Multiscale Habitat Selection and Movement of Fledgling Golden-Winged Warblers (Vermivora chrysoptera) in Two Managed Mixed-Oak Forest Communities of Northern Pennsylvania

Cameron J. Fiss

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MULTISCALE HABITAT SELECTION AND MOVEMENT OF FLEDGLING GOLDEN-WINGED WARBLERS (VERMIVORA CHRYSOPTERA) IN TWO MANAGED MIXED-OAK FOREST COMMUNITIES OF NORTHERN PENNSYLVANIA

A Thesis
Submitted to the School of Graduate Studies and Research
in Partial Fulfillment of the Requirements for the Degree
Master of Science

Cameron J. Fiss
Indiana University of Pennsylvania
May 2018
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Recent studies have demonstrated that several songbird species change habitat use patterns between nesting and post-fledging. Thus, management which focuses solely on nesting habitat may overlook habitat elements required during the full reproductive cycle. I studied the influence habitat features on movement and resource selection of fledgling Golden-winged Warblers, a species of conservation concern, from 2014 to 2016. Microhabitat including denser understory vegetation and greater vertical cover was selected by fledglings. Fledglings selected primarily for early-successional forest and secondarily for mature and sapling forest. Fledglings moved at faster rates (m/day) when in forests with higher basal area and at slower rates when in forests with reduced basal area. Along with habitat selection results, this suggests fledglings used mature forest for traveling between patches of regenerating forests. These results highlight the importance of managing landscapes to optimize the distribution and diversity of forest structure where Golden-winged Warbler conservation is a goal.
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CHAPTER I
INTRODUCTION

Conservation for Neotropical migratory songbirds on the breeding grounds has historically focused on managing nesting habitat (Vitz and Rodewald 2006, King et al. 2006), however little is known about the movements and habitat requirements for passerines during the post-fledging period -- the time between young fledging the nest and departure for migration (Morton et al. 1991, Anders et al. 1997, Pagen et al. 2000). The lack of knowledge regarding this period in songbirds is largely due to the cryptic nature of fledglings and their parents during this time and the absence of territoriality in many species, making extended observations exceptionally difficult (Sullivan 1989, Anders et al. 1998, Rush and Stutchbury 2008, White and Faaborg 2008). Nevertheless, advancements in radio-transmitter technology has given researchers the ability to attach lightweight radio-transmitters to small (<10g) songbirds without affecting their behavior (Hadley and Betts 2009). Therefore, researchers are now capable of filling in critical missing pieces of information regarding full breeding season ecology from territory establishment and nesting through the post-fledging period. Using these new advances, some researchers have reported high levels of juvenile mortality early in the post-fledging period (Anders et al. 1997, Rush and Stutchbury 2008), and shifts in habitat between cover types used for nesting and those used by fledglings and their parents after nesting (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006). Perhaps most importantly though, is the selection (i.e. nonrandom use) for cover types and habitat features within cover types that maximize fledgling survival (Rush and Stutchbury 2008, Cox et al. 2014, Streby et al. 2016). Thus, forest management guidelines based solely on nesting habitat
requirements of a species, may be overlooking important habitat requirements during the post-fledging period that afford juveniles the highest chance of surviving this critical interval.

The Golden-winged Warbler (*Vermivora chrysoptera*), a Neotropical migratory songbird, is just one of many passerines in which the post-fledging period remains understudied (Will 1986, Streby et al. 2015, Peterson et al. 2016, Streby et al. 2016), especially in the Appalachians where no studies have been conducted. This is particularly concerning for Golden-winged Warblers because these birds have suffered drastic population declines over recent years, and in 2011 were petitioned for listing under the Endangered Species Act (Rosenberg et al. 2016). North American Breeding Bird Survey data indicate over the past 45 years, Golden-winged Warblers have declined at a rate of ~2.3% annually range-wide (Sauer et al. 2017). While populations are stable to slightly increasing in the western Great Lakes segment, population declines are sustained among the Appalachian segment, ranging from 6.3% to as high as 9.8% in Maryland and New Jersey, respectively (Sauer et al. 2017). Additionally, the Appalachian segment of the Golden-winged Warbler’s breeding range now accounts for only 5% of the remaining population (Roth et al. 2012).

The availability of breeding habitat has been implicated as a primary driver of the Golden-winged Warbler’s population decline (Buehler et al. 2007, Rohrbaugh et al. 2016). Golden-winged Warblers require shrubby, early-successional forest patches within a larger forested landscape for nesting (Confer 1992). Historically, this early-successional habitat would have been created by natural disturbances on the landscape, such as forest fires, wind damage, beaver (*Castor canadensis*) activity (Short 1963, Hunter et al. 2001,
Klaus and Buehler 2001), or even the abandonment of farmland early in the 20th century (Gill 2004, Rosenberg et al. 2016). Today, natural disturbances are heavily mitigated or ceased entirely by humans, and young forest has been drastically reduced in Eastern United States as a result (Askins 2001, Degraaf and Yamasaki 2003, Shifley et al. 2014).

Research concerning Golden-winged Warblers, particularly in the Appalachians, has historically focused on hybridization (Confer and Larkin 1998, Gill 1980, Gill 2004), brood parasitism (Confer et al. 2003), and nesting habitat requirements (Bulluck and Buehler 2008, Aldinger et al. 2015, Terhune et al. 2016, McNeil et al. 2017). These studies have been used as a foundation for the development of conservation guidelines intended to stabilize and reverse Golden-winged Warbler population declines (Bakermans et al. 2011, 2015, Roth et al. 2012). Specifically, these guidelines have led to the use of timber harvests, shrubland management, surface mine reforestation, and prescribed fire to create early-successional nesting habitat for Golden-winged Warblers (Roth et al. 2012, McNeil et al. 2017). Although these management strategies provide important insight for creating high quality nesting habitat, they lack guidance regarding the species’ habitat needs during the post-fledgling period, as is the case with many species (Vega Rivera et al. 1998, Rush and Stutchbury 2008, Streby et al. 2013, Streby et al. 2016, Raybuck 2016). Additional information regarding habitat selection and movements of fledgling Golden-winged Warblers could greatly improve the effectiveness of existing habitat management guidelines, and thus increase the chances of the species population recovery.

A single study of Golden-winged Warbler post-fledging habitat selection during the dependent post-fledging period has been conducted within the western Great Lakes
segment of the species’ breeding range, which is now considered disjunct with the Appalachian breeding population (Roth et al. 2012, Rosenberg et al. 2016, Streby et al. 2016). In addition to revealing high levels of mortality in the first three days following fledging, this study also reported selection for more mature cover types than what Golden-winged Warblers require for nesting (Streby et al. 2016). Patterns of habitat selection, movement, and survival reported in the western Great Lakes segment may not carry over to the Appalachian segment because these landscapes are represented by entirely different forest community types, landscape contexts, and undergo different management practices for creating early successional forests (USDA Forest Service - Forest Inventory and Analysis Program & Remote Sensing Applications Center 2008, Shifley et al. 2014). For example, Appalachian topography is frequently characterized by rocky, rugged terrain and mixed-oak forest is marked with infrequent woody wetlands in some areas. However, the western Great Lakes region has considerably reduced topographic variation, and abundant woody wetlands are interspersed within a forested matrix dominate by aspen, birch, and spruce forests. These regional differences also dictate how forests are managed in each area, with variation in rotation lengths and silvicultural prescriptions (Nyland 2016). Thus, Golden-winged Warbler fledglings in the Appalachian Mountains are presented with distinctly different cover types and forest structures on the landscape compared with those from the western Great Lakes (Streby et al. 2016). Additionally, because reports of nesting success are quite similar across both breeding populations (i.e., Roth et al. 2014, Aldinger et al. 2015), variation in population trends across the Golden-winged Warblers breeding range could be, in part, explained by
regional differences in juvenile survival during the post-fledging period (Robinson et al. 2004).

A comprehensive investigation of fledgling Golden-winged Warbler habitat use and selection, within the Appalachian segment of the breeding range is necessary to further elucidate factors driving population declines (Rohrbaugh et al. 2016, Streby et al. 2016). Research of this nature would inform existing forest management guidelines in a way that considers juvenile habitat requirements and optimize post-fledging survival. To this end, this study measures both habitat use and habitat selection of dependent and independent Golden-winged Warbler fledglings across two managed forest landscapes in Pennsylvania. Specifically, I investigated fledgling habitat selection on the macro-scale (i.e. selection of cover types and forest stands on the local landscape, hereafter: stand-scale) and on a micro-scale (i.e. selection for vegetation and structural features within cover types, hereafter: microhabitat). Measuring movement and habitat selection on multiple scales will provide information that can guide management strategies that are needed to create structural features and landscapes that maximize post-fledging success for Golden-winged Warblers. When considered with ongoing management to create nesting habitat, this new information will allow managers to create forested landscapes that maximize full breeding season productivity of Golden-winged Warblers in the central Appalachian Mountains.

**Objectives**

1. Quantify habitat selection for fledgling Golden-winged Warblers at the stand-scale and microhabitat scale in the central Appalachian Mountains.
2. Quantify fledgling space-use and movement patterns for Golden-winged Warbler fledglings across two landscapes.

3. Compare stand-scale habitat selection by fledgling Golden-winged Warblers across two distinct managed forest landscapes in the central Appalachian Mountains.
CHAPTER II
LITERATURE REVIEW

Golden-Winged Warbler Appearance and Development

The Golden-winged Warbler (\textit{Vermivora chrysoptera}), originally described nearly 260 years ago (Edwards 1760), is a distinctive, brightly-colored songbird in the Parulidae family (Bent 1953, Confer 1992). The Parulidae family contains the wood warblers – noted for their small size and often brilliantly vibrant colors (Pyle 1997). Golden-winged Warblers, like many wood warblers, can be found throughout portions of eastern and central North America during their breeding season – between the months of May and July (Buehler et al. 2007). Although not extensively studied, mark-recapture data has indicated that Golden-winged Warblers can have a lifespan of 7 years, and possibly longer (Confer 1992). Golden-winged Warblers are relatively small birds weighing approximately 9 g and reaching a length of approximately 13 cm (Confer 1992). Males and females alike are predominantly a pearl-gray color on top with vivid white feathers covering their ventral surface (Bent 1953). The gray tail of a Golden-winged Warbler is marked with white patches on the lower portions of the three outer rectrices, which can be displayed by males while performing aggressive behaviors (Ficken and Ficken 1968a, Confer 1992). One of the most distinguishing features of Golden-winged Warblers is the prevalence of a dark facemask on males, giving the bird a chickadee-like appearance. This mask includes a large black throat patch and broad black eye line that contrast with the adjacent white malar and supercilium (Pyle 1997, Confer 1992). Further distinguishing the Golden-wing Warbler (and providing the namesake) are its bright yellow crown and wing bars (Bent 1953). Females are similar in most aspects to males,
however in general, plumage is duller. The black facial features apparent on males is
instead a soft grey in females. Additionally, the crown of a female Golden-winged
Warbler is muted with an olive tint and wing bars are often muted and smaller than in
males (Confer 1992, Bent 1953). The black bill of Golden-winged Warblers is very finely
pointed, and likely adapted for probing leaves and buds to acquire food (Ficken and
Ficken 1968b). In fact, Golden-winged Warblers are frequently observed probing dead
leaf clusters by inserting and opening their bill to glean food items within the leaves in a
characteristic foraging maneuver (Chandler et al. 2016).

Golden-winged Warblers readily interbreed with Blue-winged Warblers
(*Vermivora cyanoptera*) and produce viable hybrid offspring where the two species come
into contact (Parkes 1951, Ficken and Ficken 1968c, Gill 1980). Hybrids between
Golden-winged Warblers and Blue-winged Warbler, including the Brewster’s Warbler
and Lawrence’s Warbler, can create difficulties in correctly identifying pure Golden-
winged Warblers (Ficken and Ficken 1968a). The Brewster’s Warbler in particular,
shares the same general gray above and white underside plumage characteristics as the
Golden-winged Warbler (Confer 1992). Further increasing the Brewster’s Warbler
likeness to the Golden-winged Warbler are its own yellow crown and wing bars (Faxon
1911, Ficken and Ficken 1968a). The Brewster’s Warbler, however, does not have the
same facial pattern as the Golden-winged Warbler (Ficken and Ficken 1967). Brewster’s
Warblers have a thin black eye line, similar to that of the Blue-winged Warbler, and lack
entirely the throat patch present in Golden-winged Warblers (Brewster 1881, Confer
1992). Alternatively, Lawrence’s Warblers are mostly yellow throughout (Bishop 1905).
These hybrids have bluish gray wings punctuated by white wing bars, and are similar
overall to a Blue-winged Warbler except for the facial markings (Ficken and Ficken 1967). Lawrence’s Warblers, instead, take on the facial characteristics of Golden-winged Warblers (Brewster 1881, Bishop 1905, Ficken and Ficken 1967, Confer 1992). Although these “typical” plumage characteristics described here exist for hybrid *Vermivora*, both Brewster’s and Lawrence’s Warblers can have varying degrees of either parental species plumage characteristics (Parkes 1951).

Nestling Golden-winged Warblers develop their first feathers in the nest after undergoing a prejuvenile molt (Confer 1992). At this stage, both male and female fledglings are gray to brownish olive on their back and are often a soft yellow to whiteish underneath. The wings and tail take on a darker gray tone, and olive-yellow wing bars are present, but typically separated substantially into two bars (Bent 1953, Pyle 1997). Hatch year Golden-winged Warblers undergo their first prebasic molt between June and August on the breeding ground, in which secondary coverts are replaced (Pyle 1997). At this point, generally 18-19 days post-hatching, juvenile plumage is generally duller and male facial markings are often mottled in white, but very similar overall to adult plumage characteristics (Bent 1953, Confer 1992). Fledglings then undergo a definitive prebasic molt on the breeding grounds that leads to their bright distinctive markings, typically 36 days post-hatch, in which primaries and rectrices are replaced (Bent 1953, Confer 1992).

**Golden-Winged Warbler Distribution**

The Golden-winged Warbler is a Neartic-Neotropical migratory songbird (Bulluck and Buehler 2008, Chandler and King 2011). Thus, like many North American songbirds, Golden-winged Warblers spend the winter in the New World tropics and migrate north during the spring and summer to breed. Much of our knowledge regarding
the breeding range of Golden-winged Warblers is obtained from the USGS through North American Breeding Survey (BBS) data. These surveys, designed to monitor avian population trends in North America, have been conducted each year since 1966 and provide a useful source of information concerning avian distributions. Additionally, state programs, such as the Pennsylvania Breeding Bird Atlas provide an even finer scale look at avian population trends and distributions and help to further elucidate the Golden-winged Warblers range (Rosenberg et al. 2016). Systematic Golden-winged Warbler specific surveys also began in 1999 as part of the Golden-winged Warbler Atlas Project (GOWAP) (Swarthout et al. unpublished data), which are thought to accurately represent the most recent contraction of the warbler’s range (Rosenberg et al. 2016). On the breeding grounds, Golden-winged Warblers have a relatively wide distribution compared to most other New World Warblers (Sauer et al. 2017). Between late April and early August (Confer 1992), these warblers can be found in portions of the eastern and north central United States, as well as southern portions of central Canada (Buehler et al. 2007, Confer 1992, Sauer et al. 2017). The eastern portion of the bird’s range (often considered the Appalachian portion) covers much of the Appalachian Mountains, from extreme northern portions of Georgia in the south to parts of New York and Vermont in the north (Buehler et al. 2007, Sauer et al. 2017, Rosenberg et al. 2017). The western part of their range (often considered the Great Lakes portion) covers large sections of Michigan, Wisconsin, Minnesota, and the Canadian provinces of Quebec, Ontario, Saskatchewan, and Manitoba (Buehler et al. 2007, Rosenberg et al. 2016, Sauer et al. 2017). Although Golden-winged Warblers occur across a relatively wide geographic range, densities throughout the range vary dramatically (Sauer et al. 2017). Current estimates suggest the
Appalachian portion of the Golden-winged Warblers range constitutes only 5% of the bird’s population while the Great Lakes portion accounts for the other 95% (Roth et al. 2012).

Over at least the past 40 years, expansion and contraction of the Golden-winged Warbler’s breeding range has occurred, with the overall distribution seemingly trending northward (Buehler et al. 2007, Roth et al. 2012). Indeed, recent studies have considered the bird’s distribution over the past 150 years to be “dynamic” (Rosenberg et al. 2016). Northern portions of the Appalachian range have seen considerable population decreases (Buehler et al. 2007), and extirpation from several areas including coastal Connecticut and southern New Jersey, as well as all of Rhode Island, New Hampshire, and Massachusetts (Gill 1980, Confer and Knapp 1981, Confer et al. 2010, Rosenberg et al. 2016). In the southeast, Golden-winged Warblers have been restricted to the higher elevations of the Cumberland and Blue Ridge Mountains (Klaus and Buehler 2001, Buehler et al. 2007). Further contraction has occurred throughout southern portions of the Golden-winged Warbler’s mid-west range, including parts of Ohio, Michigan, Indiana and Illinois (Buehler et al. 2007), and the birds are now thought to be extirpated from these states (Rosenberg et al. 2017). This recent (1980’s - 1990’s) range contraction left the Appalachian and Great Lakes distributions disjunct and populations of Golden-winged Warblers are thought to remain patchily distributed among these sub-regions (Confer 1992, Rosenberg et al. 2017). However, breeding range expansion has occurred for Golden-winged Warblers in the northern most parts of the bird’s distribution. In Canada, Golden-winged Warblers have only recently been reported breeding in extreme eastern portions of Saskatchewan (Smith 1996), and have expanded into southwest
Manitoba, eastern Ontario, southwest Quebec, and northern New York (Rosenberg et al. 2017).

Our understanding of the Golden-winged Warbler’s distribution on the nonbreeding grounds is considerably weaker than our understanding of the breeding grounds distribution (Chandler and King 2011, Roth et al. 2012, Bennett et al. 2017, Kramer et al. 2017). Historically, our knowledge of the bird’s range on the wintering grounds came solely from scant historical records (Rosenberg et al. 2017). Recent research, however, has begun to focus a considerable amount of effort on understanding the distribution of Golden-winged Warblers on the nonbreeding grounds in an effort to plan conservation actions (Roth et al. 2012, Bennett et al. 2017, Kramer et al. 2017). Surveys organized by the Golden-winged Warbler Working Group (GWWG) in 2008 in Honduras, Nicaragua, Venezuela, Panama, Costa Rica, and Columbia, in addition to both historical and eBird records, have aided in the creation of occupancy and distribution models for the nonbreeding grounds (Rosenberg et al. 2016). These new models, used in conjunction with previous reports, provide the clearest picture of the Golden-winged Warbler’s nonbreeding distribution to date. Warblers occur from the southern tip of Mexico through the higher elevations portions of Central America into large sections of Columbia and eastern Venezuela (Rosenberg et al. 2016). It was previously thought that Golden-winged Warblers were distributed as far west as Ecuador on the nonbreeding grounds, though very few records exist (Degraaf and Rappole 1995).

Not surprisingly, the Golden-winged Warbler’s breeding distribution seems to be heavily influenced by the availability of breeding habitat (Rosenberg et al. 2016). As such, population trends and range expansion and contraction appear to coincide with
historical events that led to increased or decreased habitat (Confer 1992). However, other factors seem to play an important role in the birds breeding range as well. For instance, the presence of Blue-winged Warblers, which hybridize and compete with Golden-winged Warblers for nesting habitat (Gill 1980), and the range expansion of Brown-headed cowbirds (Coker and Confer 1990, Confer et al. 2003) seem to influence Golden-winged Warblers breeding distributions. All of these factors will likely need to be addressed to some degree in order to effectively conserve this species (Roth et al. 2012).

**Population Decline and Threats**

Since the initiation of the North American BBS in 1966, Golden-winged Warblers have been undergoing population declines (Sauer et al. 2017). Across the bird’s entire range, the population is estimated to be declining at a rate of approximately 2.6% per year since the mid 1960’s (Sauer et al. 2017). The Appalachian population of Golden-winged Warblers, however, is declining at a much steeper rate than the Great Lakes population (Roth et al. 2012, Aldinger and Wood 2014, Rosenberg 2017). Breeding Bird Survey data indicate a population decrease of approximately 8.0% per year across Appalachian states (Sauer et al. 2017). In light of these population trends, Golden-winged Warblers are considered to be one of the most steadily declining songbirds in North America (Rosenberg et al. 2016). Many federal, provincial, and state, actions have been taken in response to rapidly decreasing Golden-winged Warbler populations (Buehler et al. 2007). Although Golden-winged Warblers are currently listed as a “species of concern” by the U.S Fish and Wildlife Service, they were petitioned in 2011 for official listing under the Endangered Species Act (ESA). In fact, Golden-winged Warblers have one of the lowest estimated population sizes for any species not protected
under the ESA (Roth et al. 2012), with their population size recently being estimated at just 383,000 adults in 2010 (Rosenberg et al. 2016). Additionally, the bird is listed as “endangered” in the states of Massachusetts, Indiana, and Ohio. In Canada, Golden-winged Warblers are listed as “Threatened” by the Committee on the Status of Endangered Wildlife in Canada. Partners in Flight, an international avian conservation organization, lists Golden-winged Warblers as a “species of high conservation concern” (Rich et al. 2004), and the National Audubon society designates them as a “Priority Bird” species.

Researchers have also begun to pay a considerable amount of attention to Golden-winged Warblers. Much of the early work associated with *Vermivora* spp. focused on initial reports of hybridization between Golden-winged and Blue-winged Warblers (e.g. Bishop 1905, Meeker 1906, Richardson 1928) and later the effects of hybridization (Ficken and Ficken 1968a, Ficken and Ficken 1968c, Gill and Murray 1972, Confer and Knapp 1977, Gill 1980, Gill 1997). More recently, researchers have focused their attention on the breeding habitat requirements of the species (Klaus and Buehler 2001, Confer et al. 2003, Bulluck and Buehler 2008, Aldinger et al. 2015, Terhune et al. 2016). In 2007 a status review was conducted for the species and listed the loss of breeding habitat, negative interactions with Blue-winged Warblers, and range expansion of Brown-headed Cowbirds (*Molothrus aster*) as the primary threats facing Golden-winged Warblers (Buehler et al. 2007). In 2016, researchers agreed that the overarching threat to Golden-winged Warblers is land use change resulting in a loss of habitat both on the breeding and nonbreeding grounds (though the extent to which is lesser known on the nonbreeding grounds) (Rohrbaugh et al. 2016). Conversion of forest cover to
anthropogenic cover types ultimately places Golden-winged Warblers in more frequent contact with Blue-winged Warblers (Crawford et al. 2016), which is viewed as a considerable threat to Appalachian populations (Gill 2004, Buehler et al. 2007, Rosenberg et al. 2016), and reduces both nesting success and post-fledging survival (Rohrbaugh et al. 2016). Research regarding migration (Rohrbaugh et al. 2016), and post-fledging habitat associations in the Appalachians (Streby et al. 2016), are still needed to better understand threats across the full life cycle.

**Nesting Habitat**

Perhaps the most studied aspect of the Golden-winged Warbler’s ecology is its nesting habitat requirements, as evidenced by a plethora of nesting studies in both the Appalachian and Great Lakes ranges (e.g. Klaus and Buehler 2001, Confer et al. 2003, Roth et al. 2014, Aldinger et al. 2015, Terhune et al. 2016, McNeil et al. 2017). Golden-winged Warblers nest in early-successional patches within predominantly forested landscapes (Confer et al. 2003). Patches hosting nesting Golden-winged Warblers are often scrubby, and dominated by shrubs and herbaceous vegetation with few interspersed trees (Confer et al. 2003, Roth et al. 2014, Aldinger et al. 2015, Leuenberger et al. 2017). This heterogenous habitat is commonly found in both upland and lowlands, along powerline right of ways, forest edges, timber harvests, and old fields (Buehler et al. 2007, Confer 1992, Aldinger and Wood 2014). In fact, it has been postulated the Golden-winged Warblers initially expanded into New England in response to the abandonment of agricultural lands (Gill 1980). In the Great Lakes, regenerating aspen stands (i.e. <10yrs post-harvest) are frequently inhabited by these warblers (Roth et al. 2014). In the Appalachians, higher elevation clear cuts (<20yrs post-harvest) and reclaimed surface
coal mines will support breeding populations of this species (Klaus and Buehler 2001, Bulluck and Buehler 2008, Patton et al. 2010, McNeil et al. 2017). Golden-winged Warblers are also known to nest in natural shrub wetlands within both the Appalachian (Confer et al. 1998, Rossell et al. 2003, Confer et al. 2010) and Great Lakes portion (Will 1986, Streby et al. 2016) of the warbler’s range. These wetlands areas are typified by dense shrub (e.g. *Vaccinium* spp., *Alnus* spp., *Salix* spp.) layers, patches of herbaceous vegetation, and low to moderate canopy cover (Confer 1992), but the species also nests in more forested wetlands with as much as 60% canopy cover (Confer et al. 2010). Because Blue-winged Warblers are rarer in wetlands, these areas may act as a reserve for genetically pure Golden-winged Warblers, particularly within the Appalachian segment of the bird’s range (Confer 1992, McNeil et al. in press). Within early-successional communities, Golden-winged Warblers place their nests directly on, or just above the ground (Confer 1992). Typically, the nest site contains substantial ground level vegetation that acts to conceal the nest (Confer 1992). They frequently choose at least one rigid stem, either that of a woody shrub, or stiff herbaceous plant, as an anchor for their nest (Confer 1992). Many studies have indicated the close association of Golden-winged Warbler nesting sites with blackberry (*Rubus* spp.) and goldenrod (*Solidago* spp.), suggesting its importance within habitat patches (Confer 1992, Aldinger and Wood 2014, McNeil et al. 2017). In wetland cover types, Golden-winged Warblers have been known to use sedges (*Carex* spp.) as a nest substrate (Confer 1992).

Historically, the young forest patches used by Golden-winged Warblers would have been created by natural disturbances events, such as windthrow, fire, and beaver (*Castor canadensis*) activity, which serve to reset the seral stage of forest stands (Short
1963, Hunter et al. 2001, Klaus and Buehler 2001). However, forest disturbance events have largely been mitigated by humans, and have historically been viewed as a negative process (Askins 2001, Degraaf and Yamasaki 2003) resulting in decreased habitat abundance for Golden-winged Warblers (Klaus and Buehler 2001). Thus, although Golden-winged Warbler abundance initially increased in the Appalachians due to agricultural abandonment (Gill 1980), as these habitats matured, and natural disturbances were controlled, habitat availability diminished and Golden-winged Warbler populations in the region suffered (Askins 2001, Buehler et al. 2007).

**Impact of Blue-Winged Warbler and Brown-Headed Cowbird**

Interspecific hybridization, where two distinct species interbreed and combine previously isolated genetic material, is a widely occurring phenomenon (Schwenk et al. 2008). From a genetic perspective, this combination of previously distinct gene pools is called introgression. When hybridizing species are declining and have small population sizes, the effects of hybridization can be magnified (Huxel 1999), and evolutionary trajectories can be uncertain (Schwenk et al. 2008). Although, breeding habitat loss is often considered the biggest factor driving Golden-winged Warbler population declines, researchers agree that competition and hybridization with Blue-winged Warblers also plays a significant role (Buehler et al. 2007, Rohrbaugh et al. 2016). Almost since the time researchers began studying Golden-winged and Blue-winged Warblers there have been reports of hybridization between the two species (Jones 1903, Moore 1916). These hybrids, the Brewster’s Warbler and the less common Lawrence’s Warbler, were initially considered the distinct species *Helminthophila leucobronchialis* (Brewster 1881) and *Helminthophila lawrencei* (Herrick 1874) respectively. Since 1911 it has been
understood, however, that these two “species” are in fact hybrids between Golden-winged and Blue-winged Warblers (Faxon 1911).

The occurrence of *Vermivora* hybrids was thought to be driven largely by the Blue-winged Warblers range expansion north and east into that of the Golden-winged Warblers starting approximately 150 years ago (Parkes 1951, Short 1963), until which point Blue-winged Warbler typically only occurred west of the Appalachians (Gill 1980, Confer and Knapp 1981). In some ways, the range expansion of Blue-winged Warblers mimics that seen a few years previously by Golden-winged Warblers, likely due to the abandonment and subsequent succession of farmland in New England (Gill 1980, Confer and Knapp 1981). Additionally, Blue-winged Warblers began moving towards higher elevation, genetically pure, population of Golden-winged Warblers (Gill 2004). Not until more recently have we begun to better understand the interactions between these species, and the long-term implications of increasing sympatry between the two species (Confer et al. 2003, Shapiro et al. 2004, Vallender et al. 2009).

One of the most disturbing findings, that lends merit to the significance of Blue-winged Warblers as a threat, is that Blue-winged Warbler populations replace Golden-winged Warbler populations within 50 years after the arrival of Blue-winged Warblers (Gill 1980, Gill 1997). It is possible that Golden-winged Warblers are simply being evicted from areas as natural successional processes due away with the habitat they require. Indeed, some researchers have shown that Blue-winged Warblers are more of habitat generalist than Golden-winged Warblers and may just remain in successional habitats long after conditions suitable for Golden-winged Warblers disappear (Confer and Knapp 1977, 1981). Though considering the substantial amount of niche overlap, in
terms of habitat (Ficken and Ficken 1968a, Confer et al. 2003) and foraging style (Ficken and Ficken 1968a), it seems likely that there is at least some degree of competitive pressure or genetic-based influence associated with Blue-winged Warblers (Gill 1980). Reports that Golden-winged Warblers have smaller clutch sizes when their territories are adjacent to those of Blue-winged Warblers (Confer et al. 2003) seems to support this idea. In the Great Lakes segment of the Golden-winged Warblers breeding range, Will (1986) showed that Blue-winged Warblers dominate and exclude Golden-winged Warblers from dryer, more preferred breeding habitat. However, in the Appalachian segment, Confer and Larkin (1998) showed that the two species essentially ignored each other, and their breeding territories often overlapped. Thus, the processes behind this replacement, whether the result of natural habitat shifts, competition, or hybridization remains the subject of debate, especially considering Golden-winged Warblers are sometimes extirpated from areas that still support apparent habitat (Confer et al. 2003).

The fact remains however that the two species hybridize freely when sympatric and create fertile offspring (Parkes 1951, Shapiro et al. 2004). The direct result of hybridization is the appearance of F1 generation Brewster’s Warbler hybrids (Parkes 1951), followed by next generation Lawrence’s Warbler hybrids – the result of backcrossing between Brewster’s Warbler and either parental species (Gill 2004). Both recognized hybrids have their own distinct plumage, but hybrids can have widely varying degrees of each of the parental species plumage traits as well (Parkes 1951 Gill 1980). Though relatively benign on the surface, the appearance of these fertile hybrids, and the fact that they mate with either parental species suggests the introgression of Golden-winged Warbler and Blue-winged Warbler DNA (Gill 2004, Vallender et al. 2009). This
means that there are fewer genetically pure Golden-winged Warblers mating with each other each year (Shapiro et al. 2004, Buehler et al. 2007). To complicate matters further, researchers have shown in some circumstances that hybrid Brewster’s Warblers mate more frequently with Golden-winged Warblers than Blue-winged Warblers, thus unevenly diluting their genome (Confer and Larkin 1998, Gill 2004). Within hybridizing populations of Golden-wing and Blue-winged Warblers along the Pennsylvania-New Jersey border, Gill (1997) showed highly asymmetrical introgression of Blue-winged Warbler mitochondrial DNA (mtDNA) into Golden-winged Warblers. In the same study, Blue-winged Warbler genomes remained virtually unchanged. Though this trend doesn’t hold constant across the range, as Shapiro et al. (2004) showed nearly symmetrical introgression of mtDNA in Golden-winged and Blue-winged Warblers in West Virginia and Michigan.

With the expanding range of Blue-winged Warblers and the predictable schedule of Golden-winged Warbler replacement in addition to the dilution of Golden-winged Warbler genome as hybrids breed with pure Golden-winged Warblers, it’s not surprising to see why scientist consider Blue-winged warblers a threat. In fact, a range wide study involving samples from nine states across the warbler’s range suggests that cryptic hybrids are far more common than previously expected, and Manitoba may be one of the few areas in which a substantial population of genetically pure Golden-winged Warbler’s still exists (Vallender et al. 2007, Vallender et al. 2009). This study highlights the importance of hybridization in the context of uncommon and declining species, as there seems to be reasonable fear that a pure Golden-winged Warbler genome could disappear completely, rendering the species extinct. Alternatively, a recent study provided evidence
fueling a debate that Golden-winged Warblers and Blue-winged Warblers may in fact be the same species (Toews et al. 2016). In addition to surmising that hybridization between these two species has been occurring for well over two centuries, they noted striking genetic similarities between the two warblers (i.e. only six genomic regions strongly differentiated) and suggested these were mostly plumage related regions (Toews et al. 2016). However, that genetic differences are confined solely to morphological characteristics has been debated based on ecological variations between the two warblers (Bennett et al. 2017). Although the species status of Blue-winged and Golden-winged Warblers may remain somewhat mysterious, conservation actions are still necessary, even if just to conserve small genetic differences, and studying both warblers may help further elucidate the mechanisms behind the hybridization and decline of these birds (Vallender and Bull 2016).

**Current Golden-Winged Warbler Conservation Action**

In light of decades of consistent Golden-winged Warbler population declines, a considerable amount of effort has been put forth to conserve these warblers. Until the late 1990’s, this effort was essentially confined to the small-scale conservation projects in the Appalachian segment (e.g. powerline right-of-way maintenance) aimed at maintaining current Golden-winged Warbler breeding habitat, but this effort has since grown considerably (Rohrbaugh et al. 2016). The first coordinated efforts to monitor the species began in 1999 with the Golden-winged Warbler Atlas Project (GOWAP) (Swarthout et al. unpublished data). These systematic surveys targeted at monitoring Golden-winged Warbler population trends were necessary as populations fell below what could accurately be measured with North American Breeding Bird Survey routes (Rosenberg et
al. 2017). Substantial conservation planning and management strategies followed with the creation of the Golden-winged Warbler Working Group (GWWG), which formed in 2005 (Buehler et al. 2007). The primary objectives of the GWWG are to raise conservation related awareness about Golden-winged Warblers, prioritize future management related goals, and ultimately ensure the conservation of the species (Buehler et al. 2007). To this end, the GWWG facilitated the creation of the range wide Golden-winged Warbler Conservation plan and associated breeding habitat management guidelines for both segments of the species’ breeding range (Roth et al. 2012). The habitat management guidelines outline several management scenarios discussed in the conservation plan and are aimed directly at land managers looking to create habitat for Golden-winged Warblers. The conservation plan lays out an overall conservation strategy focused on the implementation of habitat management in various focal areas and subsequently monitoring the population response to those actions (Roth et al. 2012). The goals of the conservation plan are essentially to increase the population size of Golden-winged Warblers by creating early-successional nesting habitat and maximizing non-breeding season survival (Roth et al. 2012).

Breeding grounds management scenarios outlined in the Golden-winged Warbler conservation plan and management guidelines are the product of years of nest-based studies spanning many of the states where breeding populations of these warblers are found (Roth et al. 2012). Though the management technique varies from site to site, the end result of these guidelines remains fairly consistent, and achieves the structure described in the previous section on nesting habitat. In the Appalachian segment, management typically involves techniques such as timber harvesting, prescribed grazing,
mechanical shrubland maintenance, prescribed fire, or surface mine reforestation (Kubel and Yahner 2008, Patton et al. 2010, Aldinger and Wood 2014, McNeil et al. 2017). As successional habitats are ephemeral, researchers advocate for rotational management on broad scales, to ensure the constant availability of early-successional habitat on the landscape (Buehler et al. 2007, Roth et al. 2012, Bakermans et al. 2015). A key feature in many of these management scenarios is the retention of scattered canopy trees to provide song perches and forging sites. The conservation plan suggests the retention of approximately 25-37 trees/hectare (Roth et al. 2012, Bakermans et al. 2015). It is important to note that Golden-winged Warblers also use naturally occurring beaver, alder, and hardwood swamps in the Appalachians for nesting (Rossell et al. 2003, Confer et al. 2010, McNeil et al. in press) Management strategies exist to maintain these habitats as well (Roth et al. 2012). Habitat management efforts for Golden-winged Warblers in the Great Lakes population segment use many of the same techniques as in the Appalachian segment, especially shrubland management and timber harvest (Martin et al. 2007, Roth et al. 2014).

Recently the creation of breeding habitat for Golden-winged Warblers on private lands was initiated in 2012 through a joint program between the Natural Resource Conservation Service (NRCS) and the United States Fish and Wildlife Service (USFWS) called Working Lands for Wildlife (WLFW) (Ciuzio et al. 2013, McNeil et al. 2017). Working Lands for Wildlife provides conservation easements to private land owners in exchange for creating habitat on their lands. This program targets seven species throughout the US, one of which is the Golden-winged Warbler in the Appalachians. Because the majority of landholdings in the Eastern United States are privately owned...
(Wear et al. 1996, Scott et al. 2001, Shifley et al. 2014), conservation initiatives such as WLFW that target private lands for Golden-winged Warbler management, following the habitat guidelines, are likely to benefit Golden-winged Warbler population recovery (McNeil et al. 2017).

**Post-Fledging Ecology**

The post-fledging period is defined as the interval between young fledging the nest and departure for migration (Pagen et al. 2000). This time period is primarily characterized by parental care of juveniles, rapid development, and post-natal dispersal (Moreno 1984, Kershner et al. 2004, White and Faaborg 2008). Historically, the ecology of the post-fledging period was largely mysterious to biologists (Morton 1991, Baker 1993, Anders et al. 1997). Thus, little is known regarding the behaviors, survival, and habitat preferences exhibited by many bird species during this time. Unlike with conspicuous territorial adults, in-depth studies of small-sized songbirds during the post-fledging period have been virtually impossible because of the cryptic nature of passerines and their young during this time (Sullivan 1989, Anders et al. 1998, Rush and Stutchbury 2008, White and Faaborg 2008). The post-fledging interval remains the least studied aspect of many birds because of these hurdles (Cox et al. 2014). Fortunately, relatively recent technological advances have allowed for the development of miniature radio-transmitter devices such that even very small animals (e.g., Neotropical migratory birds, 10 g) can be marked and observed or tracked for extended periods (Hadley and Betts 2009). As such, studies of fledgling songbirds are now significantly more feasible (Sykes et al. 1990, Neudorf and Pitcher 1997, King et al. 2006, Berkeley et al. 2007).
First year survival of songbirds has been shown to have significant impacts on population growth rates (Donovan and Thompson 2001) which can have severe conservation implications for declining species (Anders and Marshall 2005). Perhaps more importantly, using estimates of nesting success alone has been shown to provide misleading values of population change, but knowing adult and juvenile survival can greatly improve these estimates (Anders and Marshall 2005, Streby and Anderson 2011). Thus, the ability to study the post-fledging interval has come at an opportune time, as researchers increasingly realize the importance of this life stage. Considering the implications of fledgling survival on population dynamics (Robinson et al. 2004), it’s not surprising that most post-fledging studies to date have, at least in part, focused on this aspect (Anders et al. 1997, Yackel et al. 2006, Rush and Stutchbury 2008, Vitz and Rodewald 2011).

Post-fledging survival studies have led to reports of high variability within species fledgling survival across years (Rush and Stutchbury 2008, Schmidt et al. 2008) and geographic location (Anders et al. 1997, Vernasco et al. 2017). Further suggesting the importance of this time interval are the high levels of mortality early in the post-fledging period (King et al. 2006, Rush and Stutchbury 2008, Streby et al. 2016). In a comprehensive review of fledgling survival literature, Cox et al. (2014) found that survival was lowest during the first three weeks post-fledging, but remained relatively constant after day 20 post-fledging across 35 passerine species. Some studies have reported >70% of fledgling mortalities occurring within the first three days after fledging (King et al. 2006, Rush and Stutchbury 2008). Leading some researchers to suggest that the post-fledging period is the time period in which birds experience the highest rates of

The capacity to better understand factors driving avian population fluctuations, particularly for at-risk species, is just one facet of post-fledging research, and can be better understood through habitat associations during this time (Cox et al. 2014). Interestingly, post-fledging studies in songbirds have shown shifts in habitat use between the nesting period and post-fledging period. For instance, King et al. (2006) found that juvenile Ovenbirds (*Seiurus aurocapilla*) select forest associated with more canopy gaps and greater understory vegetation density compared to nesting Ovenbirds, which use primarily closed canopy, open understory forest. Wood Thrush (*Hylocichla mustelina*) have been found to make similar habitat shifts between nesting and post-fledging. In several cases, Wood Thrush have been found to move from mature forest, typical of nesting Wood Thrush, into younger seral-stage forests with dense understory vegetation (Anders et al. 1998, Vega Rivera et al. 1998, Powell et al. 2000). In fact, many birds known to nest in mature forest have been associated with shrubby, early-successional forest. While passively sampling within young forest during the post-fledgling period, Vitz and Rodewald (2006) frequently captured juvenile Hooded Warbler (*Wilsonia citrina*), Worm-eating Warbler (*Helmitheros vermivorum*), Red-eyed Vireo (*Vireo olivaceous*) and Ovenbird. Both Marshall et al. (2003) and Pagen et al. (2000) report similar findings of mature forest nesters using early-successional forest during the post-breeding period. Habitat shifts between nesting and post-fledging are important, because most fledgling passerines have been shown to use habitat features that maximize survival (Rush and Stutchbury 2008, Cox et al. 2014). Considering habitat management on the
breeding grounds for passerines is frequently based off our knowledge of nesting needs (Vitz and Rodewald 2006, King et al. 2006, Streby et al. 2013), these results suggest management plans could be overlooking important habitat requirements through the post-fledging period, which may limit survival for some species. Thus, additional habitat information regarding the post-fledging period could greatly improve management efforts for many species (Vega Rivera et al. 1998, Berkeley et al. 2007).

The post-fledging period in Golden-winged Warblers has received minimal attention from researchers relative to other life history stages (Streby et al. 2015, Streby et al. 2016, Petersen et al. 2016). In fact, in the Appalachian segment of the Golden-winged Warbler’s breeding range, no studies have been conducted to investigate habitat use, survival, or movements during the post-fledging period. Nevertheless, within the Great Lakes portion of the warbler’s breeding range, researchers have published some interesting results regarding Golden-winged Warbler fledgling ecology. Both Will (1986) and Peterson et al. (2016) report that Golden-winged Warblers exhibit brood splitting behavior, where male and female parents each take part of the brood and go separate ways on the landscape. Although this is a relatively common phenomenon among birds (Leedman and Magrath 2003), Peterson et al. (2016) suggests that this may carry management implications. For instance, females take their sub broods significantly further distances away from the nest site compared to males, this suggests the need to manage for habitat at multiple spatial scales (Peterson et al. 2016). Habitat shifts during the post-fledging period in Golden-winged Warblers have also been reported (Streby et al. 2016). In the western Great Lakes region, fledgling Golden-winged Warblers move
from early-successional nesting stands into mature forest and sapling dominated cover types (Streby et al. 2016).

**Forest Management in the Appalachians**

After European settlement of the Appalachian region, forest structure and landscape configuration changed dramatically (Abrams 2003). The landscape went from a heavily forested system of numerous small-scale disturbances caused by storm damage (e.g. windthrow, lightning), beaver activity, and Native American agriculture activity (Brose et al. 2001, Abrams 2003), to one of unrestricted resource extraction, often in the form of extensive clearcutting and land clearing for agriculture. As a result, early settlers deforested much of the east by the late 1800s (Askins 2001, Abrams 2003). In addition, the inadvertent introduction of Chestnut Blight (*Cryphonectria parasitica*) from Asia in the early 1900s devastated arguably the most dominant tree in the Appalachians – the American Chestnut (*Castanea dentata*), thus heavily altering forest composition (Abrams 2003). One result of wide-scale forest clearcutting was the social stigma that all forest disturbance is undesirable, and the protection of forest from any disturbance essentially became conservation policy (Askins 2001). Though forest is again common on the landscape throughout the eastern United States, its relatively old and even age structure reflects this previous stigma, and young seral-stage forests are seemingly limited (Askins 2001). Fortunately, researchers and land managers have begun to realize the benefits of managing forests through silviculture methods, which often result in the creation of young and structurally diverse forests that mimic the effects of natural disturbances (Hunter 1993). In fact, timber harvesting, now accounts for the most disturbance encountered by modern forests (Shifley et al. 2006).
Forest management practices generally fall under one of two overarching categories: even-aged management, or uneven-aged management (Thompson et al. 1995, Johnson et al. 2009, Fan et al. 2015). Even-aged management, involves harvest strategies that result in the simultaneous regeneration of an entire stand, and thus stands that are managed with even-aged techniques contain trees that are the same age (Johnson et al. 2009). Over time forest landscapes managed via even-aged practices are comprised of stands of varying ages. Conversely, the goal of uneven-aged management is to create conditions characterized by trees of varying ages within a single stand, resulting in stands with trees that represent >2 age classes (Johnson et al. 2009, Nyland 2016).

A prominent silvicultural method for managing even-aged stands is clearcutting, which involves the complete removal of the overstory at once, effectively resetting the seral stage of the stand (Johnson et al. 2009). Because the success of a clearcut is largely dependent on preexisting conditions in the stand (Sander 1979), shelterwood harvests can be used to facilitate regeneration prior to overstory removal (Thompson et al. 1995, Johnson et al. 2009, Fan et al. 2015). Shelterwood harvests remove a portion of the overstory, resulting temporarily in a two-aged structured stand, but allowing sunlight to reach the forest floor initiating regeneration of desired species (Johnson et al. 2009). Partial canopy removal favors regeneration of species that tolerate shade, and would otherwise be outcompeted in full sunlight, thus shelterwood harvesting is frequently used as a mechanism to regenerate oak (*Quercus* spp.) (Sander 1979, Schlesinger et al. 1993). Under even-aged management methods, stands are allowed to regenerate to a desired rotation point, and are then harvested again, resulting in the constant turnover of forest age classes and a mosaic of age structure (Johnson et al. 2009). Uneven-aged
management of forests, involves techniques such as single tree and group selection to create small canopy gaps, resulting in forest structure with >2 age classes (Johnson et al. 2009, Nyland 2016), although this has limited benefits to early-successional species (Degraaf and Yamasaki 2003).

Silviculture, although typically considered a tool for timber production, also results in wildlife habitat (Thompson et al. 1995, Shifley et al. 2014). Thus, not only can proper forest management provide a constant supply of forest resources (Johnson et al. 2009), but also positively impact species diversity across a landscape (Thompson et al. 1995 Shifley et al. 2006). The impact of forest management on species diversity has been studied extensively among avian taxa, and many of the management techniques foresters have been using for decades can be used to managed for some of the most rapidly declining Neotropical migratory bird species, such as Golden-winged Warbler, Cerulean Warbler (Setophaga cerulean), and Prairie Warbler (Setophaga discolor) (Dickson et al. 1995, Boves et al. 2013 Bakermans et al. 2015).
CHAPTER III

STUDY AREA

This study was conducted in two distinct managed forests in Pennsylvania across three years (2014-2016). In 2014 and 2015 research was carried out primarily in Delaware State Forest (DSF) in northeastern Pennsylvania where Golden-winged Warblers reach some of their highest population densities within the state (Larkin and Bakermans 2012, Sauer et al. 2017). Some adjacent private lands were also accessed during this study. In 2016 research was conducted exclusively in Sproul State Forest (SSF) and the adjacent State Game Lands 100 (SGL 100), within the northcentral portion of Pennsylvania. Though the entire study area was not contained completely within DSF and SSF, these areas are referred to as the two primary study areas for this research (Figure 1). Much of Pennsylvania, including DSF and SSF, is characterized by the oak-hickory forest community, while northern hardwood forests become more prevalent in the most northern portions of the state (Fike 1999). As the name implies, the oak-hickory forest community is typically dominated by oaks (*Quercus* spp.) with other hardwood species interspersed, and often has an understory dominated by members of the Ericacea family (Brose 2016). In Pennsylvania, this community type is composed of virtually all second growth forest on a relatively long (~80-100 year) rotation period (Nowacki and Abrams 1992, Nyland 2016). However, common across both study areas is the prevalence of forest management in an effort to attain a more even distribution of forest age classes (PA SFRMP 2016).
Delaware State Forest

The DSF covers approximately 33,798 ha across Pike and Monroe counties in northeastern Pennsylvania (PA DCNR 2016). This area, lying amongst Pennsylvania’s Allegheny Plateau province (Sevon 2000), is broadly characterized by the presence of the Pocono Mountains. Like central PA, the region has many deep valleys and rolling hills. The Pocono region is unique, however, in that it has numerous forested and shrub wetlands (Figure 2). In fact, this area has higher densities of wetlands than any other region in Pennsylvania (Davis 1993). My study area encompassed approximately a 20 km radius bisected by state highway 402, predominantly in southwest portions of DSF. Elevation in the area ranged from 300 to 600 meters above sea level. I studied fledglings across six study sites within DSF all six of which were the result of overstory removal harvests and one underwent a prescribed fire after overstory removal. Study sites in DSF ranged in size from 7 ha to 63 ha. Mature (80+ years post-harvest) stands composed the forested matrix on the landscape, however, developed areas are interspersed throughout. Overstory composition in many upland stands across DSF is dominated by oak species such as chestnut oak (Q. montana) and white oak (Q. alba), red oak (Q. rubra), but red maple (Acer ruburm) is common as well. Hickory (Carya spp.) and pitch pine (Pinus rigida) are infrequent overstory trees in upland sites, while eastern hemlock (Tsuga canadensis) and black gum (Nyssa sylvatica) are occasional overstory trees in palustrine stands. Understory communities range widely, with occasional rhododendron and blueberry thickets occurring simultaneously with spruce (Picea spp.) in palustrine stands, while Serviceberry (Amelanchier arborea) witch hazel (Hamemelis virginiana), scrub oak (Q. ilicifolia), and mountain laurel are common among the understory of upland
stands. Palustrine stands and shrub wetlands in the Pocono Mountains are further characterized by the presence of many unique plants, including various sedges (*Carex* spp.), ferns (e.g. *Osmunda cinnamomea, Lygodium palmatum*), shrubs (e.g. *Chamaedaphne calyculata, Vaccinium corymbosum, Spiraea tomentosa*) and mosses (e.g. *Sphagnum* spp.) (Latham et al. 1996). In regenerating stands of DSF, a variety of oak saplings are present along with red maple, aspen (*Populus* spp.), black cherry (*Prunus serotina*), black birch (*Betula lenta*), hickories and pitch pine. Present in virtually all regenerating stands was *Rubus* spp. as well as grass and herbaceous vegetation often including goldenrod (*Solidago* spp.) and whorled loosestrife (*Lysimachia quadrifolia*).

**Sproul State Forest**

The SSF covers approximately 123,611 ha spanning extensive portions of both Clinton and Centre counties (PA DCNR 2016) in Pennsylvania’s Appalachian Plateau physiographic province (Sevon 2000), recognized by its steep valleys and soft rolling hills (Abrams and Ruffner 1995). The overwhelming majority of this area is forested thanks largely to the high prevalence of publicly managed lands (Stedman 2004). My study area lied within an approximate 20 km radius in the southwestern portion of SSF and the adjacent SGL 100 to the west. Elevation in the area ranged from approximately 500 to 700 meters above sea level. I studied fledglings at six study sites within SSF, of which five were the result of overstory removal and one was the result of a wildfire that occurred in 1990. These stands ranged in size between 18 ha to 96 ha. As in DSF, mature (80+ years post-harvest) stands provided the vast majority of the forested matrix on the landscape. Oak species such as white oak, red oak and black oak (*Q. velutina*) as well as hickories dominate the overstory in most stands, while black cherry and red maple
frequently comprise the majority of understory trees and saplings (Nowacki and Abrams 1992, Abrams 1998, Stedman 2004). Prevalent shrubs in the understory are rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) (Stedman 2004). Additionally, sweet fern (*Comptonia peregrine*) and huckleberry (*Gaylusaccia* spp.) comprise dominant understory shrubs in large tracts across the study area where a wildfire occurred in 1990. In regenerating stands, a variety of oak saplings are present along with red maple, aspen (*Populus* spp.), black cherry, black birch, and pitch pine. Present in virtually all regenerating stands in SSF was *Rubus* spp. as well as grass and herbaceous vegetation often including goldenrod (*Solidago* spp.) and whorled loosestrife (*Lysimachia quadrifolia*).

Common throughout the SSF study area are herbaceously maintained openings necessary due to the presence of natural gas infrastructure such as pipelines and well-pads (Stedman 2004, Drohan et al. 2012). In addition to increasing natural gas developments since the discovery of the Marcellus shale formation in 2003 (Drohan et al. 2012), over browsing from deer provide another source of forest disturbance in the northcentral region of Pennsylvania (Abrams and Ruffner 1995, Buttrick 1999). Across the Allegheny Plateau province, heavy browsing by deer has been known to alter stand composition by eliminating smaller stem classes and increasing the abundance of unfavorable species (Buttrick 1999, Nuttle et al. 2013). In SSF, the effects of over browsing are obvious in clear cuts where deer exclosure fencing was not used historically, as regeneration can be nearly absent from these stands (C. Fiss personal observation).
Figure 1. Map of Pennsylvania indicating the locations for which habitat selection by fledgling Golden-winged Warblers was studied from 2014 to 2016.
Figure 2. Map of Pennsylvania’s physiographic province subsections and wetlands with both Golden-winged Warbler study areas (Delaware State Forest and Sproul State Forest) shown in shades of grey.
CHAPTER IV

METHODS

Fledgling Data Collection

I began searching for Golden-winged Warbler nests in early-May within the 12 early-successional forest stands across both study areas (6 in DSF and 6 in SSF). To locate Golden-winged Warbler nests I used (i) active searching techniques (in areas with high-perceived probability of hosting a nest), (ii) female nest-building behaviors, and (iii) parental behavior observations (e.g., provisioning young or alarm chips). I initially monitored nest-builds from afar (>10 m) using binoculars to avoid parental abandonment of the site (Confer et al. 2003) After initiation of egg laying, I checked nests on a three-day interval to monitor progress and to ensure accurate estimates of nestling age. I monitored nests once daily when nestlings were preparing to fledge.

When nestlings were between six and seven days old (~0-2 days prior to fledging), I randomly selected two to be fitted with a VHF radio-transmitter. I chose birds of this age as they were large enough to carry a radio-transmitter in the nest but least likely to force-fledge as a result of my handling (Streby et al. 2013). I carefully removed all nestlings from the nest, placed them in a cloth bag, and carried them approximately 15 m from the nest site to minimize the distress to the adult birds. I randomly selected two fledglings, weighed them, and attached transmitters using the figure-eight harness method (Rappole and Tipton 1991). Each VHF radio-transmitter used in this study (Blackburn Transmitters Inc., Nacogdoches, TX) weighed either 0.35 g or 0.40 g and, when combined with a harness and glue, constituted less than 5% of each bird’s total mass. I cut transmitter antennae to a length of 95 mm to minimize the risk of the transmitter
interfering with fledgling behavior/survival. Harnesses were made from <1 mm black elastic thread (Fig. 3) to allow for growth (Streby and Anderson 2013). In addition to radio-transmitters, both radio-tagged birds received an aluminum United States Geologic Survey (USGS) leg band for identification purposes. Total handling time for each pair of nestlings was typically ≤10 minutes and upon completion of radio-tagging and banding, all juveniles were returned to the nest. I continued to monitor nests daily after radio-tagging to determine fledge date and begin tracking. Occasionally juveniles and, in some instances, entire broods force-fledged after radio-tagging, however, this has been shown not to influence survival in similar ground-nesting warblers (Streby et al. 2013), and these individuals were tracked daily thereafter. In addition to the juveniles I tagged prior to fledging, I also captured and tagged some individuals immediately after fledging from known nests if I was unsure of nestling age and did not want to interfere with development. Additionally, I opportunistically captured fledglings from unknown nests. Fledglings captured opportunistically were often detected by hearing frequent begging calls. In order to capture young that had already fledged, I homed in on begging, erected mist nets around the fledgling and waited for juveniles to enter, or pushed juveniles into the nets by slowly moving towards them from the opposite direction. I aged juveniles captured after fledging to the best of my ability, using physical (e.g. molt progression, tail length) and behavioral development (e.g. flight duration, foraging level) of known-age fledglings as guidelines (Fig. 4).

Technicians tracked every radio-tagged fledgling daily between 6:00 and 16:00 hours using a combination of Lotek STR 1000 (Lotek Wireless Inc., Newmarket, ON) and Telonics TR-4 (Telonics Inc., Mesa, AZ) receivers and Yagi style three-element
Figure 3. A) Diagram of radio-transmitter harness attachment method with fledgling shown in blue and gray, radio-transmitter with antenna shown in red, and elastic leg loops shown in yellow. B) Radio-transmitter (0.35g) with elastic harness attached. C) Juvenile Golden-winged Warbler with radio-transmitter.
antennae. I used the homing technique to track fledglings until I made visual confirmation with each individual to document behaviors and habitat use. Upon arriving at a fledgling’s location, I observed the target individual for a minimum of 5 minutes. Although I occasionally had to approach fledglings closely to confirm daily survival, behavioral observations of adults and juveniles were usually made from a distance (>10m) at which all birds appeared to behave in an undisturbed manner (Fig. 5). Upon visual confirmation of a fledgling, I recorded its geographic location with a handheld Garmin eTrex 20 gps unit (Garmin Intl. Inc., Olathe, KS) and documented cover type (e.g. early-successional, sapling, mature), substrate (i.e. plant species), height off the ground, and behavior (e.g. begging, foraging). Additionally, I recorded the presence and behaviors of siblings and parents when present to help determine when fledglings had become independent. I followed this tracking protocol every day until fledgling mortality or radio-transmitter battery failure (approximately 30-days post-activation). When radio-signal was lost for an individual, I conducted systematic searches to determine if the juvenile made a large movement and was out of detection range of my equipment. I started searches at the last known location for the juvenile and walked 1 km transects in each cardinal direction, which typically resulted in the fledgling’s detection. If the juvenile remained undetected, I conducted searches from automobile throughout the study area, only after which did I remove an undetected juvenile from the study.
Figure 4. Observed plumage development of fledgling Golden-winged Warblers from day 2 to day 30 post-fledging based on observations from the 2014 through 2016 breeding seasons in Delaware State Forest and Sproul State Forest in Pennsylvania.
Figure 5. Image of a fledgling Golden-winged Warbler approximately 2 days post-fledging in Sproul State Forest during the 2016 breeding season. A radio-transmitter antenna is visible on the dorsal side of the bird and the juvenile’s red color band is visible on the right tarsus.
CHAPTER V  
PROLONGED INTERSPECIFIC CARE OF TWO SIBLING GOLDEN-WINGED  
WARBLERS BY A BLACK-AND-WHITE WARBLER  

Synopsis  
I observed a fledgling abandonment and adoption event which led to an extended  
period of interspecific parental care between a male Black-and-white Warbler (Mniotilta  
varia) and two radio-tagged fledgling Golden-winged Warbler (Vermivora chrysoptera)  
siblings. Both fledglings were initially accompanied by their maternal Golden-winged  
Warbler until five and nine days after fledging. At this time, a male Black-and-white  
Warbler began feeding both fledglings, and maternal care ceased. In the 23 days I  
monitored the fledglings between onset of interspecific feeding and independence, the  
male Black-and-white Warbler was observed with at least one of the fledglings on 20 of  
those occasions. Furthermore, the Black-and-white Warbler was seen feeding at least one  
of the fledglings on 16 of those visits. Technicians photographed several feeding events.  
The Black-and-white Warbler remained with the fledglings until they successfully  
reached independence 28-days post-fledging.  

Introduction  
Until recently, the behaviors exhibited by many bird species during the post-  
fledging period have remained largely mysterious to biologists (Morton 1991, Baker  
1993, Anders et al. 1997). Unlike with conspicuous, territorial adults, in-depth studies of  
post-fledging songbirds have long remained out of reach for researchers due to the  
secretive nature of passerines and their young during this period (Sullivan 1989, Anders  
et al. 1998, White and Faaborg 2008), which is primarily characterized by parental care
of juveniles and post-natal dispersal and habitat shifts (Moreno 1984, Kershner et al. 2004, White and Faaborg 2008). Recent advances in radio-tracking technologies have allowed for the miniaturization of radio-transmitter devices such that even very small animals (e.g., Neotropical migratory birds <10g) can be tagged and tracked. As such, studies of fledgling songbirds are now possible (Sykes et al. 1990, Neudorf and Pitcher 1997, King et al. 2006). Unsurprisingly, many studies of post-fledging songbirds report fledglings being fed by their biological parents (Weelwright 2003, Grüebler and Naef-Daenzer 2010). However, interspecific feeding, where adult birds offer parental care to the non-parasitic young of another species has also been observed (Shy 1982, McNair and Duyck 1991). In fact, accounts of interspecific feeding cover a wide breadth of avian taxa, occurring in at least 22 families comprised of 71 species of non-brood parasitic birds (Shy 1982, McNair and Duyck 1991). While accounts of interspecific feeding are taxonomically widespread, the behavior is considered rare in the wild and interspecific feeding is even less commonly reported when the adopted species has reached the fledgling phase (Shy 1982). In at least 140 cases of interspecific parenting behavior in the wild, only 41 (29%) involved fledglings (Shy 1982).

Overlap of breeding ranges and overlap in habitat use during fledgling stage are clearly preconditions for instances of interspecific feeding (Shy 1982, McNair and Duyck 1991). In eastern North America, Black-and-white Warblers (*Mniotilta varia*) have been observed feeding the young of other wood warbler species in two independent reports (Rea 1945, Kendeigh 1945). Rea (1945) observed a male Black-and-white Warbler feeding Worm-eating Warbler (*Helmitheros vermivorus*) nestlings. In this case, each feeding attempt by the Black-and-white Warbler was met with aggression by the
attendant adult Worm-eating Warblers but the Black-and-white Warbler continued to feed the Worm-eating Warbler nestlings. Likewise, Kendeigh (1945) observed a male/female pair of Black-and-white Warblers feeding an evidently orphaned Ovenbird (Seiurus aurocapilla) fledgling.

The Golden-winged Warbler (Vermivora chrysoptera) has extensive breeding range overlap with the Black-and-white Warbler across large portions of eastern and central North America (Confer 1992, Kricher 1995). Within their overlapping ranges, both species use early-successional plant communities for nesting and brood rearing (Schulte and Niemi 1998, Bulluck and Buehler 2006). Habitats such as timber harvests host high rates of occupancy for both species with co-occurrence rates as high as 77% (Bakermans et al. 2011). Indeed, there appears to be a high potential for contact between these two species within their shared breeding range.

Here, I describe my extensive observations of interspecific parental care of two sibling Golden-winged Warblers by an adult male Black-and-white Warbler in northeastern Pennsylvania. My observations are the first reported instance of Golden-winged Warblers being involved in interspecific feeding activity in any capacity and represent the longest instance of interspecific care of fledglings by a wild non-captive passerine (Shy 1982, McNair and Duyck 1991). My observations and previously reported instances of interspecific care raise the question of the relative frequency of interspecific parental care in wood warblers.

Observations

The observations presented here were made during my primary study of Golden-winged Warbler fledgling ecology within Pennsylvania’s Delaware State Forest—where
breeding populations of Golden-winged Warblers are relatively common (Wilson et al. 2012). Between 10 June and 2 July 2015, I monitored one Golden-winged Warbler family closely (up to 1 hour/day) in response to an interspecific feeding observation. The nest belonging to this pair was similar to other conspecific nests ($n=156$) monitored during my primary study. This particular nest was found within a 67 ha timber harvest and was built directly on the ground, anchored to a dead goldenrod (Solidago sp.) stem. The final clutch size of six was slightly above the mean of 4.90 ± 0.09 SE for all ($n=39$) Golden-winged Warbler nests I monitored in 2015. The nest was tended by an un-banded male/female pair of phenotypically normal Golden-winged Warblers and they successfully hatched their full clutch of six eggs. I attached transmitters to two of the six young from this nest and monitored them daily after all six successfully fledged. There was no discernable difference between the two radio-tagged fledglings from this nest, and other radio-tagged fledglings ($n=33$) studied in 2015. Both radio-tagged individuals were accompanied by their mother upon fledging (5 June), and sole maternal care of the two radio-tagged fledglings continued until four days post-fledging (9 June).

On 10 June, five days post-fledging, I first observed one of the radio-tagged Golden-winged Warbler fledglings being led by a male Black-and-white Warbler. The Black-and-white Warbler produced quiet chipping calls to which the fledgling responded by following. This observation was accompanied by multiple instances of the adult male Black-and-white Warbler feeding the radio-tagged offspring. The second fledgling continued to be fed by the female Golden-winged Warbler through 10 June, however, this was the last day I observed the female caring for this offspring. I last observed the female Golden-winged Warbler on 12 June when she was chipping with a prey item near the first
radio-tagged fledgling, but she eventually ate the item herself and flew away. On 14 June, I observed the male Black-and-white Warbler feeding the second radio-tagged Golden-winged Warbler fledgling. From 14 June to independence, the two fledglings remained within close proximity of each other (on average 17.5 m across 19 relocations) and the male Black-and-white Warbler. Between fledging and reaching independence (28 days), I recorded the Black-and-white Warbler with at least one of the radio-marked Golden-winged Warbler fledglings 20 times (71% of visits).

Between 10 June and 23 June, I regularly observed the Black-and-white Warbler feeding crane flies (Order: Diptera, family: Tipulidae) to the fledglings (Fig. 6), as well as feeding unidentified moths (order: Lepidoptera) between 23 June and 2 July. On very few occasions, I observed the Black-and-white Warbler feeding caterpillars to the fledglings (Fig. 6). Between fledging and independence, I recorded the Black-and-white Warbler feeding the Golden-winged Warbler juveniles on 16 visits (57% of visits). Other radio-tagged Golden-winged Warbler fledglings I monitored (n=33) had conspecific parents and were primarily fed green caterpillars during June, with adult moths occasionally being fed from late June through early July. The Black-and-white Warbler remained with the Golden-winged Warbler fledglings until they reached independence (28 days post-fledging, 3 July). Independence was marked by the radio-tagged siblings moving away from each other as well as the absence of parental care. Based on these criteria, both radio-tagged Golden-winged Warbler fledglings reached independence on 3 July. On this date, the fledglings were >1 km apart and the male Black-and-white Warbler was not observed with either fledgling thereafter.
Discussion

I present here the first reported case of interspecific parental care involving offspring of Golden-winged Warbler and a non-
Vermivora sp. Because I studied Golden-winged Warblers using radio-telemetry, I had the ability to monitor two fledgling
Golden-winged Warblers daily and detail their interspecific relationship with an adult
Black-and-white Warbler over the course of 23 days. Despite observation bouts lasting
up to 60 minutes I never observed the fledglings being provisioned by Golden-winged
Warbler parents once the male Black-and-white Warbler was observed feeding the
fledglings. Thus, I conclude that the Black-and-white Warbler assumed parental care. The
Black-and-white Warbler was frequently seen with at least one fledgling (71% of visits)
and was often observed provisioning them (57% of visits). These patterns of behavior
suggest that the Black-and-white Warbler successfully reared both fledglings to
independence with no subsequent help from the conspecific parents after day 4 post-
fledging. Interestingly, the successful rearing of these birds occurred despite the
contrast diet offered by Golden-winged Warbler adults (mostly green leaf-roller
caterpillars), and the Black-and-white Warbler (mostly adult crane flies). Additionally, in
at least two observations, I recorded the juveniles probing leaves on their own, a
characteristic foraging behavior used by Golden-winged Warblers, believed to be
important for capturing caterpillar prey (Confer 1992).

Several other instances of fledgling abandonment (Hayward 1937, Jackson 1941,
Kendeigh 1945), reported that interspecific feeding occurred after abandonment of
young. Because I visited fledglings daily, I observed the adoption of these fledglings
while simultaneously watching parental care by the mother cease. My initial observation
of the Black-and-white Warbler male caring for the Golden-winged Warbler fledglings was not marked by immediate abandonment of fledglings by their mother. Thus, I conclude that there was a period of overlap between adoption and abandonment of the young by their mother. Additionally, in contrast to another known instance of interspecific feeding involving a Black-and-white Warbler (Rea 1945), the Golden-winged Warbler female relinquished parental duties to the Black-and-white Warbler with no apparent interspecific aggression, suggesting that the Golden-winged Warbler female willingly abandoned two of her young. Because only two of six siblings were radio-tagged, I am unable to speak to the parental care of the other four fledglings. However, because Golden-winged Warblers are a brood-splitting species (where male and female led broods part ways on the landscape) (Peterson et al. 2016), it is unlikely that the Black-and-white Warbler cared for both groups of fledglings. Further, I am unable to verify that the female Golden-winged Warbler did not care for non-radio tagged fledglings after the Black-and-white Warbler assumed care of her two radio-tagged fledglings. Perhaps her abandonment of the two-radio-tagged fledglings was facilitated by her inability to care for a higher than average brood size (n=6). Further, the absence of aggression may have been related to the fact that these juveniles had already fledged the nest, during which time Golden-winged Warblers are known to tolerate the presence of other birds, often foraging with their young in mixed flocks (Will 1986, CJF, pers. obs.).

Prolonged examples of interspecific feeding, have been documented by previous researchers. For example, McGowan (1990) observed a pair of Fish Crows (Corvus ossifragus) feeding a fledgling Blue Jay (Cyanocitta cristata) that began residing within their nest (for reasons unknown) over the course of 12 days and Carr and Goin (1965)
observed a pair of Eastern Bluebirds (*Sialia sialis*) over the course of 25 days first feeding five Northern Mockingbird (*Mimus polyglottos*) nestlings, and later the same mockingbirds after they fledged. Nevertheless, review of all known examples for passerines suggests that interspecific feeding events that extend to 23 days, and particularly those resulting in fledgling independence, are quite rare (Shy 1982, McNair and Duyck 1991). The timeframe of my observations, and the lack of any sightings of juvenile Black-and-white Warblers, suggests that the male Black-and-white Warbler lacked fledglings of its own. I conjecture that this male may have been unmated or experienced a nest failure and was thus available to provision the Golden-winged Warbler fledglings. In the case of nest failure, the Black-and-white Warbler may have used the Golden-winged Warblers as an outlet to expend excess feeding energy that accrued before losing its own young (Skutch 1961).

The begging calls of the fledgling Golden-winged Warblers, may have been enough to trigger this behavior in the Black-and-white Warbler (McNair and Duyck 1991, Dróżdż et al. 2004, Farmer et al. 2008). Farmer et al. (2008) suggested that a pair of Palila (*Loxioides bailleui*) may have been unable to provide for their higher than normal amount of young, leading one offspring to solicit food from an interspecific parent. In fact, such observations have been made before involving begging Golden-winged Warbler fledglings in Minnesota (DJM, pers. obs.), but their requests for food were unfulfilled in those cases. Such observations usually involved a fledgling loudly begging in close proximity of a heterospecific adult followed by no response by the unrelated adult.
The rarity of observed interspecific feeding events is likely due to the high energy expenditure incurred when an adult provides food for a fledgling and the seemingly absent evolutionary advantage to doing so in an interspecific context (Shy 1982, Cockburn 1998). Although the parental behavior of the Black-and-white Warbler was misdirected (Shy 1982, Brown 1987), evolutionary explanations for this type of behavior suggest that it is possible that the male acquired useful brood-rearing experience (Shy 1982). This experience may, in turn, improve the Black-and-white Warbler’s reproductive success in subsequent breeding seasons, as is the case with many after-second year birds (De Steven 1978) and birds that assist parents through cooperative breeding (Emlen 1982). Regardless of any benefit conferred, my observations suggest that an interspecific parent is capable of provisioning multiple non brood-parasitic fledglings for an extended period of time. My observations clearly demonstrate that the male Black-and-white Warbler successfully completed the rearing of two Golden-winged warbler fledglings to independence with no obvious detriment to the fledglings’ development. While it seems unlikely that I will ever know how this this interspecific brood-rearing event influences future reproductive success (i.e., pairing success, nestling and fledgling provisioning) of the two Golden-winged Warblers, the duration and outcome of these observations speaks to the resiliency of fledgling songbirds.
**Figure 6.** Two feeding sequences between the male Black-and-white Warbler and a radio-transmittered Golden-winged Warbler fledgling. A) The Black-and-white Warbler approaches the begging juvenile with a crane fly (family: Tipulidae). B) The Golden-winged Warbler fledgling with the crane fly in its mouth. C) The Black-and-white Warbler approaches the juvenile with a smooth green caterpillar and a moth and (D) places both items into the juvenile’s mouth.
CHAPTER VI

FLEDGLING GOLDEN-WINGED WARBLER STAND-SCALE HABITAT SELECTION IN TWO MANAGED FORESTS IN PENNSYLVANIA

Synopsis

Studies of songbird habitat selection during the post-fledging period are scant, yet increasing due to apparent shifts in habitat use during this time away from cover associated with nesting adults. Thus, management for birds which focuses solely on habitat associated with birds surveyed during the nesting period, may be missing key habitat associations during a critical life stage. I studied the influence of forest stand level factors on the habitat selection of fledgling Golden-winged Warblers in two managed, yet structurally distinct, forests in northcentral and northeast Pennsylvania across three breeding seasons from 2014-2016. Using radio-telemetry I monitored fledglings daily for up to 34 days or until loss of radio-transmitter signal or fledgling mortality. To model population level habitat selection, I constructed discrete-choice models within a Bayesian framework in which each fledgling was presented with a “choice set” of used vs available locations for each day it was tracked. From each location within the choice set, I measured Euclidean distance to each habitable cover type in the local landscape. In Delaware State Forest (DSF) of northeast PA, I observed a diverse use of forest cover types by fledglings \( n=59 \) that included early-successional, sapling, forested wetland and mature stands (among others) as they aged. Conversely, fledglings \( n=25 \) in SSF remained almost exclusively in early-successional cover throughout the entire tracking period (approximately 30 days). Population level habitat selection in both landscapes was primarily directed towards early-successional cover during most of the tracking period.
(day 1-20). The remainder of the dependent post-fledging period (day 21-28) was characterized by the selection of sapling stands and edge habitat in DSF and the lack of cover type selection in SSF. Across both landscapes, global models largely outperformed univariate cover type models, suggesting that landscape complexity, driven by the interspersion of different aged stands and cover types, is important to Golden-winged Warbler fledglings in Pennsylvania.

Introduction

Survival during the post-fledging period can disproportionately influence population dynamics of songbirds compared to other demographic parameters (e.g. nesting success) (Donovan and Thompson 2001, Robinson et al. 2004). Results from studies surrounding this interval have revealed high levels of fledgling mortality early in the post-fledging period (Anders 1997, Rush and Stutchbury 2008, Cox et al. 2014, Streby et al. 2016) and shifts in habitat away from typical nesting cover (Vega Rivera et al. 1998, King et al. 2006, Streby and Anderson 2013, Streby et al. 2016). Many post-fledging habitat shifts are towards forests of younger seral stages (Vega Rivera et al. 1998, Pagen et al. 2000, Vitz and Rodewald 2006). Researchers have hypothesized that habitat shifts of this nature may occur because young forest containing dense vegetation offers protection from predators (Anders et al. 1998, Vitz and Rodewald 2007), and a rich supply of food resources for developing birds (Vitz and Rodewald 2007, Streby et al. 2011). One particularly important finding from previous post-fledging research is that juveniles and their parents select habitat features that maximize their survival during this time (Rush and Stutchbury 2008, Streby and Anderson 2013, Vitz and Rodewald 2013, Cox et al. 2014). As such, identifying cover types and vegetation features that are...
selected by fledglings, may help land managers create landscapes that benefit fledgling survival, and thusly improve overall population productivity.

Many post-fledging habitat selection studies have focused on habitat influences at the micro-scale (i.e. vegetation structure; e.g. King et al. 2006, Ausprey and Rodewald 2011, Raybuck 2016, Jenkins et al. 2017). While studies of this nature are clearly important, another important scale at which to examine post-fledging habitat use and selection in songbirds is the forest stand scale (i.e. local landscape scale). Both adult and fledgling songbirds are known to respond to environmental features at this scale (Pagen et al. 2000, Hagen and Meehan 2002, Macfaden and Capen 2002, Streby and Anderson 2013). Habitat selection at this scale can help identify areas where finer scale microhabitat studies should focus attention for a given species to fully describe habitat associations during the post-fledging period. Finally, the stand is the unit with which forest managers most often work, thus, research at this scale should easily translate to on-the-ground management efforts for target species. Given the importance of research for post-fledging songbirds at the stand-scale, it’s not surprising that some recent studies have investigated habitat selection at this scale for fledgling birds of conservation concern, such as Ovenbirds (Streby and Anderson 2013) and more recently Golden-winged Warblers in the western segment of their breeding distribution (Streby et al. 2016).

The Golden-winged Warbler is a steadily declining (Sauer et al. 2017) Neotropical migratory songbird that is a focal species of conservation concern (Rohrbaugh et al. 2016). The species nests in early-successional habitat within highly forested landscapes throughout portions of the Appalachians in the eastern United States.
(US) and portions of the western Great Lakes region of the US and Canada, although the
two segments are considered disjunct (Roth et al. 2012). Golden-winged Warblers have
been experiencing rangewide population declines of approximately 2.3% since the mid
1960’s according to North America Breeding Bird Survey (BBS) data (Sauer et al. 2017).
The Appalachian population of Golden-winged Warblers is declining significantly faster
than the Great Lakes population (Sauer et al. 2017). Fortunately, conservation actions are
being taken in the Appalachian range in order to create nesting habitat for this species
following the management guidelines laid out in the Golden-winged Warbler
management plan (Roth et al. 2012) and the Best Management Practices outlined in
Bakermans et al. (2011). For instance, the US Department of Agriculture Natural
Resource Conservation Service (NRCS) has developed a private landowner conservation
easement program called Working Lands for Wildlife (WLFW) which reimburses private
landowners in exchange for creating habitat for focal species such as Golden-winged
Warblers (Ciuzio et al. 2013). Despite recent conservation efforts, our lack of knowledge
regarding habitat associations for Golden-winged Warblers during the post-fledging
period may limit the effectiveness of these actions, especially if Golden-winged Warbler
fledglings shift habitat use away from nesting cover.

Two previous study involving stand-level habitat selection by fledgling Golden-
winged Warblers were conducted in the western Great Lakes portion of the species
breeding range focusing on selection during the dependent post-fledging period (Streby et
al. 2016) and the following independent period (Streby et al. 2015). This research
revealed that fledgling Golden-winged Warblers, like many other passerines, also shift
habitat section behavior during the post-fledging period. However, unlike many previous
studies which report the use of shrubby, early-successional cover, Streby et al. (2016) reports that dependent fledglings shift habitat use away from early-successional cover to more mature forest cover as they age. This research provides valuable knowledge to incorporate into Golden-winged Warbler habitat management plans in the western Great Lakes segment of the species breeding range. However, the same patterns may not translate to the Appalachian segment of the breeding range, where forest type differs considerably (Peterken 1996). For instance, northern Minnesota (where Streby el al. 2016 work was conducted) is dominated by a more boreal spruce forest community with abundant aspen, birch, and tamarack (Peterken 1996). Portions of Pennsylvania and much of the Appalachian region are dominated by a mixed-oak hickory forest community (Peterken 1996). As such, forest management practices also differ between the Appalachians and the western Great Lakes region (e.g. PA-SFRMP, MN-SFRMP). Forest rotation periods are one main difference in the way these two forest communities are managed. Aspen/birch communities are typically harvested much sooner (e.g. 30 – 40 yrs) than their mixed-oak hickory counterparts (e.g. 80-100 yrs; Nowacki and Abrams 1992, Nyland 2016).

Given the at-risk nature of Golden-winged warbler populations in the Appalachian Mountains and the ongoing efforts to manage forest to create breeding habitat (McNeil et al. 2017), studies that examine post-fledging ecology in this region are needed to augment existing habitat guidelines. I conducted a study of fledgling stand-level habitat selection in two managed forest landscapes in the central Appalachian Mountains. Using radio-telemetry, I quantified how fledglings select for habitat at the stand-level scale during the dependent post-fledging period, and early in the independent
The primary objectives of my study were to 1) determine the influence of stand-level complexity within local landscapes on Golden-winged warbler movements and habitat selection behavior; 2) to identify if fledgling Golden-winged Warblers select for other cover types other than early-successional nesting cover; and 3) compare cover type use and selection patterns among two landscapes in Pennsylvania to what is known about Golden-winged Warbler fledgling habitat selection in the western Great Lakes.

Methods

Stand-Scale Cover Typing

I classified landscape cover (Fig. 7) across both my study areas in ArcGIS 10.3 using a combination of Pennsylvania State Forest inventory data acquired from Delaware and Sproul State Forests, Pennsylvania State Game Lands inventory data for SGL 100, National Agricultural Imagery Project (NAIP) 2011 imagery, and National Wetlands Inventory (NWI) data. In addition, I used my own observations from >3200 ground-truthed locations over three years. In Delaware State Forest, I classified cover into six different categories (Early-successional, Sapling, Shelterwood/thinned, Mature, Forested Wetland, and Shrub Wetland). In Sproul State Forest and the adjacent State Game Lands 100, I classified cover into five different categories (Early-successional, Sapling, Shelterwood/thinned, Mature, and Shrub savanna). When possible, I classified cover types based on structural (often stocking level) features, and cover types in this analysis share many of the same descriptive qualities as in the Pennsylvania Department of Conservation and Natural Resources Bureau of Forestry (PA DCNR BOF) Inventory Manual. Early-successional cover was defined as those stands which had recently
undergone overstory removal and were >50% stocked and dominated by trees <15 cm DBH. Early-successional stands in this analysis are essentially, what Golden-winged Warblers nest within or along the edge of (nesting habitat), and contain substantial amounts of shrub and herbaceous ground cover. *Sapling* cover was defined as those stands >50% stocked and dominated by trees <15 cm DBH. However, as opposed to early-successional stands, these had reached the point of stem exclusion whereby ground cover was almost entirely shaded-out by a dense sapling overstory. *Shelterwood/thinned* cover was defined as stands that were <50% stocked and dominated by trees 15-46 cm DBH. Occasionally shelterwood stands were considered amongst forest inventory data to be >50% stocked with <15 cm DBH trees being dominant (likely as a result of advanced regeneration) however, careful study of aerial imagery as well as ground-truthed locations suggested that these were not complete overstory removals. *Mature* cover was defined as stands that were >50% stocked and dominated by trees >15 cm DBH. These stands made up the forest matrix of both Delaware and Sproul State Forest. *Forested Wetland* cover was classified as palustrine stands >50% stocked and dominated by trees >15 cm DBH. Forested wetlands can be seasonally or perpetually inundated with water. *Shrub Wetland*, as the name implies, were dominated by shrubs and trees <15 cm DBH and often perpetually inundated with water. This cover type is known to be used by nesting Golden-winged Warblers, particularly along ecotones with forest wetlands. *Shrub Savanna* cover was <50% stocked and trees <15 cm DBH were dominant. This cover type was specific, but relatively prevalent and widespread across portions of Sproul State Forest.
Figure 7. An example of a digitized landscape around a Golden-winged Warbler breeding stand in Delaware State Forest of northeastern Pennsylvania. One cover type not shown is shrub savanna (SSF only). Unshaded areas indicate cover that was considered uninhabitable by fledgling Golden-winged Warblers, including developments, lawns, fields, and bodies of water.
Shrub cover in this cover type was often ubiquitous and typically a *Vaccinium* spp. or *Gaylussacia* spp. (e.g. highbush blueberry, huckleberry).

**Discrete Choice and Defining Availability**

I modelled cover type selection for fledgling Golden-winged Warblers using multinominal logistic regression (i.e. discrete choice models; Cooper and Millspaugh 1999, Manley et al. 2002). Discrete choice models have long been used for consumer decision-making studies in economics (Manski and McFadden 1981) however, these models have more recently been applied to a number of wildlife studies (McDonald et al. 2006, Carter et al. 2010, Bonnot et al. 2011, Beatty et al. 2014). Unlike compositional analysis, discrete choice models can incorporate both continuous and categorical habitat variables, and are thus capable of incorporating habitat features without physical cover in the sampling area (e.g. edge). Additionally, discrete choice models are known to be robust to noise (e.g. point misclassification) in the dataset (Connor et al. 2003).

I created choice sets for every fledgling beginning on the first day each individual was radio-tracked. Choice sets contained the point where the juvenile was observed (used) and 19 additional points that were available but not used, thus each choice set contained 20 options. This distribution of “used” to “available” points has been used in similar contexts by Bonnot et al. (2011) and Beatty et al. (2014). Available points were generated in ArcGIS using the “Create Random Points” tool. To constrain available resource units, I used methods similar to Streby et al. (2016), in which I determined a unique availability range for each age to allow availability to change as fledglings developed. I determined fledgling age-specific availability based on the 75th percentile of all daily movements for a given age, and used this value as the radius for the availability circle (Fig. 8). I chose
Figure 8. Golden-winged Warbler fledgling daily availability range (m) for each fledgling age based on the 75th percentile of all movement for juveniles of a specific age. Sproul State Forest age-specific movements are based on $n=25$ radio-tagged fledglings monitored during June and July 2016. Delaware State Forest age specific movements are based on $n=59$ radio-tagged fledglings monitored during June and July 2014 and 2015.
the 75th percentile, as the maximum distance travelled might overestimate movement capabilities fledglings in poorer condition, and using the mean may underestimate movement capabilities if several fledglings were already in preferred cover and chose not to move. If the 75th percentile of all age specific movement was higher for a younger age than an older age, the higher movement value was used for the older age as juveniles had already demonstrated their ability to move that distance. Additionally, for individual fledglings that had movements greater than the 75th percentile for a certain age, I adjusted their availability to 1m above the distance they actually moved that day to ensure that their used location fell within the availability buffer. This resulted in a scenario in which I determined availability for day i, and i + 1 always fell within that buffer (Fig. 9). I created availability buffers separately for Delaware and Sproul State Forest to account for any potential variability in fledgling movement capabilities related to each landscape. I measured Euclidian distance (m) from each of the 20 (1 used, 19 available) alternative resource units within a choice set to all cover types in each study site defined in the land cover classification (early-successional, sapling, mature, shelterwood/thinned, forested wetland, shrub wetland, and shrub savanna) to include as variables in fledgling stand-level analysis. Distance values were zero for cover types within which fledglings were observed or an available point was placed. Additionally, I included distance to edge as a variable to measure the influence of ecotones on habitat selection which are known to be important for this species (Patton et al. 2010, Streby et al. 2016). I calculated distance to edge as the distance to the closest change in cover type if that cover type consisted of a major structural change. For instance, I measured distance to mature, forested wetland, shelterwood/thinned, or sapling, if fledglings were in early-successional, shrub wetland,
Figure 9. Method for determining age-specific availability for radio-tagged Golden-winged Warbler fledglings. For any given day \((i)\) juveniles were buffered with an age-specific availability range based off the 75\(^{th}\) percentile of all fledgling movements of that age. This availability buffer always captured the next day \((i+1)\) relocation, and all available (A) locations.
or shrub savanna, and I did the opposite if fledglings were in mature, forested wetland, shelterwood/thinned, or sapling. With this method, a border between mature and forested wetland cover types would not constitute an edge. Finally, I included distance moved as a variable to assess whether fledglings were selecting locations that required less movement between consecutive locations. Thus, I modeled selection of used and available locations each day, based on proximity relative to cover types, edge, and distance from the last used location.

**Statistical Analyses**

I used a Bayesian random effects modeling approach in which selection estimates for each individual informs overall population level selection estimates (Thomas et al. 2006). Because, Golden-winged Warblers are a brood splitting species, in which the adult male and female each take part of the brood (Peterson et al. 2016), I used sub-broods as individual samples, because fledglings within the same sub-brood are not spatially independent. Thus, I modelled selection for each cover type within a study area based on each sub-brood, and based conclusions upon overall population-level selection estimates. I created a set of five *a priori* candidate models to describe fledgling habitat selection at the landscape scale based on previous findings from passerine post-fledgling habitat research, all of which contained the variable describing distance from prior location. I created three models that included, in addition to the distance moved, only a single cover type. One model included only the proximity to early-successional cover to investigate if fledglings were choosing habitat based on proximity to nesting habitat. I created two additional models including only proximity to mature cover and only proximity to sapling cover, because similar cover was selected by Golden-winged Warbler fledglings in the
Great Lakes portion of the breeding range (Streby et al. 2016). I included a global model, which would suggest that fledglings selected habitat based on proximity to every cover type (DSF = six cover types, SSF = five cover types). Finally, I included a null model, which would signify that fledglings were not selecting for cover types at the landscape scale. Because fledgling passerines may change habitat preferences as they age (King et al. 2006, Streby et al. 2016, Raybuck 2016), I applied these five candidate models to five different intervals of fledgling development based on natural breaks in all daily movement data (Fig. 10), and indicators of fledgling independence from adults. Thus, I applied models to juveniles 1 to 6 days post-fledging, 7 to 13 days post-fledging, 14 to 20 days post-fledging, 21 to 28 days post-fledging, and to juveniles during the post dependent period (29+ days post-fledging). Because different cover types were available at the two study areas, I fit models separately for each study area, for a total of 25 models per study area.

Bayesian discrete choice models were fit using WinBUGS v1.4.1 (Link et al. 2002), which I ran through the Program R package R2WinBUGS (Sturtz et al. 2005). Population-level parameter estimates and associated 95% credible intervals based on the posterior distribution for predictor variables were derived from WinBUGS output. Depending on directionality, predictor variables with 95% credible intervals not overlapping zero were assumed to be selected for or against by fledglings. Further, to rank sets of candidate models, I used deviance information criterion (DIC) scores, a Bayesian version of the frequentist AIC score. Models with ΔDIC >5 were inferred to be significantly different (Thomas et al. 2006). I ran global models for 750,000 iterations in
Figure 10. Average age-specific movement values for all radio-tagged Golden-winged Warbler fledglings across DSF and SSF with associated 95% confidence intervals. Fledglings were monitored at DSF and SSF study areas during June-July 2014-2016. Dashed lines delineate age intervals for which selection analyses were conducted. The five age intervals were chosen based on most obvious breaks in average movement values and include: days 1-6, days 7-13, days 14-20, days 21-28, and days 29-35 (independent period) post-fledging.
three chains of which I allocated the first 50,000 to burn-in to allow chains to stabilize. Additionally, I thinned chains by 10 to avoid autocorrelation in the sample. Single cover type models were run with 610,000 iterations in three chains, 10,000 burn-in, and thinning interval of 10. Thus, for global models, posterior distributions, DIC scores, and population level parameter estimates were derived from 70,000 iterations, while single cover type models were based on 60,000 iterations. I confirmed that $\hat{r} < 1.1$ for all models, indicating successful convergence of Markov chains (Gelman and Hill 2007).

**Results**

I radio-transmittered, tracked, and obtained usable habitat selection data from 84 individual Golden-winged Warbler fledglings from $n=69$ sub-broods and collected a total of 1693 relocations from 2014 to 2016. In DSF I acquired habitat selection data from 59 individuals from $n=45$ sub-broods. In SSF I acquired habitat selection data from 25 individuals from $n=24$ different sub-broods. Samples for habitat selection models varied for the dependent post-fledging period depending on age class, and were derived from 39 to 41 sub-broods in DSF (Table 1) and from 10 to 21 sub-broods in SSF (Table 2). Models for the independent post-fledging period were derived from 22 sub-broods in DSF (Table 1) and seven sub-broods in SSF (Table 2).

Fledglings used all cover type classifications in each study area throughout the duration of tracking (Fig 11). Fledglings used primarily early-successional cover during the first six days post-fledging. In DSF, fledglings began using older forest cover types including sapling, forested wetland, shelterwood and mature forest stands during later age classes, and mature forest was the most predominantly used cover type from days 14 to 28. Although, fledglings began using other cover types including sapling, mature, and
Figure 11. Percentage of forest cover types used by radio-tagged fledgling Golden-winged Warblers across five age classes in both Delaware State Forest (left) and Sproul State Forest (right). Fledglings were monitored during June and July 2014-2016. Note: Forested cover type use does not indicate selection as it does not account for cover type availability.
shrub savanna stands in SSF as well, early-successional cover remained the most predominantly used cover throughout the entire tracking period.

In both DSF and SSF, fledgling Golden-winged Warblers selected resource units based on their proximity to cover types during the entire dependent post-fledging period (i.e. days 1 to 28 post-fledging). In DSF, the global model including all cover types, edge, and distance from previous resource unit, was the top ranked model from day 1 to day 28, outperforming all single cover type models which describe selection for or against early-successional cover only, sapling cover only, or mature cover only (Table 1). In SSF, the global model was the top ranked model during days 1 to 6, however, the global model was competing (i.e. ΔDIC<5.0) as the top model with the early-successional model during days 7 to 13 post-fledging (Table 2). During days 14 to 20 post-fledging in SSF, the global model was competing with the early-successional only and shrubland only models as the top model (ΔDIC<5.0). During days 21 to 28 in SSF, all single cover type models outperformed the global model, and were all competing as the top model.

Golden-winged Warbler fledglings during the beginning of the independent period (i.e. days 29-34 post-fledging) also selected cover types in both study areas according to model rankings. The best models of cover type selection by independent fledglings in DSF were single cover type models which were all competing as the top model, while the global model performed slightly worse (ΔDIC = 5.3; Table 1). The top models of independent fledgling cover type selection in SSF were the mature forest only model, the global model, and the early-successional only model, which were all competing models and outperformed the shrubland only model (Table 2).
Table 1

*Candidate Landscape Scale Habitat Selection Models for Radio-Tagged Fledgling Golden-Winged Warblers Across Five Fledgling Age Classes in Delaware State Forest of Northeastern Pennsylvania*

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<td>Early+Dist.</td>
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*Note.* Fledglings were monitored during June and July 2014 and 2015. Models were ranked based on ΔDIC and each age class was based on n sub-broods.
Table 2

Candidate Landscape Scale Habitat Selection Models for Fledgling Golden-Winged Warblers Across Five Fledgling Age Classes in Sprouls State Forest of Northcentral Pennsylvania

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*Note.* Fledglings were monitored during June and July 2016. Models were ranked based on ∆DIC and each age class was based on n sub-broods. Asterisks represent those models which were competing.
In addition to cover type models, fledglings also selected for or against individual covariates within models. I graphed parameter estimates and 95% credible intervals for all covariates included in top models for each age class (Figs. 12 & 13). In DSF, fledglings selected for early-successional cover ($\beta = -1.73$; 95% Credible Interval = -4.16 to -0.40) from days 1 to 6 post-fledging over all other cover types and edge, which were neither selected for or against. During days 7 to 13 post-fledging in DSF, fledglings selected for early-successional cover ($\beta = -4.92$; 95% CI = -8.75 to -2.24) over all other cover types, though they also selected for mature forest ($\beta = -0.59$; 95% CI = -1.13 to -0.05) as well. During days 14 to 20 post-fledging in DSF, fledglings again selected most strongly for early-successional cover ($\beta = -2.44$; 95% CI = -4.37 to -0.97), and selected for mature cover ($\beta = -0.59$; 95% CI = -1.05 to -0.22). Fledglings in DSF then selected most strongly for sapling cover ($\beta = -0.86$; 95% CI = -1.98 to -0.04) during days 21 to 28 post-fledging over all other cover types which were neither selected for or against. During days 21 to 28, DSF fledglings also selected for edge between mature forest and young cover types ($\beta = -0.61$; 95% CI = -1.11 to -0.18). At no point in DSF did fledglings select for locations that were closer to the previous day’s location. In SSF during days 1 to 6, days 7 to 13, and days 14 to 20, fledglings selected for early-successional cover ($\beta = -7.97$; 95% CI = -19.91 to -1.91; $\beta = -3.63$; 95% CI = -9.69 to -0.78; and $\beta = -4.69$; 95% CI = -12.93 to -0.52; respectively) over all other cover types and edge, which were neither selected for or against). In SSF during days 21 to 28 fledglings selected for distance to previous location ($\beta = -2.09$; 95% CI = -3.64 to -0.84).
Figure 12. Parameter estimates and 95% credible intervals for selection of seven cover types, proximity to last used location, and edge by Golden-winged Warbler fledglings. Fledglings were monitored at Delaware and Sproul State Forest study areas during June and July 2014-2016. Negative values indicate selection for a feature, while positive values indicate avoidance. Delaware State Forest (DSF) is indicated with black circles. Sproul State Forest (SSF) is indicated with gray squares. A) Parameter estimates for days 1 to 6 post-fledge. B) Parameter estimates for days 7 to 13 post-fledge. C) Parameter estimates for days 14 to 20 post-fledge. D) Parameter estimates for days 21 to 28 post-fledge.
Figure 13. Parameter estimates and 95% credible intervals for selection of seven cover types, proximity to last used location, and edge by Golden-winged Warbler fledglings for parameters included within the top stand level habitat selection models for SSF and DSF during the independent post fledging period (day 29+). Fledglings were monitored in DSF and SSF study areas during June and July 2014-2016. Negative values indicate selection for a feature, while positive values indicate avoidance. DSF is indicated with black circles. SSF is indicated with gray squares.
In both DSF and SSF during the beginning of the independent post-fledging period (days 29 to 34), there was no significant selection for or against any covariates within selection models including cover types, edge, or distance to prior location (Figure 13).

**Discussion**

Previous post-fledging habitat selection studies have demonstrated that juvenile songbirds often use habitat that differs from those used by adult birds during the nesting period (Anders et al. 1998, King et al. 2006, Streby and Anderson 2013, Streby et al. 2016). Additionally, results from several of these studies indicate that juveniles select for habitat features that maximize their survival during a period characterized by high levels of predation (Streby and Anderson 2013, Vitz and Rodewald 2013, Streby et al. 2016). Such information highlights the need to broaden the scope of management to capture habitat associations during the full breeding season in order to maximize songbird productivity.

My results indicate that at the population level, Golden-winged Warbler fledglings selected most strongly for early-successional cover (nesting cover) throughout the first half of the dependent post-fledging period across both study areas. However, during the second half of the dependent post-fledging period, when juvenile mobility increased considerably, I observed contrasting patterns of cover type selection between study sites. In DSF, during days 7 to 20 post-fledging juveniles continued to select for most strongly for early-successional forest, but also began selecting for mature forest, and from days 21 to 28 post-fledging only selected for sapling stands. In stark contrast, fledglings in SSF selected only for early-successional forest cover throughout the
majority of the dependent post-fledging period (days 1 to 20 post-fledging), and did not select for or against any cover types during days 21 to 28 post-fledging.

The habitat selection behavior I observed during the latter part of the dependent post-fledging period in DSF is similar to what researchers observed for Golden-winged Warbler fledglings in the western Great Lakes, where fledglings selected for mature forest and sapling dominated stands over all other cover types during the first eight days of the post-fledging period and selected for mature forest throughout the remainder of the dependent post-fledging period (Streby et al. 2016). However, Streby et al. (2016) indicated mature forest was the most strongly selected for cover type in the Great Lakes region, in DSF my results suggest that mature forest was selected primarily as a medium in which to reach sapling dominated stands, and was never the most selected for cover type. Selection for mature forest in my study was comparatively weak (Figure 12), and eventually led to the selection of sapling dominated stands over all other cover types, while mature forest was neither selected for nor against during the final days of the dependent post-fledging period (i.e. days 21 to 28). This pattern makes sense, as mature forest comprised the matrix of both the DSF and SSF landscapes, and often had to be traversed through to reach other patchily distributed cover types. While selection for mature forest was relatively weak within the DSF study area and entirely absent in the SSF study area, mature forest in both study areas was compositionally and structurally different than the mature forest described in Streby et al. (2016). Mean canopy cover within mature forest of my study areas (SSF = 84%, DSF= 94%; C. Fiss chpt. 7) which was dominated by oak, maple, and hickory, was considerably greater than mature forest canopy cover in Streby et al.’s (2016) study area, which averaged >60% and was
dominated by aspen and birch. These differences likely explain the slight variation observed in DSF fledglings compared to those in the western Great Lakes. Interestingly, the pattern of movement from early-successional forest into mature forest, and ultimately into sapling stands did not occur in SSF. This raises questions about what factor(s) motivated fledglings to remain in early-successional forest for the majority (i.e. days 1 to 20 post-fledging) of the dependent post-fledging period in SSF and to seek out sapling stands in DSF.

Fledgling/parent groups remaining in early-successional cover during the post-fledging period in SSF could suggest that these family groups were able to attain all necessary resources in early-successional forest alone, that the micro-scale vegetation structure of mature forest in SSF obstructed movement, or there was no suitable alternative cover in the surrounding landscape in which to relocate. The latter argument makes sense if adults prospected for appropriate post-fledging habitat prior to rearing young, which is a hypothesis explaining fledgling movement patterns in songbirds (Reed et al. 1999, Frantz et al. 2016). In which case fledgling/parent groups would likely have remained in the cover in which they were hatched. The performance of my global models and the directionality of several cover type parameters within those models suggests that in both DSF and SSF, at least until day 20, fledglings selected areas on the landscape that were proximate to multiple cover types. Thus, if the early-successional stands in SSF were representative of the most structurally diverse areas on the landscape, fledglings may not have had reason to leave these areas. It seems unlikely that the vegetation structure of mature forest deterred the movement of fledgling Golden-winged Warblers in SSF because in a comparison of micro-scale vegetation features, mature forest structure
in both study areas was quite similar (C. Fiss, chpt 7). Fledglings in SSF may have further chose to remain in early-successional cover because it captured some of the features that would be found within sapling stands in DSF. A comparison of micro-scale vegetation features within early-successional cover between DSF and SSF indicated that saplings were significantly taller in early-successional forest in SSF (C. Fiss chpt 7). Thus, fledglings in DSF may have sought features within sapling stands that fledglings in SSF were able to exploit within the early-successional stands of that study area.

Selection for early-successional stands for the first half of the dependent post-fledging period in both landscapes is important considering that the majority of mortality in fledgling songbirds, including fledgling Golden-winged Warblers, occurs within the first five days after fledging (Cox et al. 2014, Streby et al. 2016). The overwhelming majority of early-successional stands within my study were managed in accordance to the Golden-winged Warbler Best Management Practices (BMP) (Bakermans et al. 2011, 2015). Assuming my fledglings, like those in previous fledgling studies (Cohen and Lindell 2004, Streby and Anderson 2013), selected for resource units that maximized survival, my results indicate that the management scenarios described within the BMP’s are at least partially capable of capturing the needs of fledgling Golden-winged Warblers. Thus, managing early-successional patches within forested landscapes remains important for Golden-winged Warblers during the post-fledging period in addition to the nesting period in the Appalachians. In fact, many fledgling songbirds, even those typically associated with mature forest, are known to use early-successional cover during the post-fledging period (Pagen et al. 2000, Marshall et al. 2003, King et al. 2006, Vitz and Rodewald 2006). The dense, regenerating woody vegetation of early-successional stands
may provide safety from predators (King et al. 2006, Vitz and Rodewald 2007) and ample food resources for rapidly developing fledglings (Vitz and Rodewald 2007, Streby et al. 2011).

In addition to early-successional stands, managers are likely to benefit Golden-winged Warbler fledglings by interspersing other cover types within landscapes surrounding nesting stands. For instance, sapling stands were the only cover selected for during the latter portion of the post-fledging period in DSF when fledglings were considerably more capable of landscape level movements. Sapling stands may provide fledglings with the greatest protection from both avian and ground dwelling predators (Vitz and Rodewald 2007). Vitz and Rodewald (2007) hypothesized that dense vegetation was beneficial to fledglings, but at a certain point ground level vegetation that was too dense may help to conceal predators. Areas with greater vertical regeneration, like dense sapling stands, may provide the best protection from both avian and ground predators as dense ground cover is shaded out. Additionally, because global models largely outperformed univariate cover type models and the direction of selection was typically towards several cover types within those models, Golden-winged Warbler fledglings in this study preferred areas with numerous distinct cover types within close proximity on the surrounding landscape. The fact the fledglings in DSF selected for edge between mature and early successional cover types during days 21 to 28 supports this idea. It is possible that fledgling Golden-winged Warblers and their parents select areas proximate to multiple cover types in order to diversify their prey availability, indeed I frequently watched adults forage in one cover type and then deliver food items to juveniles in a different cover type. Alternatively, multiple proximate cover types may allow parents to
shift protective cover to guard juveniles from changing predator communities as the post-nesting season progresses (Suhonen 1993).

Like past studies of habitat selection during the post-fledging period, I demonstrate that fledgling Golden-winged Warblers select for habitats that differ from what adults use for nesting. However, I found that this pattern of shifting habitat from nesting to the post-fledging period does not always occur, and that landscape complexity or vegetation structure within cover types may influence a fledglings’ stand-scale habitat selection behavior. Constant across both landscapes was the selection for locations that were proximate to multiple distinct cover types. Thus, landscapes that consist primarily of mature forest and early successional forest are not likely to be as beneficial as those which are comprised of several different aged stands. These finding suggests that for Golden-winged Warblers in the Appalachian segment of the breeding range, land managers should consider broader landscape scale habitat associations that occur throughout the full breeding cycle to create full landscapes that most benefit the species. Local landscapes that contain a mosaic of forest age classes within close proximity to Golden-winged Warbler nesting habitat are most likely to provide fledgling Golden-winged Warblers in the Appalachians with appropriate post-fledging habitat. Additionally, my results of Golden-winged Warbler fledgling habitat selection, spanning two markedly different managed forest landscapes, suggests that major variations in post-fledging habitat selection patterns can exist within a relatively small geographic range, depending on landscape context.
Studies aiming to investigate habitat selection in fledgling songbirds should attempt to explore patterns across multiple landscapes to fully characterize habitat associations during this period. Habitat selection variations such as those presented here may help explain population variability trends across a species’ range.
CHAPTER VII

INFLUENCE OF MICRO-SCALE VEGETATION STRUCTURE ON HABITAT SELECTION AND MOVEMENT OF FLEDGLING GOLDEN-WINGED WARBLERS

Synopsis

Some fledgling songbirds and their parents use vegetation conditions during the post-fledging period that differs from those associated with nesting. Further, little information exists regarding the influence of vegetation structure on fledgling movements for many species. The post-fledging period in songbirds often includes high mortality and lasting population impacts. Thus, understanding how the habitat requirements of fledglings differ from nest sites and how these requirements change as juveniles develop is critical for informing conservation strategies for declining species. Understanding what influences fledgling movements can provide greater insight into the relative importance of certain vegetation features within forest stands. Quantifying vegetation features selected by fledglings can help land managers create habitat that not only maximize nest success, but overall breeding season productivity. I studied microhabitat selection and movement of fledgling Golden-winged Warblers \( n = 84 \) during the dependent post-fledging period in two managed forest landscapes in northcentral and northeast Pennsylvania. In addition to using different habitat than nest sites, fledglings also selected for different vegetation features as they aged. Fledglings selected for denser horizontal and vertical cover across all age classes during the dependent post-fledging period (1-6, 7-13, 14-20, 21-28 days post-fledging) regardless of forest stand age. Fledgling movement rate was influenced by basal area, where fledglings moved greater distances in areas with higher basal area (i.e. mature forest). Indicating that fledglings used higher
basal area stands (mature forest) to travel between younger, lower basal area stands. Overall, fledglings from both landscapes moved on average nearly 1 km from nest sites during the tracking period. These results suggest that management for Golden-winged Warblers on the breeding grounds needs to consider the structural elements in the forests surrounding nesting habitat. Management that focuses on creating dense patches of taller vegetation amongst typical Golden-winged Warbler nesting habitat will provide habitat early in the post-fledging period. Further, interspersing areas of dense vegetation throughout mature stands surrounding early-successional nesting habitat should facilitate movement to other regenerating stands and meet the changing habitat requirements of fledgling Golden-winged Warblers as they age.

**Introduction**

Although survival during the post-fledging period can have population limiting impacts on songbirds (Donovan and Thompson 2001, Robinson et al. 2004), the factors implicated in fledgling survival (e.g. habitat use, habitat selection, movement) for many Neotropical migrant fledglings remains largely unstudied (Anders et al. 1998, Vega Rivera et al. 1998). As a result, management strategies for declining songbirds are often based solely on nesting habitat associations (Anders et al. 1998, Cox et al. 2014). In general, the post-fledging period begins upon fledging and ends when juveniles migrate (Small et al. 2015). Parental care continues through the post-fledging period, however diminishes over time (Peterson et al. 2016). In songbirds, the post-fledging stage is characterized by periodic movements to acquire food resources and avoid predation. These two resource needs (food and cover for predator avoidance) are largely reconciled through use of particular cover types, and more specifically, certain vegetation features
within cover types. Researchers have used movement patterns to quantify the relative quality of vegetation structures for young (Jenkins et al. 2017), or resource selection functions with used vs available resource units to determine selection and preference (King et al. 2006). Such studies have helped elucidate changing patterns of habitat selection as juveniles age (Raybuck 2016) and between the nesting and post-fledging period in general (King et al. 2006). Thus, research on habitat selection and movements of young during this period can help land managers create habitat conditions that are required throughout the full-breeding season.

Golden-winged Warblers are relatively well studied across their breeding range (Patton et al. 2010, Confer et al. 2010, Roth et al. 2014, Bakermans et al. 2015, McNeil et al. 2017), yet are in need of additional research regarding the habitat requirements during the post-fledging period, particularly in the Appalachian range (Rosenberg et al. 2016, Streby et al. 2016). One previous study investigating Golden-winged Warbler post-fledging habitat selection was carried out in the western Great Lakes segment of the species range, however this study investigated habitat selection at the stand-level scale (Streby et al. 2016). No previous studies have examined fledgling Golden-winged Warbler habitat selection at the micro-scale anywhere across their range.

I conducted a habitat selection and movement study in Northeast and Northcentral Pennsylvania using radio-telemetry to help fill this knowledge gap in the species breeding season ecology. I tracked 84 radio-tagged fledgling Golden-winged Warblers for approximately 30 days, documenting microhabitat use and movement patterns over five different age classes (days 1-6, 7-13, 14-20, 21-28, 29+). I then compared used and available microhabitat structures at fledgling and random locations.
for each juvenile to evaluate changes in habitat selection over time. I also quantified microhabitat selection within different forest age classes to determine whether fledglings required different structural features when using distinct cover types. To quantify fledgling movement and space-use, I evaluated daily movement and distance moved from nest sites across both study areas. This should help determine the spatial scale that land managers need to consider when managing forest to meet the full reproductive season needs of Golden-winged Warblers. Additionally, I evaluated movements of fledglings in response to microhabitat to further understand the relationship between space-use and habitat. I hypothesized fledglings would use microhabitat that was structurally different from nest sites, and that fledglings would select for different microhabitat features as they aged. However, I expected that fledglings would select for similar microhabitat features within forest stands of different age classes. Finally, I predicted that fledglings would move smaller distances in areas with vegetation structures they selected for and further distances when encountering vegetation features that they selected against.

Methods

Microhabitat Sampling

To determine fledgling microhabitat selection, technicians measured a suite of habitat variables at every location in which I relocated radio-tagged fledglings, at paired available locations and at nest sites. Thus, in addition to nest vegetation measurements, for each fledgling I recorded a used and available set of vegetation data for each day it was tracked. If fledglings remained stationary after tracking, I returned the following day to conduct vegetation surveys. Available points were determined based on daily individual fledgling movement. I calculated distance from the previous day to the current
day for each juvenile. Using this measured distance, I then plotted a point in a randomly
selected direction from the previous day’s location (Fig. 14). This methodology, in which
availability was determined daily, and on an individual basis, accounts for movement
capabilities related to fledgling age and variability in individual condition, which are
known to affect movement capabilities of fledgling songbirds (Vitz and Rodewald 2011,
Cox et al. 2014). For logistic purposes, I plotted all available locations for each bird in
ArcGIS 10.3 (Environmental System Research Institute, Redlands, CA) and conducted
these vegetation surveys after the conclusion of all radio-tracking.

The same vegetation sampling protocol was employed at both used and available
locations. At an 11.3 m radius, I counted the number of snags (standing dead trees >2 m
tall and >10 cm DBH). At a 5 m radius, I estimated average sapling (<10 cm DBH)
height and average shrub (multiple stems >1 m) height. I also quantified vegetation
density using a profile board method (Nudds 1977). The profile board consists of a sheet
containing twenty 20 x 20 cm squares. The board was held at plot center allowing an
observer to record the number of squares >50% visually obstructed by vegetation from a
distance of 5 m. The board was rotated 90° in all four cardinal directions (N, E, S, W) and
the observer’s line of sight was positioned 1 m off the ground. I recorded presence of
different woody regeneration strata (small, medium, large) within 1 m circles at each
location the density board was read (5 m from plot center in each cardinal direction) to
account for heterogeneity in vegetation structure. Small regeneration included any woody
stems <1 m tall, medium regeneration included any woody stems >1 m and <2 m tall, and
large regeneration included any woody stems that were >2 m tall. Additionally, I
recorded estimates of ground cover percentage including woody, forb, Rubus, vine, grass,
litter, and bare at a 1 m radius around plot center. From plot center, I recorded basal area and canopy cover (%) using a 10-factor cruising prism and a spherical densiometer, respectively. Finally, I recorded forest age class (e.g. early-successional, sapling, mature) for each point based on a visual inspection of forest stand structure and later verified these in situ estimates with aerial imagery and forest inventory data.

**Statistical Analyses**

I tested the differences of microhabitat variables (Table 3) within two major cover types (mature forest and early-successional forest) between both study areas using two-tailed Student’s T tests. I assumed microhabitat features were significantly different between the two study areas if p-values were <0.05.

I tested for fledgling habitat selection at the micro-scale with generalized linear mixed models using the package lme4 in program R (Bates et al. 2015, R Core Team 2016). Specifically, I modeled the ability of structural habitat variables to explain the variation between “used” and “available” fledgling locations. Prior to analyses, I scaled all environmental variables and verified that none were overly correlated (Pearson’s Correlation Coefficient <0.7). Juveniles within the same sub-brood were not spatially independent, and inherent variation between study sites may alter micro-scale habitat selection. To account for this, I included sub-brood ID and site ID (DSF or SSF) as random effects in all habitat selection models. To determine which structural variables
Figure 14. Method used to determine fledgling Golden-winged Warbler available locations for micro-scale vegetation surveys. Available locations were the same distance fledglings moved between used points on day \( i \) and day \( i+1 \) however in a random direction from the day \( i \) location.
most strongly influenced fledgling habitat selection across age classes, I created 1 to 3 variable models with all possible combinations of eight variables of interest (Table 3), resulting in a total of 224 models. I ranked models according to AICc score and assumed all models with ΔAICc < 2.00 were equivalent (Burnham and Anderson 2002). To investigate whether fledgling Golden-winged Warblers select for different habitat features as they develop, I modeled habitat selection separately for five age classes which I determined based on breaks in daily fledgling movement data (Fig 10). For top models in all age classes, I assessed the importance of each individual parameter within models and evaluated how those values changed across age classes. Based on directionality, I assumed that parameter estimates (β) with 95% confidence intervals that did not include zero were either selected for or against by fledglings.

I used the same analytical methods as described above to test which microhabitat features fledglings selected for or against within three distinct forested cover types (early successional, sapling, and mature) that were used by fledglings across both study areas. For these models, I analyzed all data within a given cover type regardless of fledgling age. Additionally, I tested whether fledgling Golden-winged Warblers used different microhabitat habitat within early-successional forest than adult Golden-winged Warblers use for nesting. This analysis used identical analytical methods as described above, however, I used only microhabitat data from fledgling locations within early-successional forest and tested the ability of nine variables (Table 4) to explain the differences between “used” vs “nest” locations. Nest models used brood ID as a random effect instead of sub-brood ID because fledglings from the same nest were not considered independent.
I also assessed fledgling space use and the influence of habitat features on fledgling movement rates. I calculated fledgling movement rates (m/day), and distance from nest sites using the haversine formula. I then summarized and compared fledgling movement rate (m/day) and distance from nest across both study areas. Using generalized linear mixed-effect models, I assessed the ability of different microhabitat features to influence movement rate (m/day). Using methods similar to Jenkins et al. (2017), I used movement rate as a response variable and applied eight vegetation measurements as explanatory variables (Table 3). I constructed and selected top models for fledgling movement using the same methods described previously for fledgling habitat selection and applied them to the entire dependent post-fledging period (days 1 to 28). Because fledgling movement ability can change as juveniles develop (Vitz and Rodewald 2010), I used age as a fixed effect in all models. I included a random effect of site (DSF or SSF) because local landscape variability within each study site may influence fledgling movement rate. I ranked models using AIC<sub>c</sub> and considered models with ΔAIC<sub>c</sub> < 2 equivalent (Burnham and Anderson 2002). I assessed parameter estimates (β) of top models for movement rate and assumed estimates with 95% confidence intervals that did not overlap zero influenced fledgling movement (Burnham and Anderson 2002).
Table 3

Vegetation Variables Used in Micro-Scale Habitat Selection Analyses for Golden-Winged Warbler Fledgling Age Classes, Selection Within Specific Cover Types, and Fledgling Movements in Northern Pennsylvania

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 VEG.DNS</td>
<td>Horizontal Vegetation Density (%)</td>
</tr>
<tr>
<td>2 CAN</td>
<td>Vertical Vegetation Density (%)</td>
</tr>
<tr>
<td>3 BA</td>
<td>Basal Area (m²/ha)</td>
</tr>
<tr>
<td>4 SNAG</td>
<td>Snags within 11.3m</td>
</tr>
<tr>
<td>5 SAP</td>
<td>Average Sapling height (m) within 5m</td>
</tr>
<tr>
<td>6 RBUS</td>
<td>Rubus spp. ground cover (%) within 1m</td>
</tr>
<tr>
<td>7 M.RGN</td>
<td>Medium (1-2m) woody regeneration (%)</td>
</tr>
<tr>
<td>8 L.RGN</td>
<td>Large (&gt;2m) woody regeneration (%)</td>
</tr>
</tbody>
</table>
Table 4

*Vegetation Variables Used in Micro-Scale Habitat Selection Analyses Investigating Differences Between Golden-Winged Warbler Nest Sites and Locations Used by Fledglings in Northern Pennsylvania*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 VEG.DNS</td>
<td>Horizontal Vegetation Density (%)</td>
</tr>
<tr>
<td>2 CAN</td>
<td>Vertical Vegetation Density (%)</td>
</tr>
<tr>
<td>3 BA</td>
<td>Basal Area (m²/ha)</td>
</tr>
<tr>
<td>4 SAP</td>
<td>Average Sapling height (m) within 5m</td>
</tr>
<tr>
<td>5 RBUS</td>
<td><em>Rubus</em> spp. ground cover (%) within 1m</td>
</tr>
<tr>
<td>6 GRASS</td>
<td>Grass ground cover (%) within 1m</td>
</tr>
<tr>
<td>7 FORB</td>
<td>Forb ground cover (%) within 1m</td>
</tr>
<tr>
<td>8 M.RGN</td>
<td>Medium (1-2m) woody regeneration (%)</td>
</tr>
<tr>
<td>9 L.RGN</td>
<td>Large (&gt;2m) woody regeneration (%)</td>
</tr>
</tbody>
</table>
Results

I radio-tagged and tracked 84 fledgling Golden-winged Warblers from 69 subbroods from 2014 to 2016. Individual fledglings had 2 to 36 relocations depending on survival and radio-transmitter battery life. Across all three years, I quantified microhabitat at 1693 used and 1693 available locations for a total of 3386 vegetation surveys.

Study Area Microhabitat Comparison

Microhabitat differed in 6 of 8 structural vegetation features of early-successional stands and 4 of 8 structural features of mature stands between DSF and SSF (Table 5). Within early-successional forests of both study areas, all microhabitat variables showed significant differences (e.g. p-value <0.05) except for vertical cover (%) and % large woody regeneration. Within mature forest across both study areas, microhabitat was significantly different. Specifically, basal area (m$^2$/ha) ($p$<0.01), snags ($p$=0.02), vegetation density (%) ($p$<0.01), and large woody regeneration (%) ($p$<0.01) were significantly different.

Microhabitat Selection Across Fledgling Age

Average basal area (m$^2$/ha) used by fledglings ranged between 4 to 10 across fledgling age classes and average basal area at points available to fledglings across age classes ranged from 5 to 13 (Fig. 15). Average used vertical vegetation density (%) ranged from 57.0 to 91.4 across age classes and average vertical vegetation density at available points ranged from 55.7 to 83.4 across age classes. Average used horizontal vegetation density (%) ranged from 63.2 to 78.1 across age classes while horizontal
vegetation density at points available to fledglings ranged from 49.6 to 74.6 across age classes (Fig 15).

During days 1-6 post-fledge, fledglings selected for areas with lower basal area, more medium (1-2m) woody regeneration, and taller saplings ($\beta = -0.23; \beta = 0.29, \beta = 0.24$; Table 6). Fledglings day 7 to 13 post-fledge selected for areas with more horizontal vegetation density and more vertical vegetation density ($\beta = 0.63; \beta = 0.23$). During days 14-20 post-fledge, fledglings selected for areas with more horizontal vegetation density, lower basal area, and higher vertical vegetation density ($\beta = 0.44; \beta = -0.25; \beta = 0.68$). Fledglings day 21 to 28 post-fledge, continued to select for areas with more horizontal vegetation density, lower basal area, and more vertical vegetation density ($\beta = 0.40; \beta = -0.39; \beta = 0.65$). Independent fledglings (day 29+) selected for areas with more horizontal vegetation density, more vertical vegetation density, and more snags ($\beta = 0.62; \beta = 0.49; \beta = 0.35$).

**Microhabitat Selection Within Cover Type and Compared to Nest**

Within early-successional cover, fledglings of all age classes selected for more horizontal vegetation density, more vertical vegetation density, and more Rubus ($\beta = 0.42; \beta = 0.34; \beta = 0.23$; Table 7). Within sapling stands, fledglings of all age classes selected for lower basal area, more vertical vegetation density, and more horizontal vegetation density ($\beta = -0.64; \beta = 2.16; \beta = 0.50$).
Table 5

Comparison of Structural Microhabitat Variables Within Early-Successional and Mature Forest Cover Types Between Delaware State Forest (DSF) and Sproul State Forest (SSF) of Northern Pennsylvania

<table>
<thead>
<tr>
<th></th>
<th>DSF (X̄)</th>
<th>SSF (X̄)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early-successional</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal Area (m²/ha)</td>
<td>4.25</td>
<td>3.26</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Vertical Cover (%)</td>
<td>52.90</td>
<td>55.00</td>
<td>0.37</td>
</tr>
<tr>
<td>Avg. Sap Ht. (m)</td>
<td>2.33</td>
<td>4.44</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Avg. Shrub Ht. (m)</td>
<td>1.62</td>
<td>1.01</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Snags</td>
<td>0.35</td>
<td>0.24</td>
<td>0.03</td>
</tr>
<tr>
<td>Veg. Density (%)</td>
<td>71.30</td>
<td>76.80</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Med. Woody Regen. (%)</td>
<td>60.40</td>
<td>33.90</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Lg. Woody Regen (%)</td>
<td>42.50</td>
<td>41.60</td>
<td>0.76</td>
</tr>
<tr>
<td>Mature</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal Area (m²/ha)</td>
<td>17.40</td>
<td>19.04</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Vertical Cover (%)</td>
<td>94.00</td>
<td>85.90</td>
<td>0.11</td>
</tr>
<tr>
<td>Avg. Sap Ht. (m)</td>
<td>4.56</td>
<td>4.53</td>
<td>0.92</td>
</tr>
<tr>
<td>Avg. Shrub Ht. (m)</td>
<td>1.80</td>
<td>1.62</td>
<td>0.18</td>
</tr>
<tr>
<td>Snags</td>
<td>2.62</td>
<td>1.96</td>
<td>0.02</td>
</tr>
<tr>
<td>Veg. Density (%)</td>
<td>37.71</td>
<td>54.70</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Med. Woody Regen. (%)</td>
<td>37.12</td>
<td>40.89</td>
<td>0.36</td>
</tr>
<tr>
<td>Lg. Woody Regen (%)</td>
<td>42.63</td>
<td>29.88</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

*Note.* P-values were derived from two-tailed t-tests. Vegetation data were collected during June and July 2014-16.
Figure 15. Mean values of habitat variables included in the top-ranked microhabitat models at used and available fledgling locations across four fledgling age classes (1-6, 7-13, 14-20, and 21-28 days post-fledge). Solid lines represent fledgling values. Dashed lines indicate available values. Error bars represent standard error of the mean.
Table 6

*Candidate Micro-Scale Model Set of Habitat Selection by Fledgling Golden-Winged Warblers Across Five Age Classes in Delaware State Forest and Sproul State Forest of Northern Pennsylvania*

<table>
<thead>
<tr>
<th>Day</th>
<th>Model</th>
<th>K</th>
<th>ΔAIC_c</th>
<th>$w_i$</th>
<th>Variable</th>
<th>β</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day 1-6</td>
<td>BA+M.RGN+SAP</td>
<td>6</td>
<td>0.00</td>
<td>0.57</td>
<td>M.RGN</td>
<td>0.29</td>
<td>0.14 to 0.45</td>
</tr>
<tr>
<td></td>
<td>RBUS+M.RGN+SAP</td>
<td>6</td>
<td>0.58</td>
<td>0.43</td>
<td>SAP</td>
<td>0.24</td>
<td>0.08 to 0.39</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>3</td>
<td>22.13</td>
<td>0.00</td>
<td>BA</td>
<td>-0.23</td>
<td>-0.39 to -0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>RBUS</td>
<td>0.22</td>
<td>0.06 to 0.39</td>
</tr>
<tr>
<td>Day 7-13</td>
<td>VEG.DNS+CAN</td>
<td>5</td>
<td>0.00</td>
<td>1.00</td>
<td>VEG.DNS</td>
<td>0.63</td>
<td>0.48 to 0.79</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>3</td>
<td>82.50</td>
<td>0.00</td>
<td>CAN</td>
<td>0.23</td>
<td>0.09 to 0.37</td>
</tr>
<tr>
<td>Day 14-20</td>
<td>VEG.DNS+BA+CAN</td>
<td>6</td>
<td>0.00</td>
<td>0.59</td>
<td>CAN</td>
<td>0.68</td>
<td>0.51 to 0.86</td>
</tr>
<tr>
<td></td>
<td>VEG.DNS+CAN+RBUS</td>
<td>6</td>
<td>0.76</td>
<td>0.41</td>
<td>VEG.DNS</td>
<td>0.44</td>
<td>0.28 to 0.61</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>3</td>
<td>108.10</td>
<td>0.00</td>
<td>BA</td>
<td>-0.25</td>
<td>-0.43 to -0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>RBUS</td>
<td>0.24</td>
<td>0.06 to 0.43</td>
</tr>
<tr>
<td>Day 21-28</td>
<td>VEG.DNS+BA+CAN</td>
<td>6</td>
<td>0.00</td>
<td>1.00</td>
<td>CAN</td>
<td>0.65</td>
<td>0.46 to 0.85</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>3</td>
<td>81.20</td>
<td>0.00</td>
<td>VEG.DNS</td>
<td>0.40</td>
<td>0.21 to 0.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>BA</td>
<td>-0.39</td>
<td>-0.59 to -0.20</td>
</tr>
<tr>
<td>Day 29+ (Ind)</td>
<td>VEG.DNS+CAN+SNAG</td>
<td>6</td>
<td>0</td>
<td>1.00</td>
<td>VEG.DNS</td>
<td>0.62</td>
<td>0.31 to 0.95</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>3</td>
<td>17.70</td>
<td>0.00</td>
<td>CAN</td>
<td>0.49</td>
<td>0.16 to 0.86</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SNAG</td>
<td>0.35</td>
<td>0.03 to 0.72</td>
</tr>
</tbody>
</table>
**Table 7**

*Candidate Model Set of Microhabitat Selection by Fledgling Golden-winged Warblers Within Three Major Cover Types in Delaware State Forest and Sprout State Forest of Northern Pennsylvania, Between Nest Sites and Sites Used by Fledglings in Early-Successional Forest, and for Explaining Juvenile Movement Rates*

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
<th>Variable</th>
<th>β</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early-Succ.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VEG.DNS+CAN+RBUS</td>
<td>6</td>
<td>0.00</td>
<td>0.51</td>
<td>VEG.DNS</td>
<td>0.42</td>
<td>0.28 to 0.56</td>
</tr>
<tr>
<td>CAN+RBUS+M.RGN</td>
<td>6</td>
<td>0.08</td>
<td>0.49</td>
<td>CAN</td>
<td>0.34</td>
<td>0.24 to 0.44</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>137.10</td>
<td>0.00</td>
<td>RBUS</td>
<td>0.23</td>
<td>0.13 to 0.33</td>
</tr>
<tr>
<td>M.RGN</td>
<td>5</td>
<td>0.32</td>
<td>0.21 to 0.43</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Sapling</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BA+CAN+VEG.DNS</td>
<td>6</td>
<td>0.00</td>
<td>1.00</td>
<td>CAN</td>
<td>2.16</td>
<td>1.08 to 3.53</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>24.50</td>
<td>0.00</td>
<td>BA</td>
<td>-0.64</td>
<td>-1.17 to -0.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mature</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VEG.DNS+BA+SAP</td>
<td>6</td>
<td>0.00</td>
<td>0.69</td>
<td>VEG.DNS</td>
<td>0.57</td>
<td>0.39 to 0.75</td>
</tr>
<tr>
<td>VEG.DNS+SAP</td>
<td>5</td>
<td>1.63</td>
<td>0.31</td>
<td>SAP</td>
<td>0.21</td>
<td>0.08 to 0.35</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>54.60</td>
<td>0.00</td>
<td>BA</td>
<td>-0.17</td>
<td>-0.34 to 0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Nest Vs. Fldg.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CAN+SAP+GRSS</td>
<td>6</td>
<td>0.00</td>
<td>0.36</td>
<td>CAN</td>
<td>0.63</td>
<td>0.27 to 1.01</td>
</tr>
<tr>
<td>CAN+GRSS+L.RGN</td>
<td>6</td>
<td>0.87</td>
<td>0.24</td>
<td>GRSS</td>
<td>-0.42</td>
<td>-0.61 to -0.25</td>
</tr>
<tr>
<td>CAN+GRSS+BA</td>
<td>6</td>
<td>0.88</td>
<td>0.24</td>
<td>SAP</td>
<td>0.79</td>
<td>0.17 to 1.47</td>
</tr>
<tr>
<td>CAN+GRSS+FORB</td>
<td>6</td>
<td>1.58</td>
<td>0.17</td>
<td>L.RGN</td>
<td>-0.02</td>
<td>-0.03 to 0.00</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>39.19</td>
<td>0.00</td>
<td>BA</td>
<td>-0.95</td>
<td>-1.68 to -0.17</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Distance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AGE+BA</td>
<td>5</td>
<td>0.00</td>
<td>1.00</td>
<td>AGE</td>
<td>0.43</td>
<td>0.40 to 0.47</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>588.01</td>
<td>0.00</td>
<td>BA</td>
<td>0.12</td>
<td>0.08 to 0.15</td>
</tr>
</tbody>
</table>
Within mature forest cover, fledglings selected for more horizontal vegetation density, lower basal area, and taller saplings ($\beta = 0.57; \beta = -0.17; \beta = 0.21$). Compared to nest sites, the best supported model suggested that fledglings selected areas of early-successional forest with more vertical cover, taller saplings, and less grass cover ($\beta = 0.63; \beta = 0.79; \beta = -0.42$; Table 7).

**Fledgling Movement**

Fledglings in both DSF and SSF showed similar movement and space use patterns. Across both study areas fledglings generally moved at higher rates as they aged and moved further from the nest site as they aged (Fig. 16). Fledgling daily movement rate did however decrease in SSF from days 21 to 28 post-fledge, but increased rapidly again during the independent post-fledging period (29+ days post-fledge). Daily movement rate was higher in SSF during the first 20 days of the post-fledging period than in DSF, however was lower than DSF for the remainder of the post-fledging period. Space-use, as determined by maximum distance from the nest site, was equivalent in both study areas. Average maximum distance from the nest in SSF ($n=24$) was $973 \pm 396 \text{ m}$ (which occurred during days 21 to 28). Average maximum distance from the nest in DSF ($n=45$) was $909 \pm 145 \text{ m}$ (which occurred during days 29+). According to $\text{AIC}_c$ ranking, fledgling movement rates were best explained by basal area (Fig. 17). My top model suggested that fledglings moved further in response to higher levels of basal area when considering fledgling age as a fixed effect ($\beta = 0.12$; Table 7).
Figure 16. A) Average movement rate (m/day) and B) maximum distance moved from nest site for 69 Golden-winged Warbler sub-broods from 2014 to 2016 in DSF (n=45 sub-broods) and SSF (n=25 sub-broods). Error bars represent standard error of the mean.
Figure 17. The relationship between movement rate of Golden-winged Warbler fledglings and basal area across both DSF and SSF. Relationship is based off the top ranked model of fledgling movement and accounts for fledgling age as a fixed effect. Light gray lines indicate the 95% confidence interval.
**Discussion**

Several recent studies of songbird post-fledging habitat selection have suggested that habitat shifts, in terms of micro-scale vegetation structure, occur between the nesting and post-fledging period. (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006, Rush and Stutchbury 2008). My results indicate a similar trend occurring with Golden-winged Warbler fledglings in the Appalachian portion of their range. Not only did I find that fledgling Golden-winged Warblers select portions of early-successional forest that are structurally different from nest sites, but I also provide evidence that Golden-winged Warbler fledglings select for different vegetation structures as they age. Features selected for at the micro-scale vary within different forest age classes as well, including early-successional forest, sapling forest, and mature forest. Finally, I provide evidence that fledgling Golden-winged Warbler movement is influenced by basal area.

Within early-successional forest, fledgling Golden-winged Warblers selected for greater vertical vegetation density, taller saplings and less grass compared to nest sites. This finding clearly indicates that fledglings require different habitat features than those indicated in the species breeding grounds conservation plan, which is structured around creating nesting habitat (Roth et al. 2012). The conservation plan highlights the importance of grass, forb, and *Rubus* cover for Golden-winged Warbler nesting habitat (Roth et al. 2012). However, I frequently relocated fledglings in ≥2m sapling dominated patches (e.g. *Betula* spp., *Populus* spp., *Quercus* spp., *Acer* spp.) or within tall (>1.5m) regenerating stump suckers (e.g. *Acer* spp.) of early-successional stands with relatively little herbaceous ground cover. These areas were often interspersed amongst the grass and herbaceously dominated trails and openings which provide Golden-winged Warbler
nesting habitat. The disparity between nesting and post-fledging habitat I observed is likely a result of the use of different forest strata during the two life history phases. Grass and forb cover serves to protect and conceal Golden-winged Warbler nests from predators (Confer et al. 2003, Aldinger et al. 2015, Terhune et al. 2016 McNeil et al. 2017). While taller regeneration conceals fledgling Golden-winged Warblers as they begin to move in search of food.

Fledglings day 1 to 6 post-fledge selected for different vegetation features than older fledglings, which selected for similar vegetation structures through day 28 post-fledge. Day 1 to 6 post-fledging was characterized by the selection of lower basal area, more medium regeneration and taller saplings. Similar to the disparity between fledgling locations and nest sites, locations selected by day 1 to 6 post-fledge juveniles likely conferred protective qualities. The selection for these vegetation structures indicates the preference for some of the most structurally complex patches available, with both high levels of 1-2m woody growth and taller saplings compared to random locations. Fledglings from day 7 to day 28 post-fledge selected for more vertical vegetation density and more horizontal density. Thus, regardless of cover type, fledglings chose locations that maximized vegetation density. Additionally, fledglings 14 to 28 days post-fledge selected for areas of lower basal area than available. Avoidance of higher basal area locations throughout much of the post-fledging period is not surprising, in the context of previous post-fledging studies, as this would indicate a preference for more mature stands which often host lower prey abundance (Streby et al. 2011) and lack the understory complexity (C. Fiss, pers. obs.) desired by fledgling Golden-winged Warblers at this age.
Lower basal area stands likely supports denser and faster understory regeneration across more of a stand, for which fledglings selected across all age classes. Indeed, I frequently observed radio-tagged Golden-winged Warbler fledglings in the understory, even when using mature forest. Dense understory vegetation including tall saplings and greater medium (1-2m) woody regeneration may provide several benefits to fledglings. It is possible that denser vegetation provides fledglings with greater protective cover from predators. For example, both King et al. (2006) and Vitz and Rodewald (2011) have indicated that vegetation density increases fledgling survival in Ovenbirds. Others have suggested that dense vegetation provides more invertebrate prey items (Streby et al. 2011) or thermoregulatory properties (DeWoskin 1980). Post-fledging studies on Wood Thrush (Hylocichla mustelina) have indicated preferences for similar vegetation features (Anders et al. 1998, Vega Rivera et al. 1998). Similar to habitat use I observed in fledgling Golden-winged Warblers, juvenile Wood Thrush selected for dense understory vegetation including Rubus and saplings in Virginia (Vega Rivera et al. 1998), and in southern Missouri (Anders et al. 1998). Regardless of factors driving fledglings to use these vegetation structures, juvenile songbirds, including Golden-winged Warblers in the Appalachians, clearly rely on these features to survive and gather resources necessary for migration.

Fledgling Golden-winged Warblers in my study also selected for unique vegetation structures when using different cover types. For example, although horizontal vegetation density was selected for across all cover types, Rubus was important only when fledglings used early-successional forest. Vertical vegetation density was important in both sapling and early-successional stands, but not in mature stands – where taller
saplings were important. Finally, in both sapling and mature stands, lower basal area was selected. Selection for *Rubus* by fledgling Golden-winged Warblers in early-successional stands suggests the importance of this vegetation feature throughout the full Golden-winged Warbler breeding cycle. For instance, *Rubus* has been shown to influence probability of territory occupancy in male Golden-winged Warblers (Luenberger et al. 2017) and daily survival rate of nests (McNeil et al. 2017). It’s likely that *Rubus* thickets provide protection from predators as well as a food source for fledglings. Adult Golden-winged Warblers selectively forage on *Rubus* in the Appalachians (Bellush et al. 2016), and it is a common invertebrate host plant in the Great Lakes (Streby et al. 2011).

Selection for lower basal area in sapling and mature stands suggests that fledglings selected portions of these stands that had experienced disturbance, promoting both dense horizontal and vertical vegetation cover. Other researchers have revealed similar findings (Vega Rivera et al. 1998, Rush and Stutchbury 2008). Vega Rivera et al. (1998) indicated that Wood Thrush fledglings used portions of mature forest with dense understory growth where Gypsy Moth (*Lymantria dispar*) mortality had occurred. Rush and Stutchbury (2008), found that fledgling Hooded Warblers (*Wilsonia citrina*) used areas more structurally complex than nest sites. Generally, in mature stands fledgling Golden-winged Warblers seem to select microhabitat features that resemble sapling stands, including taller saplings and lower basal area. Selection for sapling dominated stands in the Appalachian segment is apparent on the landscape scale as well for older fledglings (i.e. >20 days post-fledging, Fiss chpt. 6). These selection preferences are important as they indicate structures within specific stands that forest managers should consider when managing habitat for fledgling Golden-winged Warblers. Because fledgling Golden-
winged Warblers of the same age often inhabit different cover types, selection preferences among juvenile age classes may not indicate selection for true habitat features, but rather overall trends across all cover types. Thus, selection for structures within a given cover type should provide land managers a clearer picture of fledgling habitat preferences.

Fledgling Golden-winged Warblers could benefit from future research that investigates the ecological mechanisms driving habitat selection in both the Appalachians and Great Lakes portion of their ranges. It is likely that predator communities, prey availability, or even other ecological phenomena (e.g. mixed flocking) play an important role in determining what habitat Golden-winged Warbler fledglings select or avoid. Knowing why certain habitat decisions are made can provide better understanding of the broader habitat needs of fledglings, and perhaps help land managers create habitat for fledglings where predator, prey, and avian communities are drastically different. Additionally, future research should investigate factors influencing Golden-winged Warbler fledgling survival in the Appalachian range. It is possible that fledglings could be selecting habitat that is detrimental to survival, resulting in an ecological trap (Streby and Anderson 2013). Overall, my results suggest that management efforts for Golden-winged Warblers in the Appalachian portion of their range should consider aspects beyond what adults require for nesting. Although some of the features needed for nesting (e.g. Rubus) are important for very young fledglings (i.e. 1 to 6 days post-fledge), dense areas of woody regeneration not typically used for nesting are highly sought after across all age classes. Ensuring the availability of areas with more advanced regeneration within early-successional stands should allow for a more complete breeding season landscape.
Additionally, management efforts could further benefit fledgling Golden-winged Warblers by creating areas of lower basal area, increased vertical and horizontal vegetation density, and taller saplings within mature and sapling dominated stands proximate to nesting habitat. Both fledgling movement and habitat selection data across age classes and cover types suggests that lower basal area patches throughout the landscape are important for fledgling Golden-winged Warblers. In a landscape where higher basal area is prevalent in the surrounding matrix, fledglings move more rapidly and select lower basal area and microhabitat features consistent with lower basal area.
CHAPTER VIII
CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Given recent population trends, Golden-winged Warblers face a precarious future in the Appalachian segment of their breeding distribution (Sauer et al. 2017). This species faces considerable management challenges brought about by factors ranging from hybridization to nesting habitat loss (Buehler et al. 2007, Rosenberg et al. 2016). One such factor that has only relatively recently been considered, is habitat required during the post-fledging period (Cox et al. 2014, Streby et al. 2016). Considering the drastically contrasting population trends between the disjunct breeding distributions, yet relatively stable nesting success range wide, post-fledging habitat may play an important role in population recovery.

My research suggests that land managers in the Appalachians can take several measures to create habitat for Golden-winged Warblers during the post-fledging period and, in turn, benefit a rapidly declining population of an imperiled songbird. My results indicate that current management for Golden-winged Warblers on the breeding grounds is not considering full breeding cycle habitat components. I found that Golden-winged Warbler fledglings use different microhabitat features and different landscape scale habitat than what adult Golden-winged Warblers are currently known to use on the breeding grounds in the Appalachian segment of their range.

At the landscape scale, fledglings displayed different habitat selection patterns depending on the context of the surrounding landscape. In one landscape, DSF, stand level structural variability was high and fledglings selected for an assortment of habitat types, but when structural variability was low (as in SSF), fledglings selected exclusively
for early-successional forest. However, when considered with microhabitat selection results, fledglings made similar choices in both DSF and SSF. In DSF fledglings eventually moved out of early-successional habitat into a variety of cover types but selected weakly for mature forest and eventually selected for sapling aged forest. Although this pattern was not repeated in SSF, fledglings did indeed select microhabitat consistent with sapling aged stands across both study areas. Thus, fledglings in SSF selected only for early-successional forest at the landscape scale, but microhabitat selection suggests that they preferred areas of early-successional forest with advanced regeneration (e.g. taller saplings), with structure resembling sapling aged stands. As such, I recommend that land managers maximize forest stand structural heterogeneity on the landscape peripheral (within 1.5km) to Golden-winged Warbler nesting habitat patches. This increased heterogeneity will provide early-successional stands, and later sapling aged stands that Golden-winged Warblers in the Appalachians select for throughout the dependent post-fledging period. This management recommendation will likely benefit a suite of additional imperiled avian species including Wood Thrush, Ovenbird, and Scarlet Tanager (Piranga olivacea), who are also known to use a variety of cover types to fulfill their breeding cycle (Marshall et al. 2003, Vitz and Rodewald 2006).

Golden-winged Warbler fledglings selected for early-successional forest at the landscape scale in both DSF and SSF throughout the first 14 days of the post-fledging period. Although early-successional forest is already being managed for nesting Golden-winged Warblers in the Appalachians, managers can create these stands with the post-fledging period in mind as well. For instance, it is known that Rubus cover, forb cover, and grass cover are important for nest sites (Aldinger et al. 2015, Terhune et al. 2016,
Mcneil et al. 2017), but taller saplings and greater vertical vegetation density was selected by fledglings. Further, across most fledgling age classes, regardless of cover type, fledglings selected for increased horizontal vegetation density, increased vertical vegetation density, and often lower basal area. Together these features represent very dense patches of advanced regeneration (Fig. 18). Land managers can seek to carry these features of mature forest over to early-successional nesting stands using variable retention harvest methods like life-boating. (Franklin et al. 1997).

In the Great Lakes segment of the Golden-winged Warbler’s breeding range, fledglings selected mature forest over all other cover types during the post-fledging period (Streby et al. 2016). Although mature forest does not appear to play as important a role in the Appalachians during this period, juveniles in a structurally diverse forest landscape exhibited weak selection for mature forest between days 7 to 20 post-fledging. However, movement models indicate rapid movement in response to higher basal area (i.e. mature forest). This could indicate that fledglings use mature forest to travel between patches of early-successional and sapling stands. My cover type specific microhabitat models suggest that fledglings using mature forest selected for areas with greater horizontal vegetation density, taller saplings, and lower basal area. In other words, fledglings selected areas of mature forest with canopy openings resulting in advanced understory regeneration. These features are often naturally created through normal ecological processes in healthy mature forest (Franklin et al. 2002). However, across extensive portions of the Appalachian segment of the Golden-winged Warbler’s breeding distribution, mature forest is degraded due to deer over browsing (Marquis and Brenneman 1981, Baiser et al. 2008) and nonnative forest pest outbreaks (Shifley et al. 2002).
Land managers should select landscapes with healthy mature forest within which to manage for Golden-winged Warbler nesting and post-fledging habitat. If factors degrading mature forest (e.g. deer browse, pest outbreaks) cannot be easily mitigated or avoided on the landscape, it should not impede the creation of young forest, as this is already underrepresented on the landscape (Shifley et al. 2014).

Like several previous post-fledging studies (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006) I found that fledgling Golden-winged Warblers select for different habitat than adults use for nesting. Past Golden-winged Warbler fledgling research in the Great Lakes has indicated this trend on the landscape scale as well (Streby et al. 2016). Unlike Streby et al. (2016), fledglings in the Appalachians did not select for mature forest over other forest cover types throughout the post-fledging period. These differences may be a result of different forest community types, different forest management strategies, or other undetected differences between the Great Lakes and Appalachian breeding segments. Fledglings in my study relied on early-successional forest cover early in the post-fledging period (day 1-20) in both landscapes, and selected sapling stands over everything else later in the post-fledging period (day 21-28 post-fledge) in one landscape. Within early-successional forest cover, fledglings selected for structural features indicative of more advanced regeneration than Golden-winged Warbler adults use for nesting. Overall these findings suggest a need for forest managers to create landscapes in the Appalachians with a mosaic of forested cover types within proximity of Golden-winged Warbler nesting stands. This could be achieved through rotational harvest.
Appalachian forest landscapes with both stand level diversity and within stand structural complexity of regenerating vegetation, should provide habitat for Golden-winged Warblers during the post-fledging period.
Figure 18. Examples of fledgling Golden-winged Warbler microhabitat in the central Appalachians of northern Pennsylvania. A) Patch of advanced regeneration consisting of taller (~3m) saplings and dense vegetation within a Golden-winged Warbler nesting stand. B) Older overstory removal dominated by saplings (~3-5m). C) Mature forest with disturbed canopy and significant understory woody regeneration.
References


Edwards, G. (1760). *Gleanings of natural history, exhibiting figures of quadrupeds, birds, insects, plants, &c: Most of which have not, till now, been either figured or described. With descriptions of seventy different subjects, designed, engraved, and coloured after nature, on fifty copper-plate prints.* Printed for the author, at the Royal College of Physicians, in Warwick-Lane.


Appendix A

Information for Golden-winged Warbler fledglings radio-tagged in Pennsylvania from 2014 to 2016 including year of study, radio-frequency, study area, study site, date radio-tagged, and the number of relocations recorded.

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