RESEARCH ARTICLE

Post-fledging Golden-winged Warblers require forests with multiple stand developmental stages

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ABSTRACT
Our understanding of songbird habitat needs during the breeding season stems largely from studies of nest success. However, growing evidence shows that nesting habitat and post-fledging habitat often differ. Management guidelines for declining species need to be reevaluated and updated to account for habitat shifts that may occur across the full breeding cycle. The Golden-winged Warbler (*Vermivora chrysoptera*) is a declining songbird species for which best management practices (BMPs) are based overwhelmingly on nesting habitat. We studied stand-scale habitat selection by fledgling Golden-winged Warblers during May–July, 2014–2017, in 2 landscapes (2 yr of data for each landscape), 200 km apart in Pennsylvania. Across 4 yr, we radio-tagged and tracked 156 fledglings. We used discrete-choice models to evaluate habitat selection during 2 post-fledging time periods (days 1–5, days 6–28). Fledglings used a variety of cover types, but most telemetry relocations (i.e. 85%) occurred in forest in the stand initiation stage, stem exclusion stage, or mature forest upland. Fledglings primarily selected stand initiation forest during the first 5 days, but preferred habitats differed between regions during days 6–28 post-fledging. Fledglings in one landscape favored stands in the stem exclusion stage while fledglings in the other landscape continued to select stands in the initiation stage. Fledglings moved greater distances as they aged and dispersed ~750 m by day 28 post-fledging. These findings suggest the need to update Golden-winged Warbler BMPs to account for the broader habitat needs of fledglings during the breeding season. In addition, these results indicate that regional studies of habitat requirements can help guide management of dynamic forest landscapes for birds.

Keywords: discrete-choice, forest management, Golden-winged Warbler, habitat selection, movement, post-fledging

LAY SUMMARY
- Little is known about the post-fledging ecology and habitat requirements of many migratory songbirds.
- We used VHF radio-transmitters to track 156 fledgling Golden-winged Warblers (*Vermivora chrysoptera*) from two subpopulations in Pennsylvania, USA, and describe their movements, habitat use, and habitat selection.
- On average fledglings dispersed ~750 m from nest sites by day 28 post-fledging with the maximum dispersal distance being 3.6 km.
- Fledglings used all cover types but 85% of relocations occurred in stand initiation, stem exclusion, or mature forest uplands.
- Habitat selection was directed primarily toward forest in the stand initiation stage, however fledglings in one landscape also selected for stem exclusion stands.
- Managers should consider promoting additional forest stand age class diversity (especially forest in the stem exclusion stage) in areas proximate to Golden-winged Warbler nesting habitat to provide the structure necessary for fledglings.

Los individuos post-emplumamiento de *Vermivora chrysoptera* requieren bosques con rodales en múltiples estadios de desarrollo

RESUMEN
Nuestro entendimiento de las necesidades de hábitat de las aves canoras durante la estación reproductiva surge en gran medida de estudios del éxito del nido. Sin embargo, hay evidencia creciente que sugiere que el hábitat de anidación y el

hábitat post-emplumamiento usualmente difieren entre sí. Las recomendaciones de manejo para las especies en disminución necesitan ser reevaluadas y actualizadas para tener en cuenta los cambios de hábitat que pueden ocurrir a través de todo el ciclo reproductivo. *Vermivora chrysoptera* es una especie de ave canora en disminución para la cual las mejores prácticas de manejo se basan principalmente en el hábitat de anidación. Estudiamos la selección de hábitat a escala de rodal por parte de los volantones de *V. chrysoptera* durante mayo a julio de 2014–2017, en dos paisajes (2 años de datos para cada paisaje) separados por 200 km en Pensilvania. Durante cuatro años, marcamos con radio y seguimos 156 volantones. Usamos modelos de elección discretos para evaluar la selección de hábitat durante dos periodos de tiempo posteriores al emplumamiento (días 1–5, días 6–28). Los volantones usaron una variedad de tipos de cobertura, pero la mayoría de las relocalizaciones de telemetría (i.e. 85%) se registraron en bosques con rodales en la etapa de inicio, en la etapa de exclusión de tallos o en tierras altas de bosque maduro. Los volantones seleccionaron principalmente bosque con rodales de inicio durante los primeros cinco días, pero los hábitats preferidos difirieron entre regiones durante los días post-emplumamiento 6 a 28. Los volantones en un paisaje favorecieron rodales en la etapa de exclusión de tallos, mientras que los volantones en el otro paisaje continuaron seleccionado rodales en la etapa de inicio. Los volantones se movieron distancias mayores a medida que crecieron y se dispersaron ~750 m al día 28 de post-emplumamiento. Estos hallazgos sugieren la necesidad de actualizar las mejores prácticas de manejo para *V. chrysoptera* para tener en cuenta las necesidades más amplias de hábitat de los volantones durante la estación reproductiva. Adicionalmente, estos resultados indican que los estudios regionales de requerimiento de hábitat pueden ayudar a guiar el manejo de paisajes forestales dinámicos para las aves.

Palabras clave: elección discreta, manejo de bosque, movimiento, post-emplumamiento, selección de hábitat, *Vermivora chrysoptera*

INTRODUCTION

Understanding factors that limit reproduction is critical for effective wildlife conservation (Norris 2004). For most songbirds, reproductive success is typically evaluated using the proportion of nests that fledge young as a proxy for productivity (Faaborg et al. 2010, Marra et al. 2015). While vital to our understanding of breeding season ecology, nest-focused studies do not provide a complete picture of reproductive success because they fail to address the "population bottleneck" that often occurs during the post-fledging period (Cox et al. 2014, Jones et al. 2017). Immediately following the nesting cycle, many fledgling songbirds experience ~1 mo under parental care in which they remain vulnerable to predation (i.e. the post-fledging period; Pagen et al. 2000, Yackel Adams et al. 2006). In fact, the post-fledging period in songbirds has been identified as an important driver of population dynamics in that population growth rates may be highly sensitive to fledgling survival (Robinson et al. 2004). While nesting habitat requirements are well studied for many songbirds, our understanding of post-fledging habitat needs remains limited for most species.

Early studies of habitat use during the post-fledging period relied on color-banding individuals and attempting to follow their movements for as many days as possible, often in the vicinity of the nest (Nolan 1978, Weise and Meyer 1979). More recent studies, using radio-transmitter technology, revealed that habitat shifts between nesting and post-fledging periods are relatively common among songbirds (Naef-Daenzer and Gruebler 2016). Such habitat shifts are understood to be critical for fledgling survival as birds seek habitats with reduced predation pressure or high-quality foraging opportunities (Cox et al. 2014). Moreover, researchers are increasingly aware that post-fledging habitat selection patterns are dynamic for some species in that habitat preferences may change over the course of a few days (Jenkins et al. 2017, Raybuck et al. 2020). Less recognized is that post-fledging habitat preferences can vary among regions for a single species. For example, fledgling Ovenbirds (*Seiurus aurocapilla*) in Minnesota selected strongly for sapling-dominated clearcuts (Streby and Andersen 2013), but the same species avoided regenerating forest and, instead, selected for mature hardwood stands in New Hampshire (King et al. 2006). The potentially enormous demographic consequences of post-fledging habitat selection make it imperative that researchers quantify habitat features required by fledglings and the extent to which those needs vary regionally.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Nearctic–Neotropical migratory songbird that has undergone steady population declines for over a half century (Rosenberg et al. 2016). On the breeding grounds, the species occurs in 2 disjunct regions including a larger population in the Great Lakes and a smaller Appalachian Mountains population (Rosenberg et al. 2016). In contrast to the relatively stable Great Lakes population (–0.89% yr^{-1}), the Appalachian population is experiencing a rapid decline (–8.56% yr^{-1}; Sauer et al. 2017). In recent decades, the Golden-winged Warbler has increasingly become the focus of conservation efforts aimed at stemming population declines. These efforts largely focused on understanding the habitat factors affecting nest success, and these formed the basis of best management practices (BMPs) for the species (Bakermans et al. 2011, Roth et al. 2012). The Golden-winged Warbler BMPs have since been extensively implemented on public and private lands (Aldinger et al. 2015, Lutter et al. 2019, McNeil et al. 2020). However, the BMPs' focus on nesting habitat could overlook important habitat needs during

the post-fledging period. In recent years, post-fledging habitat selection of Golden-winged Warblers has been studied in the Great Lakes region (Peterson et al. 2016, Streby et al. 2016), but to a much lesser extent in the Appalachians (Lehman 2017). Stark regional differences in topography between the Appalachian Mountains region and the lower-elevation Great Lakes, in addition to a shift in forest type from aspen-birch communities in the Great Lakes to mixed-oak communities in the Appalachians, suggest that additional post-fledging studies of Golden-winged Warblers are warranted in the Appalachians to better understand habitat requirements in the region and to evaluate the existing BMPs' applicability to this life stage (Roth et al. 2012, Rohrbaugh et al. 2016).

We studied post-fledging habitat selection of Golden-winged Warblers within 2 geographically and demographically distinct subpopulations in Pennsylvania. One subpopulation in northeast Pennsylvania has exhibited high reproductive output (nest success and fledgling survival) and generally stable demography similar to that experienced by Golden-winged Warblers in the western Great Lakes region (McNeil et al. 2020). However, our other study subpopulation in north-central Pennsylvania has low reproductive output and is more representative of Golden-winged Warbler populations throughout much of the Appalachians (McNeil et al. 2020). Our study had 2 objectives: (1) describe and compare space use, movement, and stand-scale habitat selection by fledgling Golden-winged Warblers between 2 demographically distinct Appalachian populations; and (2) provide habitat recommendations to inform BMPs in the Appalachian region.

METHODS

Study Area
From 2014 to 2015, we collected data in the Pocono Mountains (Pike and Monroe Counties) of northeastern Pennsylvania (PA; hereafter NE; Figure 1) where Golden-winged Warblers historically have occurred at their highest population densities within the state (Larkin and Bakermans 2012). From 2016 to 2017, we collected data within north-central PA (Centre and Clinton counties; hereafter NC). Forests in both study areas are characterized by the broad-leaved oak-hickory community (Fike 1999) where stands are dominated by an overstory of oak (*Quercus* spp.) or hickory (*Carya* spp.) with other hardwood species interspersed (e.g., red maple [*Acer rubrum*]), and an ericaceous understory. These forests are overwhelmingly second-growth with relatively long harvest rotations (80–100 yr; Nowacki and Abrams 1992). The primary difference between our study areas was the abundance of wetlands in the NE and the absence/rarity of similar wetlands in the

NC. Shrub and sapling species composition varied in early-successional stands between the NE and NC; however, all stands contained blackberry (*Rubus* spp.) thickets, sedges (e.g., *Carex pennsylvanica*), and broadleaf herbaceous vegetation like goldenrods (*Solidago* spp., *Euthamia* spp.), whorled loosestrife (*Lysimachia quadrifolia*), and ferns (e.g., *Pteridium aquilinum*, *Dennstaedtia punctilobula*).

Our NE study area encompassed a ~20 km radius in the Delaware State Forest. Dominant land cover within this study area included broad-leaved forest (75%), emergent wetlands (8%), and low-intensity developed (12%). Elevation ranged from 300 to 600 m above sea level. We studied fledglings from 6 discrete nesting habitat sites, all of which were the result of recent (2–12 yr post-harvest) timber harvests ranging in size from 7 to 63 ha. These regenerating timber stands were composed of a variety of sapling species including oaks, red maple, aspen (*Populus* spp.), black cherry (*Prunus serotina*), black birch (*Betula lenta*), hickories, and occasional pines (*Pinus rigida*, *P. strobus*). These stands also had well-established shrub layers dominated by scrub oak (*Q. ilicifolia*), lowbush blueberry (*Vaccinium angustifolium*), and hillside blueberry (*V. pallidum*). Understory communities in mature forests were distinct between forested wetlands and upland sites with forested wetlands often hosting great rhododendron (*Rhododendron maximum*) and highbush blueberry (*V. corymbosum*) thickets while uplands supported species like scrub oak, witch hazel (*Hamemelis virginiana*), and mountain laurel (*Kalmia latifolia*).

Our NC study area encompassed a ~30 km radius in southwest Sproul State Forest and the adjacent State Game Lands 100. Land cover within NC included broad-leaved forest (87%), agriculture/grasslands (6%), and low-intensity developed (5%). Elevation ranged from 500 to 610 m above sea level. We studied fledglings from 11 discrete nesting habitat sites (18–96 ha) within the NC, of which 10 were the result of overstory removal (2–10 yr post-harvest) and one was the result of a wildfire that occurred in 1990. In these early-successional stands, a variety of saplings were present including oaks, red maple, aspen, black cherry, pin cherry (*P. pennsylvanica*), black birch, and pines; however, the shrub component was sparse and consisted mostly of black huckleberry (*Gaylusaccia baccata*), lowbush blueberry, and sweet fern (*Comptonia peregrina*). Within surrounding mature forest in the NC, understory shrubs typically included mountain laurel and occasionally witch hazel.

Data Collection
We searched for Golden-winged Warbler nests from May to June within early-successional forests and along edges of adjacent mature forest across both study areas. We used active searching techniques (e.g., parental behavior cues) to locate nests. For each nest discovered, we conducted
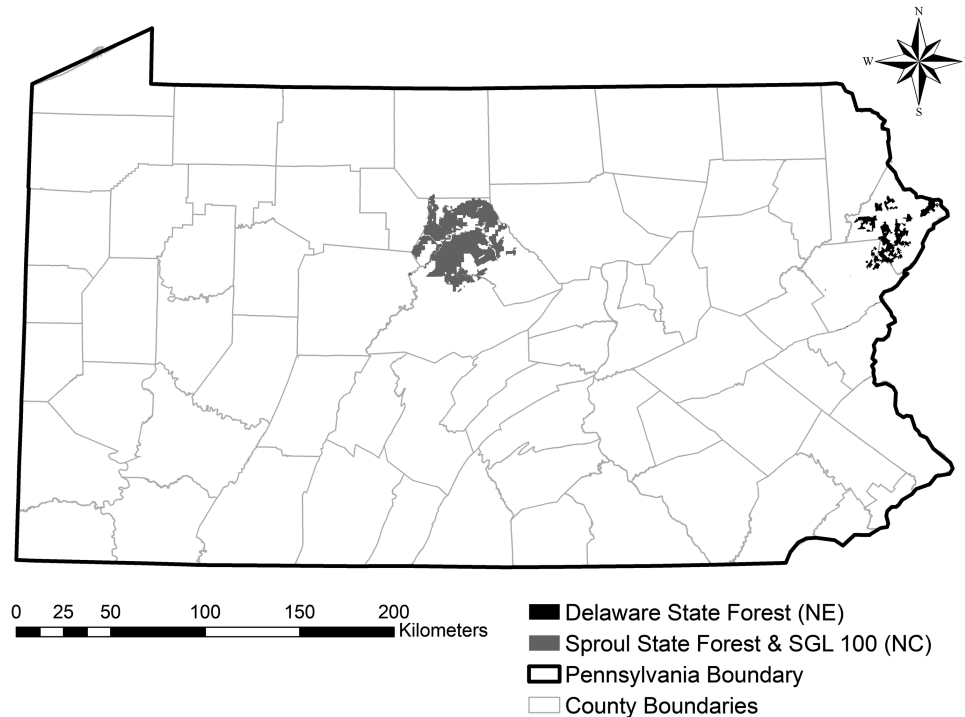
FIGURE 1. Map of Pennsylvania (PA) indicating the locations of study areas in northcentral (NC) and northeast (NE) PA. Fledgling Golden-winged Warblers were radio-tagged and monitored throughout the duration of the dependent post-fledging period from 2014 to 2015 in the NE and from 2016 to 2017 in the NC.

checks on a 3-day interval to monitor progress and to ensure accurate estimates of nestling age (Martin and Geupel 1993). As nestlings approached fledging (8 days old; Confer et al. 2020), we monitored nests daily.

Immature Golden-winged Warblers were usually marked as nestlings 8 days after hatching. However, individuals that fledged prior to nest checks on day 8 were caught by hand, typically within 10 m of the nest. We randomly selected 2 members of each brood to be fitted with a VHF radio-transmitter (Blackburn Transmitters, Nacogdoches, Texas, USA) with 95 mm antenna. Two fledglings were chosen because parents split broods shortly after fledging (Peterson et al. 2016), and we wanted to increase the chance of monitoring separate sub-broods. Both birds received an aluminum USGS leg band and a radio transmitter affixed using the figure-8 harness method (Rappole and Tipton 1991). We constructed harnesses from <1 mm black elastic thread to allow for growth (Streby et al. 2015). VHF radio transmitters used in this study weighed either 0.35 g or 0.40 g and, when combined with a harness and leg band, constituted <5% of each bird's mass. There was no obvious indication that transmitters affected mobility or survival of fledglings, and radio-tagged individuals were often seen behaving in a similar fashion to brood-mates without radio transmitters. Handling time for each brood was ≤10 min and, upon completion of radio-tagging and banding, all birds were returned to their nest

(nestlings) or perch (recently fledged young). In addition to fledglings from monitored nests, we opportunistically captured dependent fledglings that we encountered during nest searching and telemetry. We aged these birds to the nearest day by comparing their plumage characteristics to known-age fledglings.

Each radio-tagged fledgling was tracked daily between 0600 and 1600 hours using a Lotek STR 1000 (Lotek Wireless, Newmarket, Ontario, Canada) receiver and Yagi 3-element antenna. We tracked each fledgling once per day using the homing technique until we visually confirmed its location. Upon arriving at a fledgling's location, we recorded the presence and behaviors of siblings and parents to determine fledgling independence. We recorded coordinates at the first location the fledgling was observed using a Garmin eTrex 20 GPS unit (Garmin International, Olathe, Kansas, USA). We followed this tracking protocol until fledgling mortality or radio-transmitter battery failure (~30 days). When radio-signal was lost for an individual, we conducted systematic searches to determine if the fledgling had moved outside the normal detection range of our equipment. Searches were centered on the fledgling's last known location and extended along 1-km transects in each cardinal direction. If a fledgling remained undetected, we conducted daily searches from automobile throughout the study area for ≥1 week before ceasing searches.

Movement and Space Use

We assessed fledgling movements and space use separately for each study area. Because Golden-winged Warblers are a brood-splitting species and multiple radio-tagged fledglings occasionally went with the same parent, we treated sub-broods as a random effect. To assess movement rate, we averaged daily straight-line movements across all sub-broods during 2 periods (low survival [~70% of mortalities]: days 1–5 post-fledging, and high survival [~30% of mortalities]: days 6–28 post-fledging; McNeil 2019). We averaged Euclidean distance from each sub-brood location to its nest of origin to determine dispersal distance. During the high-survival period, we compared fledgling dispersal range between study areas using a Student's t-test.

Cover Type Classification

We classified cover types in both study areas with ArcGIS 10.3 (ESRI, Redlands, California, USA) using a combination of Pennsylvania State Forest and State Game Lands forest inventory data, ArcGIS online aerial imagery (ESRI, Redlands, California, USA), National Wetlands Inventory data, and records of recent (<10 yr) timber harvests on public lands in PA. In addition, technicians visited >3,800 randomly selected locations in our study areas and classified forest developmental stage. We used these ground-based samples to assist in classification of cover types. We classified most cover types based on tree size, stocking level (i.e. tree density relative to the stand's capacity), and age class of the timber stand as described in the PA Department of Conservation and Natural Resources (DCNR) Bureau of Forestry Inventory Manual (PA DCNR 1999). We classified Stand Initiation (SI) cover as stands that had recently (approximately <10 yr) undergone overstory removal harvest and were >50% stocked by trees <15 cm DBH (diameter at breast height). Stand Initiation cover closely represented Golden-winged Warbler nesting habitat and contained substantial shrub and herbaceous ground cover in addition to a diverse mixture of regenerating seedlings/saplings. We defined Stem Exclusion (SE) cover as older (~10–25 yr post-harvest) even-aged stands >50% stocked by trees <15 cm DBH. These stands were distinct from SI cover due to the dominance of a dense sapling layer such that herbaceous vegetation and most shrubs were shaded out by the overstory. Mature forest (i.e. stands in the understory reinitiation stage) was characterized by the dominance of trees >15 cm DBH. We divided mature forests into 3 sub-categories: Shelterwood/Understocked, Mature Forest Wetland, and Mature Forest Upland. We classified Shelterwood/Understocked (SH) cover as mature forest <50% stocked. These stands were treated (e.g., shelterwood harvest) or had experienced non–stand replacing natural disturbance. We classified Mature Forest Upland (MU) as mature even- or uneven-aged stands that were >50% stocked. These stands were ~60–90 yr old. We classified Mature Forest Wetland (MW; NE only) as mature palustrine stands >50% stocked. Mature Forest Wetlands were seasonally or perpetually inundated with water. We classified Shrub Wetland (SW; NE only) as stands dominated by shrubs and trees <15 cm DBH and, in many cases, perpetually inundated with water. We classified Upland Shrubland (US; NC only) as stands dominated by shrubs and <50% stocked with trees <15 cm DBH being dominant. Shrub cover in these stands was predominantly *Vaccinium* spp. or *Gaylussacia* spp. Upland Shrubland cover was largely derived from a forest fire that occurred in 1990.

Statistical Analyses

We used mixed-effects conditional logistic regression (i.e. discrete-choice) to model stand-scale habitat selection by fledgling Golden-winged Warblers and their parents (Thomas et al. 2006). As such, we created daily choice sets for fledglings beginning on the first day an individual was radio-tracked. Choice sets contained the fledgling's observed location (used) and 19 available points. Similar ratios of used to available points have been used in local-scale habitat selection studies (Bonnot et al. 2011, Cheeseman et al. 2018). Available points were generated in ArcGIS using the *Create Random Points* tool. We restricted available points to a circle centered on a fledgling's last used location, the radius of which was equal to the 75th percentile of all fledgling movements for a particular age, similar to Streby et al. (2016). As such, the range of available points expanded as fledglings developed and became more mobile. We measured Euclidean distance from all used and available points to each cover type to explain habitat selection (Conner et al. 2003). Specifically, use of a given alternative in the choice set acted as a binary response that varied as a function of the distance (continuous) to each cover type variable. Additionally, we included distance to edge to measure the influence of ecotones on habitat selection. Edge was calculated as the distance to the closest intersection between an early-successional stand (SI, SE, US, SW) and a mature stand (MU, MW, SH).

We fit habitat selection models within a Bayesian framework using JAGS (Plummer 2003) run from program R 3.5.1 (R Core Team 2018) with the *jagsUI* (Kellner 2015) package. Because individuals can respond differently to habitat, and because sub-broods occasionally had >1 radio-tagged fledgling, sub-broods were treated as random effects. We modeled each study area separately, and we modeled the post-fledging period in 2 parts for each study area (days 1–5 and days 6–28). Prior to model fitting we assessed collinearity using Pearson's correlation coefficient with a cutoff of 0.6. One variable (distance to edge) was removed from the NC day 1–5 model due to collinearity.

TABLE 1. Summary of 4 models used to explain habitat selection by fledgling Golden-winged Warblers in Pennsylvania (PA). Sample sizes (*n*) represents the number of sub-broods used in each model. Goodness of fit results (based on *k*-fold cross validation) are reported as % predictive-success. Data were collected from May to July, 2014–2015 (NE PA) and 2016–2017 (NC PA). Abbreviations: SI = Stand Initiation, SE = Stem Exclusion, SW = Shrub Wetland, US = Upland Shrubland, MW = Mature Forest Wetland, MU = Mature Forest Upland, SH = Shelterwood/Understocked, Edg = Edge.

	Model	*n*	% Predictive-success
Day 1–5 NE	SI + SE + SW + MW + MU + SH + Edg	41	33%
Day 1–5 NC	SI + SE + US + MU + SH	40	34%
Day 6–28 NE	SI + SE + SW + MW + MU + SH + Edg	43	41%
Day 6–28 NC	SI + SE +US + MU + SH + Edg	35	52%

Because we were interested in evaluating habitat preferences for each cover type and edge, we constructed models for each study area and age class that included all variables, resulting in 4 models (O'Hara and Sillanpää 2009, Cheeseman et al. 2018; Table 1). We ran 3 concurrent Markov chains for each model for 100,000 iterations of which 20,000 were allocated to a burn-in period. We assessed model convergence based on $IS\hat{R}$ values <1.1 (Gelman and Rubin 1996). We inferred selection for or against cover types based on regression coefficients with 95% credible intervals not overlapping zero (Kéry 2010).

Model Fit
Traditional goodness-of-fit (GOF) methods are not appropriate for discrete-choice models (Womack et al. 2013), so we adopted the *k*-fold cross-validation approach to test the fit of our models (Boyce et al. 2002, Bonnot et al. 2011). Briefly, for each model, we randomly subset the data into a training set (80%) and a testing set (20%). We fit each model using the training set and then evaluated the rate at which the fit model accurately predicted used locations in the testing set vs. 3 randomly selected available locations. We repeated this process 5 times for each model and report the average predictive-success as a measure of GOF. Given that we evaluated 4 choices, we would expect 25% predictive-success to be due to chance alone and predictive-success >25% suggesting adequate model fit (Bonnot et al. 2011).

RESULTS

We radio-tagged 156 Golden-winged Warbler fledglings and relocated individuals 2,128 times from 2014 to 2017. Habitat selection data were collected for 47 sub-broods in the NE and 43 sub-broods in the NC. The number of fledgling relocations ranged from 2 to 28 days in both the NE ($\bar{x}$ = 22.3 ± 1.2 relocations per fledgling) and NC ($\bar{x}$ = 16.8 ± 1.5 relocations per fledgling). In both study areas, sub-broods used all available cover types. Habitat use was heavily skewed toward stand initiation forest (nesting habitat) during the first 5 days post-fledging (87% of relocations) but became more diverse during the latter portion of the dependent post-fledging period, particularly in the NE. During days 6–28 post-fledging in the NE, stand initiation cover was used in similar proportion to mature forest (Figure 2).

Movement and Space Use
Sub-broods in both study areas increased their movement rate as they aged. During days 1–5 post-fledging, sub-broods made average daily movements of 38.7 m (range: 5.3–127.5 m) in the NE and 44.9 m (range: 3.0–104.7 m) in the NC. During days 6–28, sub-broods made average daily movements of 155.9 m (range: 61.1–322.8 m) in the NE and 156.7 m (range: 56.9–369.1 m) in the NC (Figure 3). Golden-winged Warbler sub-broods also moved farther from nest sites as they aged. In both study areas, sub-broods remained proximate to nesting locations during days 1–5 (NE: $\bar{x}$ = 92.5 m, range: 6.1–278.9 m; NC: $\bar{x}$ = 106.0 m, range: 4.1–266.1 m). Sub-broods in both study areas were substantially farther from nest sites during days 6–28 post-fledging (NE: $\bar{x}$ = 749.3 m, range: 207.4–2042.8 m; NC: $\bar{x}$ = 694.3 m, range: 38.9–3600.2 m; Figure 3), and there was no significant difference in dispersal distance between study areas during this time ($P > 0.05$).

Habitat Selection
Cross validation indicated that all models had adequate predictive-success. Models for days 6–28 preformed slightly better (predictive-success: 41–52%; Table 1) than models for the early post-fledging period (predictive-success: 33–34%). Habitat selection analyses revealed that sub-broods selected cover types nonrandomly in both study areas and across both time periods (1–5 and 6–28 days post-fledging). Sub-broods selected for forest in the stand initiation stage during days 1–5 post-fledging in the NE (β = 2.20; 95% CI: 0.57–5.45) and in the NC (β = 2.98; 95% CI: 0.85–7.34) over all other cover types (Figure 4). During days 1–5, sub-broods in the NE also avoided edges (β = –0.87; 95% CI: –0.43 to –0.06) between early-successional (SI, SE, SW, US) and mature (MU, MW, SH) cover types. No other cover types were selected or avoided during the first 5 days post-fledging in either study area. During days 6–28 of the post-fledging period, sub-broods in the NE selected for stands in the stem exclusion stage (β = 1.30; 95% CI: 0.29–2.45) and stand initiation stage (β = 0.97; 95% CI: 0.42–1.61; Figure 4). Sub-broods in the NC continued selecting forest in the stand initiation stage (β = 14.17; 95% CI: 7.46–22.78) during days 6–28 but also selected for upland shrublands (β = 6.73; 95% CI: 0.94–12.50).
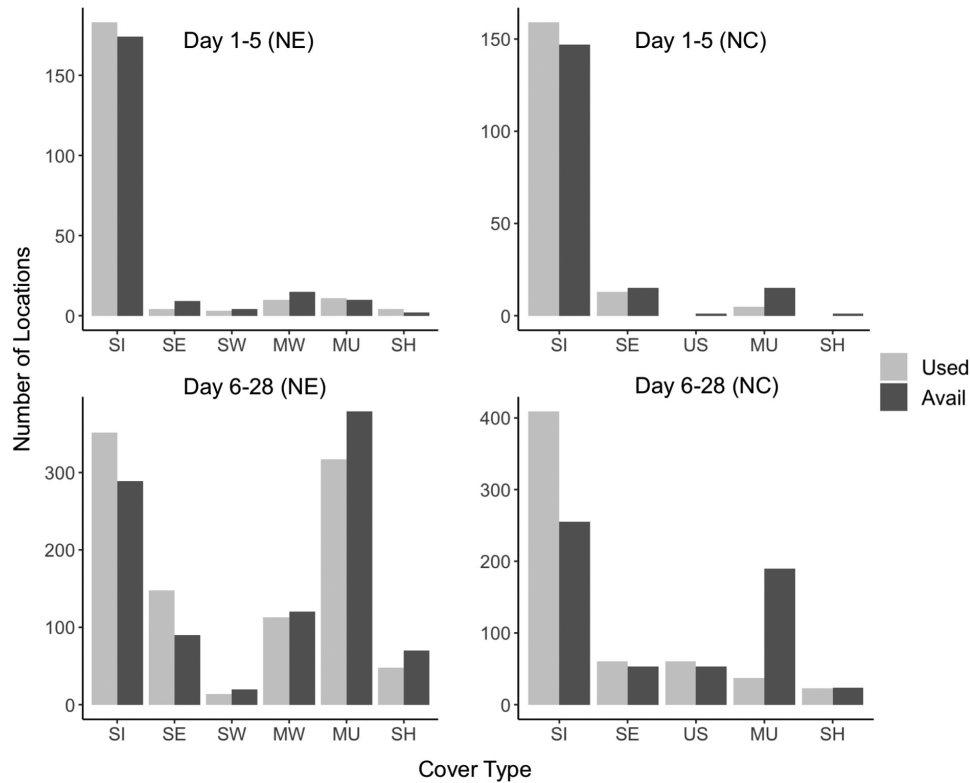
FIGURE 2. Comparison of Golden-winged Warbler habitat use and availability based on the number of radio-telemetry relocations within a given cover type (use) and the relative frequency of available points for each cover type (availability). Data are summarized for ages 1–5 days and ages 6–28 days post-fledging. Habitat use data were collected throughout the entire dependent post-fledging period in NE Pennsylvania (2014–2015) and NC Pennsylvania (2016–2017). Abbreviations: SI = Stand Initiation, SE = Stem Exclusion, SW = Shrub Wetland, US = Upland Shrubland, MW = Mature Forest Wetland, MU = Mature Forest Upland, SH = Shelterwood/Understocked, Edg = Edge.

DISCUSSION

Our study demonstrates both similarities and differences in post-fledging habitat selection at the stand scale for 2 subpopulations of Golden-winged Warblers. Across both subpopulations, Golden-winged Warbler fledglings were consistent in their use of stand initiation stage forest during the early post-fledging period. However, like other songbirds, Golden-winged Warblers have the capacity to switch habitats between nesting and post-fledging periods and switch from early-successional to later seral stages in certain regions. In particular, we detected regional differences in habitat selection toward the end of the post-fledging period when fledglings were more mobile. Fledglings in the NE dispersed to ultimately relocate in older overstory removals (i.e. stem exclusion stands) but fledglings in the NC (200 km away) primarily restricted their habitat use and selection to forest in the stand initiation stage (approximately <10 yr post-harvest.) These results underscore the importance of regional and subregional studies to improve conservation guidelines on the breeding grounds.

During the high-mortality phase of the post-fledging period (days 1–5), we documented similar habitat selection patterns between the NE and the NC study areas. Specifically, we found sub-broods from both regions selected for forest in the stand initiation stage (i.e. nesting habitat) and sub-broods in the NE avoided edge habitat. This finding is consistent with studies that investigated post-fledging habitat use by mature forest–nesting species. Using passive mist-netting surveys, studies have revealed extensive use of forest in the stand initiation stage during the post-breeding period for species including Red-eyed Vireos (*Vireo olivaceus*), Black-throated Blue Warblers (*Setophaga caerulescens*), and American Redstarts (*S. ruticilla*) (Vitz and Rodewald 2006, Chandler et al. 2012). These species also preferred interior portions of clearcuts <10 yr since harvest (i.e. stand initiation) compared to edges (Vitz and Rodewald 2006). Further, radio-telemetry studies revealed nonrandom (i.e. selective) use of clearcuts by mature forest species during the post-fledging period (e.g., Ovenbird, Wood Thrush [*Hylochichla mustelina*]; Anders et al. 1998, Streby and Andersen 2013).
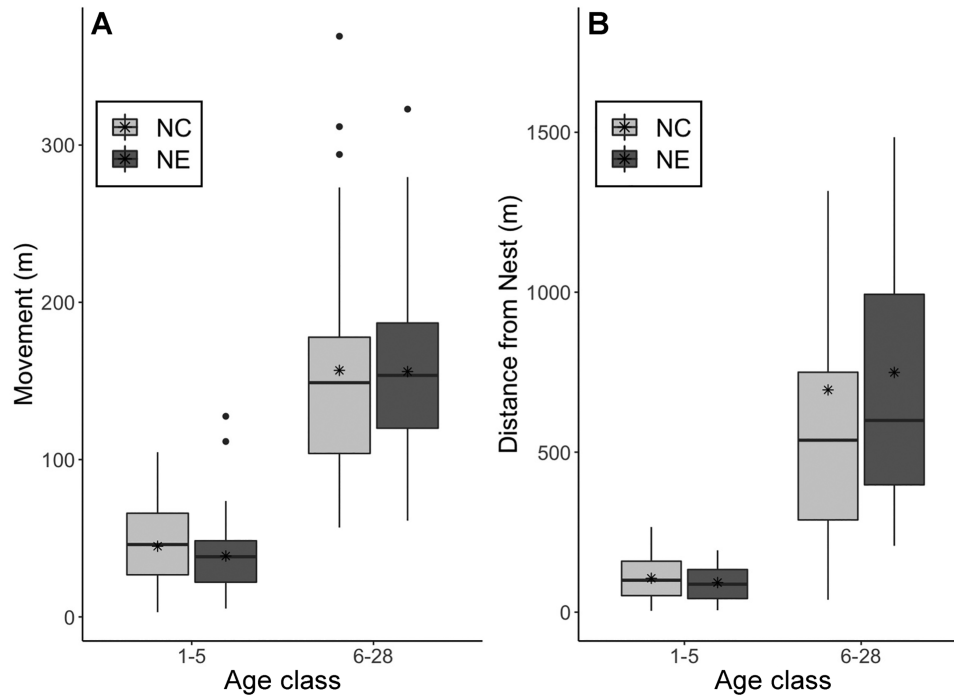
FIGURE 3. (**A**) Summarized daily movement and (**B**) maximum dispersal distance (i.e. distance moved from nest) for fledgling Golden-winged Warblers in the NE (2014–2015) and NC (2016–2017) study areas in Pennsylvania (PA). Asterisk (*) represents the mean value for each category. Outliers for dispersal not shown for data visualization purposes. Maximum dispersal distance in the Poconos was 1.4 km and maximum dispersal distance in the PA Wilds was 3.6 km.

Hypotheses for why some forest-nesting bird species prefer early-successional forest during post-fledging have been postulated. For instance, researchers have hypothesized that early-successional forest stands have greater food availability than adjacent mature forest (Streby et al. 2011, Major and Desrochers 2012). However, an alternate hypothesis suggests that denser vegetation within early-successional forest could protect vulnerable fledglings from predation (King et al. 2006, Vitz and Rodewald 2007, Raybuck et al. 2020). This latter hypothesis provides the most intuitive explanation for selection of forest in the stand initiation stage by fledgling Golden-winged Warblers during days 1–5 because predation, not starvation, was the primary cause of mortality during this phase (McNeil 2019). Our evidence of selection for forest in the stand initiation stage by day 1–5 fledglings clearly demonstrates that the importance of this cover type extends beyond nesting for Golden-winged Warblers.

Most documented shifts in habitat selection during the breeding season occur from mature forest to early-successional forest (Anders et al. 1998, King et al. 2006, Vitz and Rodewald 2011). However, we show that habitat shifts from forest in stand initiation to forest in stem exclusion also occurs. Indeed, Golden-winged Warbler fledglings in Minnesota showed a similar pattern of selection for sapling stands later in the post-fledging period after using early-successional nesting stands (Streby et al. 2016). However, a shift from early-successional to sapling-dominated stands did not occur for Prairie Warblers (*S. discolor*), which use early-successional forest in both nesting and post-fledging periods (Nolan 1978). Similar to our results, fledgling Wood Thrushes and Ovenbirds preferred clearcuts with taller (>4.5 m) saplings and less low (<1.5 m) vegetation (Vitz and Rodewald 2007), and clearcuts 6–9 yr post-harvest contained a greater abundance of mature forest birds during post-fledging than clearcuts <6 yr post-harvest (Porneluzi et al. 2014). Our results in the NE reveal that dense stem exclusion stands produced by past even-aged forest management are also important to a shrub-nesting specialist during later portions of the post-fledging period. While nesting habitat seems to meet the needs of breeding Golden-winged Warblers during days 1–5 post-fledging, older forest stands may be important for the species over the remainder of the post-fledging period.

Across most of the post-fledging period (days 6–28), fledgling Golden-winged Warblers selected for other cover types in addition to their nesting habitat. From a conservation perspective, this behavior is somewhat problematic because only nesting habitats are explicitly considered in the definition of "breeding habitat" detailed by the species' conservation guidelines (Bakermans et al. 2011, Roth
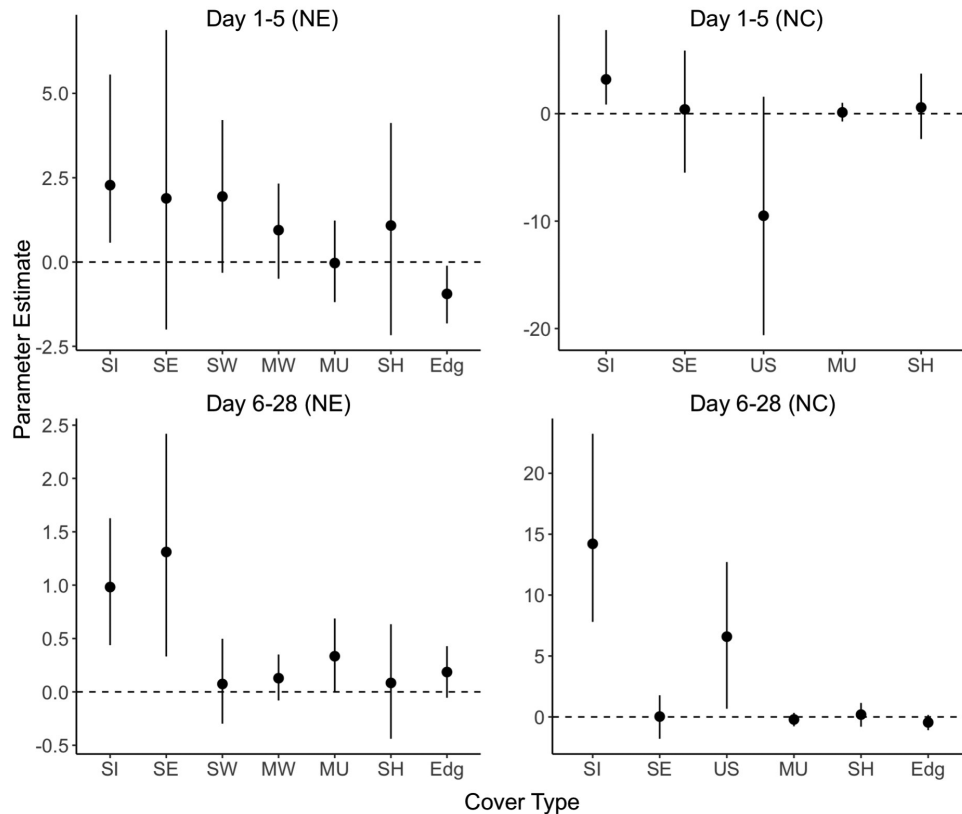
FIGURE 4. Beta coefficients and 95% credible intervals for 7 (NE) and 6 (NC) cover type variables used in habitat selection models for dependent fledgling Golden-winged Warblers. Data were collected from 2014 to 2017 in Pennsylvania. Abbreviations: SI = Stand Initiation, SE = Stem Exclusion, SW = Shrub Wetland, US = Upland Shrubland, MW = Mature Forest Wetland, MU = Mature Forest Upland, SH = Shelterwood/Understocked, Edg = Edge.

et al. 2012). Our study (although only in the NE) indicates that older fledglings select regenerating stands that have reached stem exclusion (~10–25 yr post-harvest) and frequently used mature forest. This notable shift in habitat between nesting/early post-fledging and the later post-fledging period supports the mounting evidence that forest birds require "dynamic" landscapes with multiple seral stages to complete their full breeding cycle (King et al. 2006, Raybuck et al. 2020). Further, our results of region-specific habitat selection during days 6–28 post-fledging, whereby one subpopulation selected for stand initiation and upland shrubland cover and the other selected for stand initiation and stem exclusion stands, indicates the importance of region-specific studies to best understand local variation in habitat needs of a species. Additional post-fledging studies of early-successional-nesting species would be valuable in determining the extent to which habitat shifts occur as well as the relative value of different cover types, including older clearcuts in the stem exclusion stage.

Our study found that fledgling Golden-winged Warblers in the central Appalachian Mountains used mature forest upland frequently in the NE but did not select for mature forest upland in either study area (i.e.

use relative to availability; Figure 2). This aligns with a similar study of fledgling Golden-winged Warblers in Tennessee (Lehman 2017). However, this is a notable difference from fledgling Golden-winged Warblers in the Great Lakes region, which selected mature forest over other cover types during days 9–25 post-fledging (Streby et al. 2016). This discrepancy between the Appalachians and the Great Lakes could be related to differences in mature forest structure at a broader scale between the regions; indeed, the forest community in the central Appalachians is dominated by mixed oak whereas those in many portions of the western Great Lakes are dominated by aspen and birch. In fact, Streby et al. (2016) reported that fledglings often utilized mature forests with complex understories consisting of aspen and hazel (*Corylus* spp.). Complex understory structure may be more common in aspen-birch stands that experience frequent tree mortality and have greater light penetration than closed-canopy mixed-oak hickory stands (Perala 1990). In our study areas, understory vegetation was seldom structurally complex in mature forests, especially in the NC study area (Fiss 2018). Indeed, the simplification and/or homogenization of forest

structure and species composition in eastern mixed-oak forests (Shifley et al. 2014, Kelly 2019) may compromise the value of mature forest cover to fledgling Golden-winged Warblers in the Appalachians. Ericaceous shrubs (e.g., mountain laurel), in particular, can outcompete oak seedlings and inhibit regeneration in Pennsylvania (Brose 2016, Bolstad et al. 2018). Such a change in species composition could limit food availability in mature forest for Golden-winged Warblers (Bellush et al. 2016). Interestingly, when fledglings in our study used mature forest, they moved 1.4 times more rapidly (meters per day) than fledglings using regenerating (e.g., early-successional or sapling) forest (Fiss 2018). This suggests that fledglings in our study may have used the mature forest matrix to traverse local landscapes in search of patchily distributed higher-quality cover types (i.e. early successional forest or upland shrublands).

The process of habitat selection is fundamentally linked to fitness, whereby the resources selected by an individual are assumed to increase fitness (Morris 1989). Nevertheless, individuals occasionally select for habitat that has deleterious effects on survival (Catlin et al. 2019). We observed varied habitat use and clear signs of habitat selection by fledgling Golden-winged Warblers, but a concurrent study on these same fledglings indicated no relationship between forest stand developmental stage and survival (McNeil 2019). Thus, stand-scale habitat selection by fledglings conveyed no negative fitness consequences during the post-fledging period. Habitat selection during post-fledging could have carryover effects (negative or positive) on other portions of the life cycle (Van De Pol et al. 2006, van Oosten et al. 2017), thus we urge managers to consider providing the forest conditions selected by fledglings because these could have undetected benefits. Additionally, by promoting the habitat conditions described herein (i.e. increased stand age class diversity) managers should be providing fledglings with greater options and creating habitat for other species with dynamic habitat needs (e.g., Wood Thrush).

CONCLUSIONS

Our study of Golden-winged Warbler habitat selection during the post-fledging period revealed dynamic (i.e. changing throughout the post-fledging period) habitat selection patterns and region-specific habitat needs. While it is possible that year effects influenced differences in habitat selection between our study areas, we consider this unlikely given the similar weather conditions across years (McNeil 2019). Similarly, habitat selection differences mainly occurred during the high survival time period when predator communities are less likely to influence

selection. In general, our findings indicate that habitat conditions for fledgling Golden-winged Warblers in the central Appalachians overlap with BMPs, but additional habitat recommendations and novel information regarding the spatial context of landscapes are necessary to improve these guidelines.

In our study, fledgling dispersal was restricted to local landscapes within a maximum of 3.6 km of nest locations. We recommend that land managers create landscapes with diverse forest stand developmental stages, including abundant stand initiation forest following existing species management guidelines (Bakermans et al 2011, Roth et al. 2012) to best meet Golden-winged Warbler habitat needs during the nesting and post-fledging period. Land managers should prioritize new projects in areas proximate to even-aged stands that have reached stem exclusion (i.e. 10–25 yr post-harvest) or areas with persistent upland shrubland cover to provide additional habitat for Golden-winged Warbler fledglings later in the post-fledging period. Stands in later developmental stages should be intermixed to maintain commercial viability and operability. Given that we located most sub-broods ~750 m from nest sites (maximum: 3,600 m) during days 6–28 post-fledging, forest age-class mosaics should be created or maintained within 2 km^2 landscapes to maximize their value to dispersing sub-broods. Land managers attempting to create habitat for Golden-winged Warblers throughout the entire breeding season should carefully consider spatial and temporal aspects of forest landscapes when planning and implementing forest management activities such as timber harvests and forest stand improvements.

Our study contributes to a growing body of literature suggesting that forest songbirds require diverse forest age classes to fulfill their entire breeding cycle (Chandler et al. 2012, Raybuck et al. 2020). Indeed, our management recommendations echo those of recent studies suggesting that local landscapes with forest age class mosaics could benefit birds irrespective of nesting guild. A pertinent example is the Cerulean Warbler (*S. cerulea*), a rapidly declining forest songbird in need of management action (Buehler et al. 2020). While the species nests in mature forest with small canopy gaps, its fledglings require closed canopy forest, sapling stands, and dense understory structure within 2 km of nesting locations (Raybuck et al. 2020). Other species share similar full breeding season habitat needs (e.g., Wood Thrush; Anders et al. 1998, Rivera et al. 1998). Ultimately, these studies and our results indicate that land managers need not decide between management for one species or another, but that sound forest management to improve age structure within local landscapes should benefit a wide suite of eastern forest birds.

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