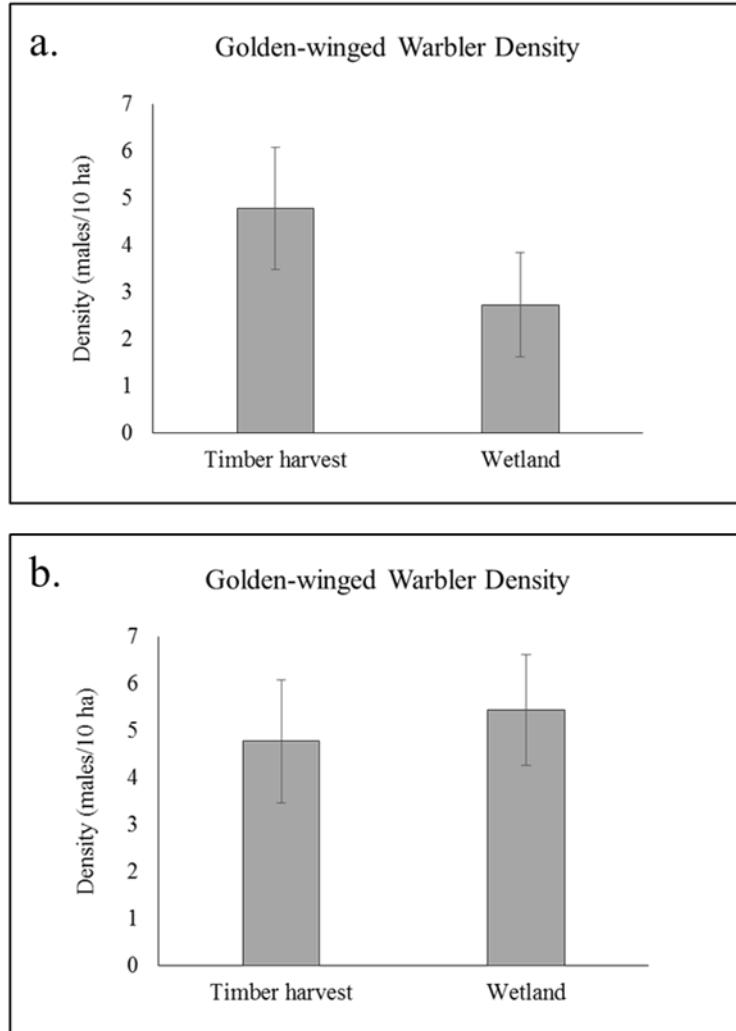
Figure 7. (a) Golden-winged Warbler densities for all point count locations and (b) only sites where Golden-winged Warblers were detected. Surveys were conducted in wetland and timber harvests during May-June 2014 in northeastern Pennsylvania, USA. Densities were generated in program DISTANCE where observations were truncated to exclude birds detected >150 m from the observer.

where Golden-winged Warblers were observed, the density estimate for wetland sites

increases to 5.5 (±1.3 SE) males/10 ha (Fig. 7b.).

Associated Bird Species of Timber Harvests and Wetlands

Although Golden-winged Warblers are the focus of this study, avian surveys

allowed me the opportunity to record all bird species using timber harvests and natural

wetlands of the Poconos region. During the Golden-winged Warbler survey period, I

made 2,885 individual bird observations of 89 separate species (listed in Apendix B). On

the whole, timber harvest and shrub wetlands hosted similar species. Chestnut-sided

Warbler, Common Yellowthroat, Gray Catbird, and Red-eyed Vireo were some of the

most common species, regardless of community type. While the bird communities were

similar in most respects, small differences were apparent. Eastern Towhees and American

Redstarts were detected on 2.61 and 4 times more occasions in timber harvests than

wetlands, respectively. Red-winged Blackbirds were detected on 27.5 times more

occasions in wetlands than in timber harvests. There were also several species that were

each detected almost exclusively in one community or another (Fig. 8, Appendix B).

Factors Affecting Golden-winged Warbler Detection Probability

I modeled detection probability as a function of two survey-specific habitat

covariates: *Julian date* and *time*. Of the four-model candidate set, there were no models

competing with the top-ranked model (Table 1). The second-best model "$\psi(.)$, $p(time)$"

was >13 ΔAIC_c from the top model which had an AIC_c ω of 1.0. Because of the strong

support for this model, all occupancy models exploring how occupancy varied as a

function of habitat covariates also included *Julian date* and *time* (minutes since sunrise)

as detection covariates. Model-averaged estimates of detection suggested that Golden-

Some breeding birds of early-successional communities of northeastern Pennsylvania
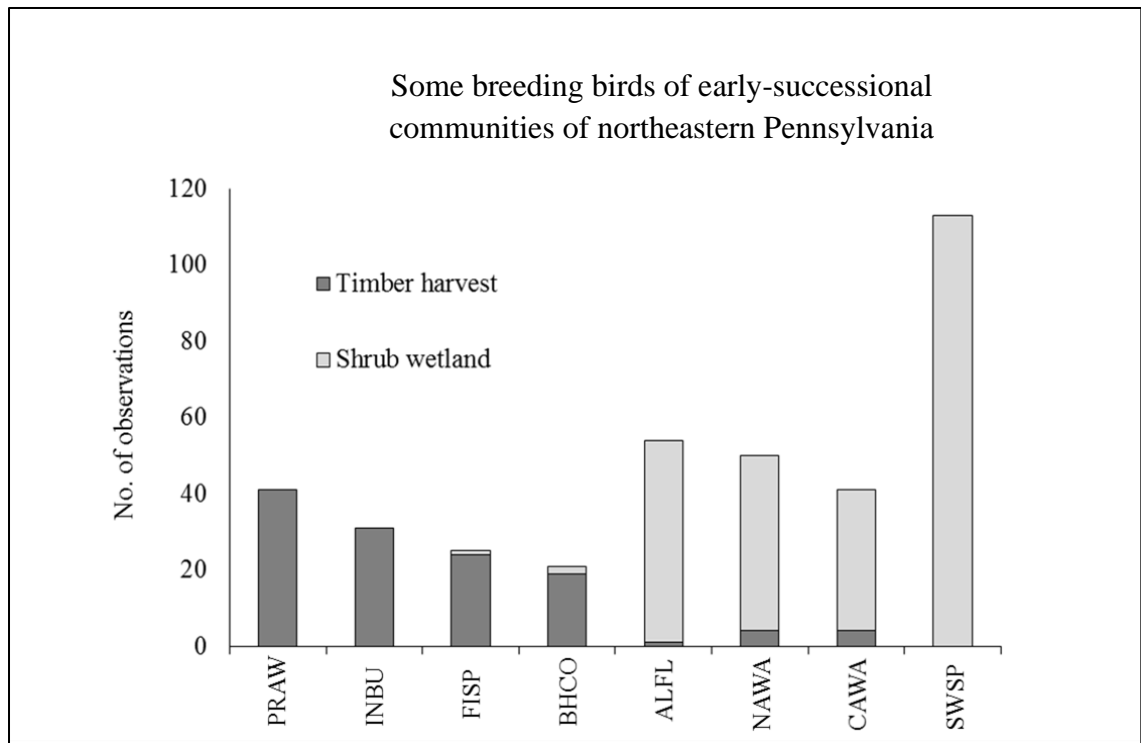
Figure 8. Bird species occurrence data from point count surveys conducted in northeastern Pennsylvania May-June 2014. Shown are a subset of eight species (89 species detected in total) showing apparent habitat distinctions. Birds are shown using their American Ornithologist's Union (AOU) banding code: Prairie Warbler: PRAW, Indigo Bunting: INBU, Field Sparrow: FISP, Brown-headed Cowbird: BHCO, Alder Flycatcher: ALFL, Nashville Warbler: NAWA, Canada Warbler: CAWA, and Swamp Sparrow: SWSP. Scientific names can be found in Appendix C.

Table 1.

Ranking of candidate detection models for Golden-winged Warblers. Surveys were conducted May-June, 2014 in northeastern Pennsylvania, USA. AIC_c = Akaike's Information Criterion adjusted for small sample size. ω = the weight of evidence in favor of the model i being the best model in the candidate set. K = the number of parameters. LL is the -2*Log Likelihood.

Model	K	AIC_c	ΔAIC_c	ω	Cum. ω	LL
$\psi(.)$, p(julian + time)	4	256.42	0.00	1	1	-123.47
$\psi(.)$, p(time)	3	270.03	13.61	0	1	-131.585
$\psi(.)$, p(julian)	3	276.87	20.45	0	1	-135.005
$\psi(.)$, $p(.)$	2	293.04	36.62	0	1	-144.315

winged Warbler detection probability on 2-minute sub-surveys was 0.67 (SE:0.04).

Golden-winged Warbler Occupancy as a Function of Wetland Microhabitat

I measured the microhabitat at 32 wetland point count locations during the 2014

field season (Table 2). The wetlands that I surveyed were structurally diverse and hosted

a variety of plant species (Appendix C). Although more than a dozen tree species were

detected across all wetlands, red maple was by far the most abundant in both its sapling

and tree forms. Red maple saplings (n=572) were >31 times more abundant than the next-

most abundant sapling (willow sp., n=18). Moreover, red maple trees (n=65) were

approximately three times more abundant than the next-most abundant tree species, red

spruce (n=22). The dominant shrub species in the wetlands surveyed were highbush

blueberry (n=1,629 counted), meadowsweet (n=643 counted), and swamp azalea (n=452

counted). The dominant understory herbaceous plants were species such as interrupted,

marsh, and sensitive ferns. Easily the most ubiquitous plant species among all of the

wetlands that I surveyed was the tussock sedge which was observed on 97% of surveys

and was anecdotally observed within 100% of the sites in at least some capacity.

Occupancy methods produced a single model set (of models each considering up

to 3 predictor variables) consisting of 470 models compared within the AIC$_c$ framework.

Twelve models competed with the top model (n=13 models with ΔAIC$_c$ <2.0; models

shown in Appendix D). Of these competing models, all included the covariate for *small

shrub count*. Additionally, most of the competing models also included a covariate

describing sapling abundance (10/13): *sapling count* was within seven of 13 top models.

Finally, *ocular tube sedge* was a component of four of the 13 top models. The top model

appeared to be a reasonably good predictor of Golden-winged Warbler occupancy on

Table 2.

Covariates considered among occupancy models for Golden-winged Warblers. Covariates were used to evaluate occupancy of Golden-winged Warblers (GWWA) in wetlands located in the Poconos region of PA from May-June, 2014. Microhabitat features were measured as either an absolute count, height (meters), area (m^2/ha), standardized Shannon-Weiner Diversity Index (H'), or mean percentage cover (as measured through an ocular tube). Macro-scale habitat features are reported as either a coefficient of variation (for texture) or as percent coverage of a total area for a given extent (100, 250, or 500 m radius). Range of observed values describes the total range and median for values recorded in this study. Observed differences differentiates values seen in sites where GWWA were detected ("*GWWA- yes*") and where GWWA were not detected ("*GWWA- no*") as well as the difference between the two values ("Diff"= "GWWA- yes" – "GWWA- no").

		Range of observed values			Observed differences (Naïve occupancy)		
Covariate name	Covariate code	Minimum	Median	Maximum	GWWA- yes	GWWA- no	Diff
Microhabitat							
Total "small" shrubs (#/5m)	smshrubcount	0	40	140	38	82	-44
Total "large" shrubs (#/5m)	lgshrubcount	2	47	247	62	49	+13
Total saplings (#/5m)	sapcount	0	10.5	115	26	11	+15
Woody plant diversity (H')	woodydiv	1.2	2.59	10.4	3.74	2.89	+0.85
Average shrub height (m)	shrubheight	0	4.5	10	4.59	4.88	-0.29
Average sapling height (m)	sapheight	1.5	2.63	6	2.87	3.02	-0.15
Distance to forest edge (m)	forestdistance	10	77	176	82.11	75.62	+6.49
Total snags (count)	snagcount	0	0	13	1	1	0
Basal area (m^2/ha)	basalarea	0	0	22.05	3.33	3.53	-0.20
Sedge (% cover)	sedge_cov	0	75%	100%	70%	55.4%	+14.6
Herbaceous (% cover)	herb_cov	0	27.6%	90%	31.8%	23.8%	+8.0
Shrubs (% cover)	shrub_cov	20%	85%	100%	78.6%	70.8%	+7.8
Saplings (% cover)	sap_cov	0	15%	60%	21.4%	10%	+11.4

Table 2.

Continued.

		Range of observed values			Observed differences (Naïve occupancy)		
Covariate name	Covariate code	Minimum	Median	Maximum	GWWA- yes	GWWA- no	Diff
Macro-scale habitat							
100 m radius							
Texture (mean coef. of var.)	texture100	0.26	0.38	0.60	0.40	0.38	0.02
Deciduous forest (% area)	decid100	0	0	43%	4.58%	9.43%	-4.85%
Emergent wetland (% area)	emerg100	0	9%	95%	27.91%	20.15%	7.76%
Woody wetland (% area)	woodywet100	5%	68%	100%	62.36%	68.25%	-5.89%
250 m radius							
Texture (mean coef. of var.)	texture250	0.30	0.35	0.51	0.38	0.37	0.01
Deciduous forest (% area)	decid250	0	33%	70%	33.79%	37.62%	-3.83%
Emergent wetland (% area)	emerg250	0	7%	67%	15.03%	8.50%	6.53%
Woody wetland (% area)	woodywet250	14%	44%	88%	44.78%	48.87%	-4.09%
Mixed forest (% area)	mixed250	0	0	32%	1.49%	4.06%	-2.57%
500 m radius							
Texture (mean coef. of var.)	texture500	0.30	0.35	0.59	0.35	0.37	-0.02
Deciduous forest (% area)	decid500	12%	63%	88%	60.75%	56.43%	4.31%
Emergent wetland (% area)	emerg500	0	3%	38%	7.14%	3.83%	3.31%
Woody wetland (% area)	woodywet500	10%	26%	60%	2.54%	0.76%	1.78%
Mixed forest (% area)	mixed500	0	1%	28%	2.04%	5.26%	-3.22%
Shrub/scrub (% area)	shrub500	9%	26%	60%	25.27%	31.00%	-5.73%

point counts as the ROC (Fig. 9") was characterized by an AUC=0.79 (95%CI: 0.63-0.94). The top model was also found to not be overdispersed with ĉ < 1.

Using my model-averaged estimates, there were four microhabitat variables (*small shrub count, sapling count, percent sapling cover,* and *percent sedge cover*) that had 85% confidence intervals not overlapping with zero (Table 3). The nine remaining variables appeared to be poor predictors of Golden-winged Warbler presence on point counts as their 85% confidence intervals overlapped with zero and their importance values were low (<0.21 of the informative variables; i.e., those with 85% confidence intervals not encompassing zero). *Small shrub count* was the microhabitat covariate that had the strongest effect on the occupancy rate for Golden-winged Warblers (estimate = -1.77; 95%CI: -3.11, -0.43) with a relative importance = 0.83. Other variables were somewhat less important though still significant with *sapling count* (estimate = 1.57; 95%CI: 0.05, 3.08), *percent cover sedge* (estimate = 0.92; 95%CI: -0.13, 1.71) and *percent cover sapling* (estimate = 1.08; 95%CI: 0.15, 2.02) having relative importance values of 0.30, 0.24, and 0.21, respectively. My unconditional model-averaged estimate of Golden-winged Warbler site occupancy (corrected for imperfect detection probability) was 0.61 (SE: 0.04).

Golden-winged Warbler occupancy as a function of wetland macro-scale habitat

Because many landscape-scale habitat covariates were correlated with adjacent spatial extents, I produced three candidate model sets to evaluate the effects of macro-scale habitat on Golden-winged Warbler occupancy (one model set for each radius). The 100m radius candidate model set produced 15 different models including a
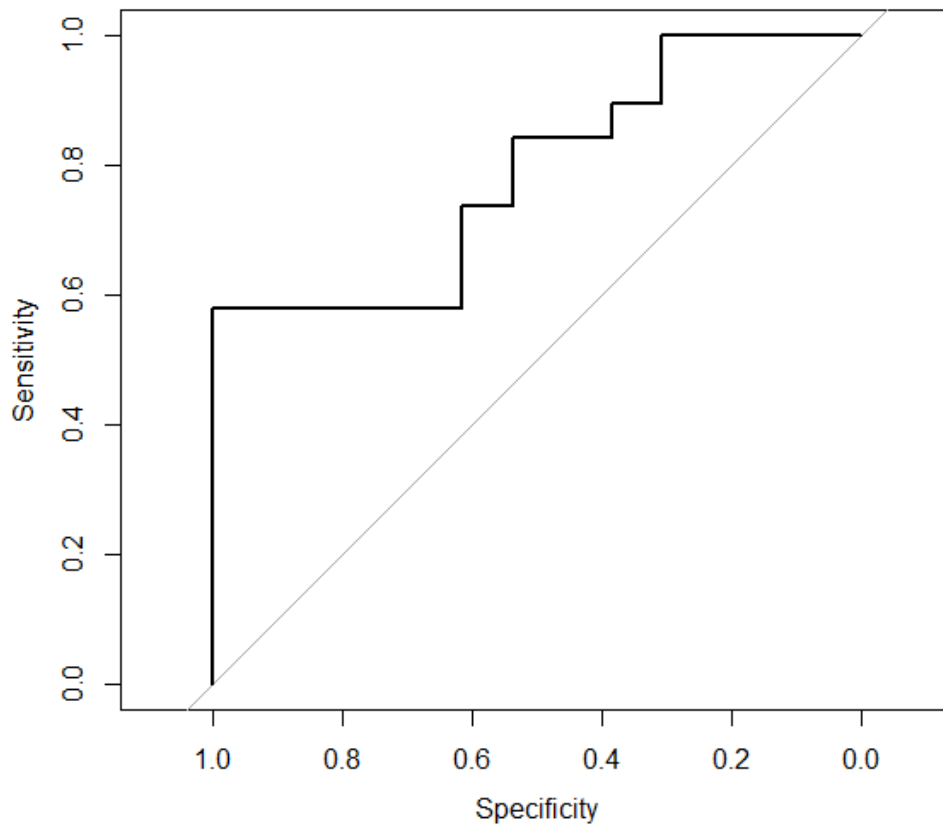
Figure 9. A receiver operator curve for the top microhabitat occupancy model for Golden-winged Warblers in wetlands surveyed in northeastern Pennsylvania during May-June, 2014. The top model, "ψ(smshrubcount + sapcount), p(julian + time)" allows detection to vary as a function of Julian date and time of day while allowing occupancy to vary as a function of the site's abundance of small shrubs, saplings, and trees. This model appeared to be a good predictor of Golden-winged Warbler occupancy on point counts as the AUC (area-under-the-curve)=0.79 (95%CI: 0.63-94). AUC=1.0 would suggest a model that perfectly predicts the occurrence of Golden-winged Warblers whereas an AUC value of 0.5 would suggest a model that performed as effectively as randomly guessing the site's occupancy state (Fielding and Bell 1997).

Table 3.

Model average results for microhabitat variables. Listed microhabitat variables were used to predict Golden-winged Warbler occupancy in wetlands of northeastern Pennsylvania, USA, 2014. Thirteen microhabitat components were incorporated into all-subsets occupancy modeling including up to three covariates each. Each variable occurred within the same number of models in the complete set. Relative importance values were calculated for variable j as a sum of all model weights within which variable j was included. Variable estimates (Estimate), standard errors (SE) and upper and lower bounds of 85% confidence intervals (Lower C.I., Upper C.I.) are also reported. Variables were considered significant if their 85% confidence intervals did not overlap with zero and are shown here in order of descending relative importance values.

Variable	Relative importance	Estimate	SE	Lower C.I.	Upper C.I.
small shrub count	0.83	-1.77	0.93	-3.11	-0.43
sapling count	0.3	1.57	1.05	0.05	3.08
percent cover sedge	0.24	0.92	0.55	0.13	1.71
percent cover sapling	0.21	1.08	0.65	0.15	2.02
woody diversity	0.13	0.99	0.78	-0.14	2.12
shrub height	0.11	-0.77	0.68	-1.75	0.21
percent cover shrub	0.11	0.68	0.54	-0.1	1.46
large shrub count	0.1	0.7	0.68	-0.27	1.68
basal area	0.09	-0.74	0.75	-1.82	0.35
sapling height	0.07	-0.54	0.67	-1.51	0.43
snag count	0.05	0.71	0.93	-0.63	2.04
distance to forest	0.04	0.33	0.52	-0.42	1.08
percent cover herb	0.03	0.18	0.47	-0.5	0.87

null model (see appendix E). There were two competing models in the set, however, the

null detection model "$\psi(.)$, p(*julian date + time*)" was ranked as the top model. This trend

was repeated at the other radii, as well; the top model for both the 250 m model set (26

total models, appendix F) and 500 m model set (42 models, appendix G) were the null

detection models. Although these model sets had greater numbers of competing models.

All models in all three candidate sets were considered to have at least some level of

support as no models within the landscape analyses (at any scale) had $\Delta AIC_c > 10$. Model

averaging supported these findings as all macro-scale habitat variables (at each of the

three spatial extents examined) has 85% confidence intervals that overlapped with zero

(Table 4).

Table 4.

Model average results for standardized macro-scale habitat variables predicting Golden-winged Warbler occupancy in wetlands of northeastern Pennsylvania, USA, 2014. Model averaged estimates were produced as a result of three occupancy model sets (one at each of three spatial scales: 100, 250, and 500 m radii) using structural heterogeneity (texture) and National Land Cover Data as covariates. Relative importance values were calculated for variable j as a sum of all model weights within which variable j was included. Variable estimates, standard errors (SE) and bounds of 85% confidence intervals (Lower C.I., Upper C.I.) are also reported.

Scale	Variable	Relative importance	Estimate	SE	Lower C.I.	Upper C.I.
100 m	Texture	0.22	0.26	0.40	-0.31	0.83
	Deciduous forest	0.31	-0.45	0.41	-1.05	0.14
	Emergent wetland	0.22	0.21	0.60	-0.65	1.07
	Woody wetland	0.20	-0.23	0.59	-1.08	0.61
250 m	Texture	0.19	0.21	0.40	-0.36	0.79
	Deciduous forest	0.27	-0.84	1.06	-2.37	0.68
	Mixed forest	0.44	-0.91	0.82	-2.08	0.27
	Emergent wetland	0.33	0.71	0.63	-0.2	1.61
	Woody wetland	0.27	-0.76	0.97	-2.16	0.65
500 m	Texture	0.22	-0.5	0.59	-1.34	0.34
	Deciduous forest	0.18	0.02	0.73	-1.03	1.08
	Mixed forest	0.44	-0.78	0.57	-1.60	0.04
	Emergent wetland	0.41	0.91	0.74	-0.15	1.97
	Woody wetland	0.23	-0.5	0.52	-1.25	0.25
	Shrub/scrub	0.24	0.55	0.56	-0.26	1.36

CHAPTER V

DISCUSSION

Ecological restoration use reference conditions as a way to achieve desired outcomes and to evaluate progress and success (Dey & Schweitzer, 2014). My study was the first to compare Golden-winged Warbler breeding season demographics between a natural reference system and sites that conformed to recently-published, species-specific best management practices (Bakermans et al, 2011; Bakermans et al, 2015). Previous comparisons of Golden-winged Warbler demographics for various habitat types were largely limited to those among anthropogenic communities such as managed shrublands, utility rights-of-way, timber harvests, reclaimed surface coal mines, and abandoned farmland (Terhune et al, *in press*; Aldinger et al, 2015). Indeed, only one previous study compared Golden-winged Warbler demographics between an anthropogenic community and a natural reference system (Confer et al, 2010). When considering only sites where I detected Golden-winged Warblers, density estimates of territorial males in timber harvests and naturally-occurring wetlands did not differ. This finding is important as it further demonstrates the potential for using forest management as a conservation tool to meaningfully contribute to the recovery of Golden-winged Warbler populations in the Appalachian Region.

Although this finding is encouraging, similarity in male density alone is not synonymous with the capacity of timber harvests and wetlands to contribute equally to the recovery of the Golden-winged Warbler (Van Horne, 1983). Such an understanding will only be possible through studies that compare nest success and fledgling survival between timber harvests and wetlands. Although nest success was not a focus of my

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study, there was a concurrent study that quantified Golden-winged Warbler nest success

across many of the same timber harvests I surveyed (Aldinger et al, 2015). Results from

this study revealed that over four years nesting success ranged between 50-63%

(Aldinger et al, 2015; C. Fiss unpub. data). While nesting success was not studied for the

wetlands I surveyed, the rates reported for the timber harvests are comparable to those

reported for nests in forested wetlands of southeastern New York (65%; Confer et al,

2010). The distance between my study area and that of Confer et al, (2010) was only

<80km. Additionally, an ongoing study examining fledgling survival in many of the

timber harvests for which I generated male densities estimates has found fledgling

survival (from fledging to independence) to be high (66-80%; Aldinger et al, 2015; C.

Fiss unpub. data). These fledgling survival values are equivalent to survival rates for

fledglings in managed forests/shrublands of Minnesota (52%; Streby et al, 2015) and

much higher than survival rates for fledglings on reclaimed mine lands in Tennessee (30-

33%; Aldinger et al, 2015; J. Lehman unpub. data). A future study that directly compares

Golden-winged Warbler nesting success and fledgling survival in timber harvests created

via the implementation of Golden-winged Warbler habitat management guidelines and

nearby natural wetlands would be worthwhile. Nonetheless, my results regrading natural

wetlands and timber harvests having similar male densities combined with results from

ongoing studies that report high rates of Golden-winged Warbler nest success and

fledgling survival in these same timber harvests are encouraging for the potential success

of existing conservation efforts intended to benefit this imperiled songbird.

My finding that timber harvests and wetlands supported similar densities of male

Golden-winged Warblers is important for two primary reasons. First, wetlands alone will

likely not allow for land managers to achieve the ambitious habitat and population goals outlined in the Golden-winged Warbler Conservation Plan (Roth et al, 2012). Timber harvesting activities that implement species-specific best management practices (Bakermans et al, 2011) is one of only a few methods for producing biologically meaningful amounts of additional habitat for breeding Golden-winged Warblers (Fig. 10). Moreover, it is perhaps the only method that can be implemented without landowners or resource agencies incurring heavy financial costs (Zedler, 2000; Bakermans et al, 2011). Secondly, the physical structure of BMP-generated timber harvests can be controlled to maximize the potential number of Golden-winged Warbler pairs a site can support, whereas local hydrology dictates plant community structure in each wetland, particularly as it relates to the distribution of trees. Rossell et al, (2003) found that Golden-winged Warbler territories within high-elevation wetlands of the southern Appalachian Mountains tended to incorporate wetland edges. I also observed that Golden-winged Warbler males were usually confined to wetland edges, whereas this was not true in timber harvests where males were distributed within the interiors of timber harvests and along their edges. It is well known that Golden-winged Warblers require large trees within their territories for foraging and other activities (i.e., song perches, Roth et al, 2012; Bellush et al in press), and recent studies have demonstrated that Golden-winged Warbler densities in timber harvests were higher in stands with more residual trees (Roth et al, 2014; Bakermans et al, 2015). Ultimately, the fact that land managers have greater control over resulting plant community structure in BMP-generated timber harvest compared to wetlands should allow managers to 1) maximize the number of potential breeding pairs at a given sites and 2) more reliably extrapolate

Figure 10. A regenerating timber harvest in the Poconos of northeastern Pennsylvania. Such timber harvests are conducted in a manner which leaves healthy residual trees throughout the stand to facilitate stand regeneration and structural complexity. Communities under such circumstances provide breeding season habitat for Golden-winged Warblers for 12-15 years post-harvest.

the number of breeding pairs that BMP-generated timber harvests may support.

Although BMP-generated timber harvests appear to act as quality habitat for Golden-winged Warblers over the short term, these young forest habitats are highly ephemeral and only provide habitat for nesting Golden-winged warblers for about 12-15 years (Bakermans et al, 2015; Klaus & Buehler, 2001). This is in contrast to wetland communities which persist on the landscape over the long-term, often in a perpetual state of early-succession (Majumdar et al, 1989). Both historic glaciation events and the presence of beaver influence wetland communities of the Poconos (Majumdar et al, 1989; see Fig. 11). Beaver-made/maintained wetlands often promote complex regrowth of early-successional plant species in a manner that supports many declining shrubland bird species (Wright et al, 2002; Chandler et al, 2009; Fig. 12). The long-term persistence of many early-successional wetlands in our study area likely allows them to act as refugia for Golden-winged Warbler populations on the landscape, even when forest disturbances (e.g., wildfire, wind events, timber harvests) are locally rare/absent. Indeed, highly forested portions of Pennsylvania where wetlands are uncommon have experienced the loss and subsequent restoration of upland early successional habitats, but have failed to thus far see the return of the Golden-winged Warbler. This is in contrast to the Poconos region of the state where the species has persisted over the long-term even during periods when young forest communities were less common (Larkin & Bakermans, 2012).

Given the importance wetlands have likely had in maintaining long-term Golden-winged Warbler populations in the Poconos, it is surprising that no previous studies examined the ecology of this species in this vital community. As such, my study serves as an important first step in exploring how Golden-winged Warblers use wetland

Figure 11. A red maple (*Acer rubrum*) tree that was recently felled by a beaver (*Castor canadensis*) near a wetland point count location in northeastern Pennsylvania, USA. I anecdotally observed beaver sign within a significant proportion of the wetland communities used by Golden-winged Warblers in the Poconos.

Figure 12. A typical shrub-wetland in northeastern Pennsylvania used by Golden-winged Warblers during May-June 2014. Many such wetlands are either the byproduct of slow-moving streams or the result of beaver (*Castor canadensis*) activity. Most are characterized by larger trees around the periphery with the core of the wetland often supporting open water (ponds, streams, etc.).

communities in this region. The results presented here reveal a variety of habitat similarities and differences among the wetlands I surveyed. At the macro-scales, land cover compositions surrounding the wetlands I surveyed had no influence on Golden-winged Warbler occupancy rates. This is not surprising as wetlands I surveyed were small in area (mean = 16.5 ha) and were embedded within large, continuous tracts of deciduous forest (Majumdar et al, 1989). Bakermans et al (2015) found that the landscape context of regenerating timber stands within my study area (i.e., landscape-scale forest cover and distance to neighboring stands) was important in explaining the occurrence of Golden-winged Warblers within managed areas. A future study that includes more wetland sites that represent a variety of surrounding landscape contexts may better elucidate macro-scale patterns that influence wetland-nesting Golden-winged Warblers in the region.

Similar to other community types used by nesting Golden-winged Warblers, microhabitat structure appeared to be important in predicting the occurrence of Golden-winged Warblers within the wetlands I surveyed. Numerous studies have shown that there are several structural requisites within anthropogenic early successional communities that influence use by Golden-winged Warblers (Roth et al, 2004; Roth et al, 2014; Bakermans et al, 2011; Aldinger et al, 2014; Bakermans et al, 2015). The relationships between Golden-winged Warblers and many habitat features are understood to be complex with many nonlinear (i.e., quadratic) patterns emerging (Aldinger et al, 2015). For example, the retention of trees can increase the density of Golden-winged Warblers within a habitat patch, however, too many remaining trees results in non-nesting habitat (Bakermans et al, 2011; Roth et al, 2014). Similarly, herbaceous plant

cover (e.g., grasses, forbs) has been positively associated with the occurrence of the species, however, the too much herbaceous cover has also been shown to contribute to lowered levels of nesting success in upland communities (Terhune et al, in press). These examples serve as evidence to the complex structural requisites of Golden-winged Warbler nesting habitat.

At the micro-habitat scale, small shrubs (<1m tall) were the most important vegetation feature for predicting Golden-winged Warbler occupancy in the wetlands I surveyed. Small shrub count relative importance value (RI= 0.83, 95%CI= -3.11 - -0.43; Table 3) was more than twice the value of the next most important variable (sapling count, RI= 0.30, 95%CI: 0.05-3.08). Further, this covariate was included in every top model within the microhabitat occupancy model set (Appendix D). The number of small shrubs had a strong negative relationship with Golden-winged Warbler occupancy. This relationship may be the result of several wetland sites where no Golden-winged warblers were detected were dominated by a continuous layer of small shrubs (usually leatherleaf, *Chamaedaphne calyculata*). The dense monoculture of small shrubs at these sites sometimes resulted in decreased presence of other vegetation features that are known to be important components of Golden-winged Warbler breeding habitat (e.g., saplings and sedges; see Fig. 13). Indeed, small shrubs are known to be an important component of Golden-winged Warbler habitat as nesting substrate, fledgling habitat, and as a general component of breeding season habitat (Confer et al, 2013; Aldinger & Wood, 2014; Aldinger et al, 2015). As such, I hypothesize that there is likely nonlinear relationship between small shrub abundance and Golden-winged Warbler occupancy. It seems possible that my study would have identified the minimal density of small shrubs

Figure 13. A wetland point count location surveyed for Golden-winged Warblers in northeastern Pennsylvania, May-June 2014. Some wetlands (such as this one) were largely dominated by small shrubs (e.g., leatherleaf *Chamaedaphne calyculata*). The over-abundance of such shrubs inhibits the growth of other vegetative strata such as tussock sedges (*Carex stricta*), highbush blueberry shrubs (*Vaccinium corymbosum*, some seen here), and red maple (*Acer rubrum*) saplings. Though some structural complexity exists around the periphery of this site, the core wetland is largely homogeneous.

required by wetland-breeding Golden-winged Warblers had I sampled a continuum from open emergent wetland through dense shrub swamps. Ultimately, because sites with small shrubs still supported Golden-winged Warblers, a desired level may resemble the average abundance for small shrubs among sites where Golden-winged Warblers were detected. I found that wetlands that support an average of 4,838 small shrubs/hectare are more likely to host Golden-winged Warblers than those with more densely-concentrated small shrubs. Wetlands where the species was not detected hosted, on average, more than twice this density of small shrubs.

My analysis also revealed that saplings (stem count and percent cover) had a significant positive relationship with Golden-winged Warbler occupancy (count: RI= 0.30, 95%CI= 0.05 – 3.08 and percent cover sapling: RI=0.21, 95%CI=0.15-2.02; Table 3). This finding, though novel in my study system, has been found previously during upland Golden-winged Warbler studies and it is likely that saplings serve similar functions for the species within both habitat types (Aldinger et al, 2015, Patton et al, 2010, Roth & Lutz, 2004). Saplings are known to be not only important for foraging adults (Frantz et al., in press; Bellush 2013) but also critical for nesting (Aldinger & Wood, 2014) and post-fledging (Streby et al, 2015) Golden-winged Warblers. Sedges were also found to be important in predicting Golden-winged Warbler occupancy in the wetlands of northeastern Pennsylvania (RI=0.24, 95%CI=0.13-1.71; Table 3). Like small shrubs and saplings, grasses/sedges are also a habitat feature previously described as important to the species in upland systems (Confer, 1992; Klaus & Buehler, 2001; Bakermans et al, 2011). Furthermore, Confer et al (2010) found that tussock sedge, the dominant sedge observed in my study, was the primary nest substrate for Golden-winged

Warblers nesting in wetlands in southern New York. My study ultimately suggests that wetlands hosting abundant saplings (3,310 stems/ha) and high sedge cover (70%) will ultimately host more Golden-winged Warblers, especially when small shrubs are not excessively abundant (e.g., >6,000 small shrubs/ha).

Conclusions

If the decline of the Golden-winged Warbler is to be slowed and ultimately reversed, the creation of high quality breeding habitat will be important (Buehler et al 2007; Roth et al, 2012). As such, quantifying Golden-winged Warbler demographic parameters in reference systems such as natural wetlands is helpful for evaluating and maximizing the success of ongoing efforts to implement breeding habitat guidelines for this imperiled species. My study contributes to the growing body of literature that suggest regenerating timber harvests with adequate residual trees have the capacity to support breeding male Golden-winged Warblers. Moreover, the timber harvests I surveyed supported equal densities of male Golden-winged Warblers compared to those observed in local wetland references systems. Collectively, my finding regarding wetlands and timber harvests having similar male densities and those findings that demonstrate the same timber harvests support high reproductive success (nest and fledgling survival) suggests that both communities are important contributors to the persistence and further recovery of the species in this region. While recent studies have identified landscape-scale and within-stand structural characteristics that are important to the occurrence and density of Golden-winged Warblers in timber harvests (Bakermans et al, 2015), a similar assessment for all wetland types (i.e., emergent to forested) that occur in the Poconos region is lacking. Such information will ultimately help researchers and managers better

understand the relative contribution of various wetland types to the persistence of

Golden-winged Warblers in this region.

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Appendix A.

All Poconos sites (Delaware State Forest and Promised Land State Park) surveyed for Golden-winged Warblers from May-June 2014. Values indicated with refer to sites where density was estimated to be 0 despite Golden-winged Warblers detected at the site (due to distance truncation) and [**] indicates birds not included in DISTANCE analysis because they were attracted to the surveyor using a playback recording.

Site name	Habitat type	Area (ha)	Estimated GWWA dens. ($\male$ /ha)	Max GWWA detected	Max *Vermivora* detected
Big Wide Open	Timber harvest	42.4	0.46	2	2
Brewster Road	Timber harvest	31.6	0.23	3	3
Burnt Mills	Timber harvest	9.2	0.11	1	1
Dancing Ridge 1	Timber harvest	18.9	0.23	2	2
Dancing Ridge 2	Timber harvest	37.9	0.76	6	6
Elbow Swamp E.	Timber harvest	14.1	0.46	2	2
Elbow Swamp W.	Timber harvest	8.8	0.46	1	1
Flat Ridge	Timber harvest	10.7	0.80	4	4
Laurel Run	Timber harvest	49.4	0.34	4	4
Minisink	Timber harvest	10.0	1.15	3	3
Painter Swamp	Timber harvest	17.9	0.34	2	2
Rattle	Timber harvest	20.5	0.69	2	2
Thunderbird	Timber harvest	27.7	0.69	2	2
White Birch Swamp	Timber harvest	12.6	0.23	2	4
Whittaker Lane	Timber harvest	24.6	0.23	1	1
William Penn	Timber harvest	67.2	0.46	4	5
Bald Hill Swamp	Natural wetland	7.7	0.46	1	1
B. Mills Wetland	Natural wetland	2.3	0.46	1	1
Cheecho Center	Natural wetland	12.5	0.46	2	2
Cheecho N.	Natural wetland	8.3	0.69	2	2
Cheecho S.	Natural wetland	10.7	0.69	2	3
Elbow Swamp N.	Natural wetland	3.1	0	0	0
Elbow Swamp S.	Natural wetland	5.0	0.46	1	1
Fivemile Meadow 1	Natural wetland	4.3	0	0	0
Fivemile Meadow 2	Natural wetland	13.6	0.46	2	2

Site name	Habitat type	Area (ha)	Estimated GWWA dens. ($\male$ /ha)	Max GWWA detected	Max *Vermivora* detected
Fivemile Meadow 3	Natural Wetland	17.4	0.69	2	2
Fivemile Meadow 4	Natural Wetland	4.9	1.15	3	3
Fivemile Meadow 5	Natural wetland	6.8	0.69	2	2
Gamete Pond	Natural wetland	9.1	0.23	1	1
Hay Rd N.	Natural wetland	7.7	0[*]	1	1
Hay Rd S.	Natural wetland	4.0	0	0	0
Little Bushkill Crk	Natural wetland	61.4	0[*]	2	2
Minisink Wetland	Natural wetland	11.8	0.23	1	1
Painter Drainage	Natural wetland	33.9	0	1[**]	2
Peck's Pond N.	Natural wetland	15.2	0	0	0
Promised Land 1	Natural wetland	11.2	0	0	0
Promised Land 2	Natural wetland	3.0	0	0	0
Promised Land 3	Natural wetland	10.5	0	0	0
Promised Land 4	Natural wetland	12.2	0	0	0
Promised Land 5	Natural wetland	23.0	0	0	0
Rattle Beaver Pond	Natural wetland	2.5	0	0	0
Saw Creek	Natural wetland	6.8	0.46	2	2
Shahola Lake S.	Natural wetland	17.3	0	0	0
Silver Lake N.	Natural wetland	8.3	0	0	0
Silver Lake S.	Natural wetland	9.4	0.23	1	1
Taylor Creek	Natural wetland	12.3	0.46	2	2
Whittaker Wetland	Natural wetland	17.8	0.97	4	4

Appendix B.

A complete list of all species and occurrence records for timber harvests and shrub wetlands surveyed for birds May-June 2014 in northeastern Pennsylvania. Birds were sampled using 10-munite passive point count surveys in which all species of bird detected by vocalization or sight were recorded. * refers to species exclusively observed flying over habitat.

Common name	Scientific name	Total	Timber harvests	Wetlands
Great Blue Heron*	*Ardea herodias*	1	0	1
Canada Goose*	*Branta canadensis*	2	1	1
Mallard	*Anas platyrhynchos*	2	0	2
Hooded Merganser	*Lophodytes cucullatus*	3	0	3
Turkey Vulture*	*Cathartes aura*	1	1	0
Red-shouldered Hawk	*Buteo lineatus*	8	3	5
Ruffed Grouse	*Bonasa umbellus*	7	4	3
Wild Turkey	*Meleagris gallopavo*	4	4	0
Mourning Dove	*Zenaida macroura*	45	28	17
Yellow-billed Cuckoo	*Coccyzus americanus*	5	4	1
Black-billed Cuckoo	*Coccyzus erythropthalmus*	25	15	10
Barred Owl	*Strix varia*	2	2	0
Ruby-throated Hummingbird	*Archilochus colubris*	6	3	3
Red-bellied Woodpecker	*Melanerpes carolinus*	15	11	4
Yellow-bellied Sapsucker	*Sphyrapicus varius*	19	6	13
Downy Woodpecker	*Picoides pubescens*	1	1	0
Hairy Woodpecker	*Picoides villosus*	4	2	2
Northern Flicker	*Colaptes auratus*	16	6	10
Pileated Woodpecker	*Hylatomus pileatus*	7	2	5
Eastern Wood-Pewee	*Contopus virens*	26	18	8
Alder Flycatcher	*Empidonax alnorum*	54	1	53
Least Flycatcher	*Empidonax minimus*	21	14	7
Eastern Phoebe	*Sayornis phoebe*	3	0	3
Great Crested Flycatcher	*Myiarchus crinitus*	33	8	25
Eastern Kingbird	*Tyrannus tyrannus*	2	0	2
Red-eyed Vireo	*Vireo olivaceus*	136	74	62
Yellow-throated Vireo	*Vireo flavifrons*	34	26	8
Blue-headed Vireo	*Vireo solitaries*	3	0	3
Blue Jay	*Cyanocitta cristata*	53	18	35
American Crow	*Corvus brachyrhynchos*	32	11	21
Fish Crow	*Corvus ossifragus*	1	1	0
Common Raven*	*Corvus corax*	2	0	2
N. Rough-winged Swallow	*Stelgidopteryx serripennis*	1	1	0
Tree Swallow	*Tachycineta bicolor*	12	0	12
Barn Swallow	*Hirundo rustica*	4	0	4
Tufted Titmouse	*Baeolophus bicolor*	20	9	11
Black-capped Chickadee	*Poecile atricapillus*	32	9	23
White-breasted Nuthatch	*Sitta carolinensis*	17	7	10
Carolina Wren	*Thryothorus ludovicianus*	1	0	1

Common name	Scientific name	Total	Timber harvests	Wetlands
Blue-gray Gnatcatcher	*Polioptila caerulea*	14	7	7
Eastern Bluebird	*Sialia sialis*	1	0	1
American Robin	*Turdus migratorius*	5	4	1
Wood Thrush	*Hylocichla mustelina*	12	10	2
Veery	*Catharus fuscescens*	166	66	100
Swainson's Thrush	*Catharus ustulatus*	2	2	0
Hermit Thrush	*Catharus guttatus*	21	5	16
Gray Catbird	*Dumetella carolinensis*	164	89	75
Brown Thrasher	*Toxostoma rufum*	1	0	1
Cedar Waxwing	*Bombycilla cedrorum*	80	26	54
Northern Parula	*Setophaga americana*	1	1	0
Tennessee Warbler	*Oreothlypis peregrina*	1	1	0
Blue-winged Warbler	*Vermivrora cyanoptera*	1	1	0
Golden-winged Warbler	*Vermivora chrysoptera*	117	67	50
Brewster's Warbler	*V. chrysoptera* x *V. cyanoptera*	4	2	2
Lawrence's Warbler	*V. chrysoptera* x *V. cyanoptera*	1	0	2
Nashville Warbler	*Oreothlypis ruficapilla*	50	4	46
Yellow Warbler	*Setophaga petechia*	89	31	58
Chestnut-sided Warbler	*Setophaga pensylvanica*	199	116	83
Magnolia Warbler	*Setophaga magnolia*	8	4	4
Black-throated Blue Warbler	*Setophaga caerulescens*	12	7	5
Cerulean Warbler	*Setophaga cerulea*	4	3	1
Blackburnian Warbler	*Setophaga fusca*	9	5	4
Yellow-rumped Warbler	*Setophaga coronata*	1	1	0
Black-throated Green Warbler	*Setophaga virens*	5	3	2
Prairie Warbler	*Setophaga discolor*	41	41	0
Pine Warbler	*Setophaga pinus*	11	4	7
Blackpoll Warbler	*Setophaga striata*	3	2	1
Black-and-white Warbler	*Mniotilta varia*	122	61	61
American Redstart	*Setophaga ruticilla*	85	68	17
Ovenbird	*Seiurus aurocapilla*	130	75	55
Northern Waterthrush	*Parkesia noveboracensis*	20	3	17
Common Yellowthroat	*Geothlypis trichas*	193	80	113
Canada Warbler	*Cardellina canadensis*	41	4	37
Hooded Warbler	*Setophaga citrina*	2	0	2
Scarlet Tanager	*Piranga olivacea*	71	40	31
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	54	33	21
Indigo Bunting	*Passerina cyanea*	31	31	0
Eastern Towhee	*Pipilo erythrophthalmus*	141	102	39

Common name	Scientific name	Total	Timber harvests	Wetlands
Field Sparrow	*Spizella pusilla*	25	24	1
Chipping Sparrow	*Spizella passerine*	10	8	2
White-throated Sparrow	*Zonotrichia albicollis*	3	0	3
Song Sparrow	*Melospiza melodia*	12	0	12
Swamp Sparrow	*Melospiza georgiana*	113	0	113
Brown-headed Cowbird	*Molothrus ater*	21	19	2
Red-winged Blackbird	*Agelaius phoeniceus*	57	2	55
Common Grackle	*Quiscalus quiscula*	10	0	10
Baltimore Oriole	*Icterus galbula*	33	22	11
Purple Finch	*Haemorhous purpureus*	16	5	11
American Goldfinch	*Spinus tristis*	11	6	5

Appendix C.

All species of plant observed as part of my floristic sampling methods. Saplings, shrubs and trees were detected using both count and percent cover data where sedge and forb strata plants were only quantified using the ocular-tube (percent cover).

Strata level	Common name	Scientific name	All survey locations (n=32)	Locations w/ GWWA detections (n=18)
Sapling				
	Serviceberry	*Amelanchier canadensis*	0.13	0.16
	Black birch	*Betula lenta*	0.13	0.11
	Quaking aspen	*Populus tremuloides*	0.03	0.05
	Black cherry	*Prunus serotina*	0.03	0.05
	Willow sp.	*Sailx* sp.	0.03	0.05
Sapling/tree				
	Red maple	*Acer rubrum*	0.91	0.95
	Yellow birch	*Betula alleghaniensis*	0.03	0.00
	Gray birch	*Betula populifolia*	0.06	0.11
	Red spruce	*Picea rubens*	0.16	0.05
Tree				
	Shagbark hickory	*Carya ovata*	0.03	0.05
	Black tupelo	*Nyssa sylvatica*	0.03	0.05
	White oak	*Quercus alba*	0.03	0.05
	Northern red oak	*Quercus rubra*	0.03	0.05
	Eastern hemlock	*Tsuga canadensis*	0.03	0.00
Shrub				
	Speckled alder	*Alnus incana*	0.09	0.05
	Chokeberry	*Aronia* sp.	0.22	0.11
	Buttonbush	*Cephalanthus occidentalis*	0.03	0.05
	Leatherleaf	*Chamaedaphne calyculata*	0.06	0.00
	Red osier dogwood	*Cornus sericea*	0.13	0.05
	Beaked hazel	*Corylus cornuta*	0.03	0.05
	Witch hazel	*Hamamelis virginiana*	0.03	0.05
	Sheep laurel	*Kalmia angustifolia*	0.16	0.16
	Spicebush	*Lindera benzoin*	0.03	0.00
	Maleberry	*Lyonia ligustrina*	0.31	0.53
	Swamp azalea	*Rhododendron viscosum*	0.56	0.74
	Swamp rose	*Rosa palustris*	0.13	0.21
	Am. elderberry	*Sambucus canadensis*	0.06	0.11
	White meadowsweet	*Spirea alba*	0.45	0.74
	Poison sumac	*Toxicodendron vernix*	0.38	0.53
	Highbush blueberry	*Vaccinium corymbosum*	0.94	0.84
	Viburnam sp.	*Viburnam* sp.	0.19	0.21

Strata level	Common name	Scientific name	All survey locations (n=32)	Locations w/ GWWA detections (n=18)
forb				
	Water arum	*Calla palustris*	0.09	0.05
	Hay-scented fern	*Dennstaedtia punctilobula*	0.03	0.05
	Bedstraw sp.	*Galium sp.*	0.03	0
	Common jewelweed	*Impatiens capensis*	0.03	0.05
	Sensitive fern	*Onoclea sensibilis*	0.06	0.11
	Royal fern	*Osmunda regalis*	0.16	0.16
	Cinnamon fern	*Osmundastrum cinnamomeum*	0.34	0.26
	Goldenrod sp.	*Solidago sp.*	0.09	0.16
	Marsh fern	*Thelypteris palustris*	0.47	0.58
	Violet sp.	*Viola sp.*	0.06	0.11
Sedge				
	Tussock sedge	*Carex stricta*	0.97	1.00
	Rush sp.	*Juncus sp.*	0.03	0.00
	Reed canarygrass	*Phalaris arundinacea*	0.03	0.00

Appendix D.

Ranking of occupancy models (in order of increasing AIC$_c$) for Golden-winged Warbler occupancy using microhabitat features around surveyed locations. Golden-winged Warbler surveys were conducted from May-June 2014 in northeastern Pennsylvania, USA. AIC$_c$ = Akaike's Information Criterion adjusted for small sample size. ω = the weight of evidence in favor of the model i being the best model in the candidate set. K = the number of parameters. LL is the -2*Log Likelihood. Covariate codes for all occupancy covariates can be referenced in Table 2.

Model	K	AIC$_c$	ΔAIC$_c$	ω	Cum. ω	LL
ψ(smshrubcount + sapcount), p(julian + time)	6	267.84	0	0.06	0.06	-126.24
ψ(smshrubcount + sapcount + sedge_cov), p(julian + time)	7	268.18	0.34	0.05	0.1	-124.76
ψ(smshrubcount + sedge_cov + sap_cov), p(julian + time)	7	268.44	0.59	0.04	0.14	-124.88
ψ(smshrubcount + sapcount + shrub_cov), p(julian + time)	7	268.76	0.91	0.04	0.18	-125.04
ψ(smshrubcount + sap_cov), p(julian + time)	6	269.03	1.19	0.03	0.21	-126.84
ψ(smshrubcount + lgshrubcount + sedge_cov), p(julian + time)	7	269.04	1.2	0.03	0.24	-125.19
ψ(smshrubcount + lgshrubcount + sapcount), p(julian + time)	7	269.28	1.44	0.03	0.27	-125.31
ψ(smshrubcount + woodydiv + shrubheight), p(julian + time)	7	269.29	1.45	0.03	0.29	-125.31
ψ(smshrubcount + sedge_cov), p(julian + time)	6	269.39	1.54	0.03	0.32	-127.01
ψ(smshrubcount + sapcount + basalarea), p(julian + time)	7	269.45	1.6	0.02	0.34	-125.39
ψ(smshrubcount + sapcount + woodydiv), p(julian + time)	7	269.6	1.76	0.02	0.37	-125.47
ψ(smshrubcount + sapcount + shrubheight), p(julian + time)	7	269.76	1.92	0.02	0.39	-125.55
ψ(smshrubcount + shrubheight + sap_cov), p(julian + time)	7	269.79	1.95	0.02	0.41	-125.56
ψ(smshrubcount + woodydiv + sedge_cov), p(julian + time)	7	270.05	2.21	0.02	0.43	-125.69
ψ(smshrubcount + woodydiv + basalarea), p(julian + time)	7	270.16	2.31	0.02	0.44	-125.74
ψ(smshrubcount + sedge_cov + shrub_cov), p(julian + time)	7	270.29	2.45	0.02	0.46	-125.81
ψ(smshrubcount + basalarea + sap_cov), p(julian + time)	7	270.35	2.51	0.02	0.48	-125.84
ψ(smshrubcount + sapcount + sapheight), p(julian + time)	7	270.44	2.59	0.02	0.49	-125.88
ψ(smshrubcount + woodydiv), p(julian + time)	6	270.51	2.67	0.01	0.51	-127.58
ψ(smshrubcount + sapcount + snagcount), p(julian + time)	7	270.53	2.69	0.01	0.52	-125.93

Appendix E.

Ranking of candidate models for Golden-winged Warbler occupancy using land cover and texture covariates at the 100m radius area around surveyed locations. Golden-winged Warbler surveys were conducted from May-June 2014 in northeastern Pennsylvania, USA. AIC_c = Akaike's Information Criterion adjusted for small sample size. ω = the weight of evidence in favor of the model i being the best model in the candidate set. K = the number of parameters. LL is the -2*Log Likelihood.

Model	K	AIC_c	ΔAIC_c	ω	Cum. ω	LL
$\psi(.)$, p(julian + time)	4	256.42	0	0.32	0.32	-123.47
ψ(decid), p(julian + time)	5	257.97	1.55	0.15	0.47	-122.83
ψ(emerg), p(julian + time)	5	258.71	2.30	0.10	0.58	-123.2
ψ(texture), p(julian + time)	5	258.89	2.47	0.09	0.67	-123.29
ψ(woody), p(julian + time)	5	258.95	2.53	0.09	0.76	-123.32
ψ(texture + deciduous), p(julian + time)	6	260.21	3.80	0.05	0.81	-122.43
ψ(decid + woody), p(julian + time)	6	260.38	3.96	0.04	0.85	-122.51
ψ(decid + emerg), p(julian + time)	6	260.80	4.38	0.04	0.89	-122.72
ψ(texture + emerg), p(julian + time)	6	261.38	4.97	0.03	0.92	-123.01
ψ(texture + woody), p(julian + time)	6	261.75	5.33	0.02	0.94	-123.20
ψ(emerg + woody), p(julian + time)	6	261.76	5.34	0.02	0.96	-123.20
ψ(texture + decid + woody), p(julian + time)	7	263.07	6.65	0.01	0.97	-122.20
ψ(decid + emerg + woody), p(julian + time)	7	263.22	6.80	0.01	0.98	-122.28
ψ(texture + decid + emerg), p(julian + time)	7	263.32	6.90	0.01	0.99	-122.33
ψ(texture + emerg + woody), p(julian + time)	7	264.56	8.15	0.01	1.00	-122.95

Appendix F.

Ranking of candidate models for Golden-winged Warbler occupancy using land cover and texture covariates at the 250m radius area around surveyed locations. Golden-winged Warbler surveys were conducted from May-June 2014 in northeastern Pennsylvania, USA. AIC_c = Akaike's Information Criterion adjusted for small sample size. ω = the weight of evidence in favor of the model i being the best model in the candidate set. K = the number of parameters. LL is the -2*Log Likelihood.

Model	K	AIC_c	ΔAIC_c	ω	Cum. ω	LL
$\psi(.)$, p(julian + time)	4	256.42	0	0.18	0.18	-123.47
ψ(mixed), p(julian + time)	5	257.69	1.27	0.10	0.28	-122.69
ψ(emerg + mixed), p(julian + time)	6	257.73	1.31	0.09	0.37	-121.18
ψ(emerg), p(julian + time)	5	257.80	1.38	0.09	0.47	-122.75
ψ(decid + woody + mixed) p(juliandate+sunrise)	7	257.81	1.39	0.09	0.56	-119.57
ψ(texture), p(julian + time)	5	258.85	2.43	0.05	0.61	-123.27
ψ(woody), p(julian + time)	5	258.95	2.53	0.05	0.66	-123.32
ψ(decid), p(julian + time)	5	258.98	2.57	0.05	0.71	-123.34
ψ(decid + mixed), p(julian + time)	6	259.80	3.38	0.03	0.75	-122.22
ψ(texture + emerg), p(julian + time)	6	260.25	3.83	0.03	0.77	-122.45
ψ(woody + mixed), p(julian + time)	6	260.26	3.84	0.03	0.80	-122.45
ψ(texture + mixed), p(julian + time)	6	260.68	4.26	0.02	0.82	-122.66
ψ(decid + emerg + mixed), p(julian + time)	7	260.71	4.29	0.02	0.84	-121.02
ψ(decid + woody), p(julian + time)	6	260.75	4.33	0.02	0.86	-122.69
ψ(emerg + woody), p(julian + time)	6	260.84	4.43	0.02	0.88	-122.74
ψ(decid + emerg), p(julian + time)	6	260.85	4.43	0.02	0.90	-122.74
ψ(texture + emerg + mixed), p(julian + time)	7	260.93	4.51	0.02	0.92	-121.13
ψ(emerg + woody + mixed), p(julian + time)	7	261.03	4.61	0.02	0.94	-121.18
ψ(texture + decid), p(julian + time)	6	261.58	5.17	0.01	0.95	-123.11
ψ(texture + woody), p(julian + time)	6	261.62	5.20	0.01	0.97	-123.13

Appendix G.

Ranking of candidate models for Golden-winged Warbler occupancy using land cover and texture covariates at the 500m radius area around surveyed locations. Golden-winged Warbler surveys were conducted from May-June 2014 in northeastern Pennsylvania, USA. AIC_c = Akaike's Information Criterion adjusted for small sample size. ω = the weight of evidence in favor of the model i being the best model in the candidate set. K = the number of parameters. LL is the -2*Log Likelihood.

Model	K	AIC_c	ΔAIC_c	ω	Cum. ω	LL
$\psi(.)$, p(julian + time)	4	256.42	0	0.09	0.09	-123.47
ψ(mixed), p(julian + time)	5	256.71	0.29	0.08	0.17	-122.20
ψ(emerg + mixed), p(julian + time)	6	256.75	0.33	0.08	0.25	-120.69
ψ(woody), p(julian + time)	5	257.44	1.03	0.06	0.31	-122.57
ψ(emerg), p(julian + time)	5	257.61	1.19	0.05	0.36	-122.65
ψ(shrub), p(julian + time)	5	257.96	1.54	0.04	0.40	-122.82
ψ(texture + emerg + mixed), p(julian + time)	7	258.07	1.65	0.04	0.45	-119.70
ψ(texture), p(julian + time)	5	258.22	1.81	0.04	0.48	-122.96
ψ(emerg + shrub), p(julian + time)	6	258.27	1.85	0.04	0.52	-121.46
ψ(emerg + shrub + mixed), p(julian + time)	7	258.35	1.94	0.04	0.56	-119.84
ψ(decid), p(julian + time)	5	258.66	2.25	0.03	0.59	-123.18
ψ(woody + mixed), p(julian + time)	6	258.70	2.28	0.03	0.62	-121.67
ψ(texture + mixed), p(julian + time)	6	258.72	2.30	0.03	0.65	-121.68
ψ(shrub + mixed), p(julian + time)	6	259.07	2.65	0.02	0.67	-121.85
ψ(decid + mixed), p(julian + time)	6	259.07	2.65	0.02	0.70	-121.85
ψ(texture + emerg), p(julian + time)	6	259.16	2.74	0.02	0.72	-121.90
ψ(emerg + woody), p(julian + time)	6	259.24	2.82	0.02	0.74	-121.94
ψ(decid + woody + mixed), p(julian + time)	7	259.51	3.09	0.02	0.76	-120.42
ψ(emerg + woody + mixed), p(julian + time)	7	259.60	3.18	0.02	0.78	-120.46
ψ(woody + shrub), p(julian + time)	6	259.72	3.30	0.02	0.80	-122.18