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Research Paper

Using a natural reference system to evaluate songbird habitat restoration

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ABSTRACT. The Golden-winged Warbler (*Vermivora chrysoptera*) is an imperiled songbird that breeds in early-successional plant communities of eastern North America. Conservation efforts on the breeding grounds have become a priority because population declines are thought to be driven, in part, by the loss of breeding habitat. Although the species is known to use a variety of upland and wetland cover types, the majority of previous research on the species has been conducted in uplands. Although patterns of Golden-winged Warbler habitat use within anthropogenic upland communities are well understood, such information within naturally occurring habitats are scant. We compared Golden-winged Warbler densities in natural shrub-wetlands and nearby upland timber harvest that conformed to species-specific habitat guidelines of the Poconos Region of Pennsylvania. We also identified vegetation characteristics of natural shrub-wetlands associated with high warbler abundance. Our analyses suggest that timber harvests and natural shrub-wetlands of the Poconos supported similar densities of Golden-winged Warblers. N-mixture models suggested that natural shrub-wetlands with low canopy cover and high densities of 1-2 m tall woody stems hosted more Golden-winged Warblers. Wetland complexes comprising more edge and those with more emergent wetland types supported the highest warbler abundances. This suggests that the species requires edges when it occurs within shrub-wetlands, a pattern not observed within our timber harvests, which were designed to have adequate tree cover throughout. Findings from our study combined with those from concurrent research evaluating Golden-winged Warbler reproductive success suggests that timber harvests following Golden-winged Warbler habitat guidelines have similar capacity as natural shrub-wetlands to support breeding populations. A future effort to quantify the potential of different wetland types to host breeding Golden-winged Warblers is warranted. Such information used in combination with timber harvest planning will provide insight for landscape-level conservation that considers maintaining appropriate amounts of nesting habitat to sustain Golden-winged Warblers in this region.

Utilisation d'un système de référence naturel pour évaluer la restauration de l'habitat d'un passereau

RÉSUMÉ. La Paruline à ailes dorées (*Vermivora chrysoptera*) est un passereau en danger qui niche dans les communautés végétales de début de succession de l'est de l'Amérique du Nord. Les efforts de conservation sur les aires de nidification sont maintenant prioritaires parce qu'on pense que les baisses de population sont imputables, en partie, à la perte d'habitat de nidification. Même si cette espèce est connue pour fréquenter une variété de milieux se trouvant en terrains secs ou humides, la majorité des recherches antérieures sur l'espèce ont été menées sur des hautes terres. Si on connait bien les tendances de l'utilisation de l'habitat par cette paruline dans les milieux d'origine anthropique se trouvant en terrain sec, cette information pour les milieux naturels est toutefois limitée. Nous avons comparé les densités de cet oiseau dans des milieux arbustifs humides naturels et des terrains secs avoisinants qui ont été récoltés selon des recommandations spécifiques à l'habitat de cette espèce dans la région des Poconos en Pennsylvanie. Nous avons aussi déterminé les caractéristiques de la végétation des milieux humides arbustifs naturels hébergeant un grand nombre de parulines. Nos analyses indiquent que les milieux récoltés et les milieux humides arbustifs naturels des Poconos avaient des densités similaires de Parulines à ailes dorées. Des modèles de type N-mélange ont indiqué que les milieux humides arbustifs naturels qui avaient une voûte basse et une densité élevée de tiges ligneuses de 1 à 2 m étaient ceux qui hébergeaient le plus de Parulines à ailes dorées. Les complexes de milieux humides qui présentaient plus de bordures et ceux qui avaient plus de plantes émergentes étaient ceux qui hébergeaient les densités de parulines les plus élevées. Ces résultats indiquent que cette paruline recherche les bordures dans les milieux humides arbustifs, une tendance qui n'a pas été observée dans les milieux récoltés, qui ont été conçus pour offrir un couvert forestier propice partout. D'après nos résultats et ceux d'autres recherches évaluant le succès de reproduction de la Paruline à ailes dorées, les parterres dans lesquels la récolte forestière a respecté les recommandations pour l'habitat de la Paruline à ailes dorées ont une capacité similaire à celle des milieux humides arbustifs naturels pour héberger des populations nicheuses. Dans le futur, il serait important de quantifier le potentiel de divers types de milieux humides à héberger la Paruline à ailes dorées. Cette information, combinée à la planification de la récolte forestière, servira à la conservation à l'échelle du paysage tenant compte du maintien de suffisamment d'habitat de nidification pour soutenir les Parulines à ailes dorées dans cette région.

Key Words: *early-successional habitat; management; N-mixture models; reference system; songbirds; timber harvest; wetlands*

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INTRODUCTION

The Golden-winged Warbler (*Vermivora chrysoptera*) is a Neotropical-Neartic migratory songbird that nests in early successional habitats in eastern North America (Confer et al. 2011). The species has experienced long-term population declines throughout much of its North American breeding range (Rosenberg et al. 2016, Sauer et al. 2017). Researchers largely agree that breeding habitat loss is, in part, a driver behind Golden-winged Warbler population declines, particularly in the Appalachian portion of the species' range (Rohrbaugh et al. 2016, Rosenberg et al. 2016). In fact, the species and its early successional nesting habitat are listed as priorities in several State Wildlife Action Plans (e.g., Pennsylvania Game Commission 2015). As such, efforts that increase the availability of breeding habitat for this imperiled species have been identified as a conservation priority (Buehler et al. 2007, Rohrbaugh et al. 2016).

To address this issue, a large-scale study was conducted to generate habitat management guidelines for the Golden-winged Warbler (Aldinger et al. 2015, Bakermans et al. 2015, Terhune et al. 2016). The products of this extensive effort included species-specific habitat management guidelines and a breeding grounds conservation plan (Bakermans et al. 2011, Roth et al. 2012). Both documents provide science-based guidance for the use of various management practices to create Golden-winged Warbler nesting habitat. These habitat guidelines are currently being implemented by several state and federal agencies on publicly managed lands. Additionally, the USDA-Natural Resources Conservation Service and U.S. Fish and Wildlife Service have initiated an incentive program called Working Lands for Wildlife (https://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/programs/initiatives/?cid=stelprdb1046975) to promote the creation of Golden-winged Warbler nesting habitat on private lands in the Appalachian Mountains (Ciuzio et al. 2013).

Although implementation of timber harvest-based guidelines is the prominent method used to create Golden-winged Warbler nesting habitat in the Appalachian Mountains, naturally occurring wetlands also support breeding populations of this species in this region (Gill and Murray 1972, Confer et al. 2010). It was suggested by Hunter et al. (2001) that the historical abundance of naturally occurring wetlands may have been an important factor in the evolutionary history of the Golden-winged Warbler. Golden-winged Warbler nest success in southern New York was higher in wetland communities as compared to adjacent upland communities associated with either power line right-of-ways or managed shrublands (Confer et al. 2010, however, see Streby et al. 2016). Confer et al. (2010) postulated that the long-term persistence of wetland-nesting Golden-winged Warblers in close proximity to upland-nesting Blue-winged Warblers (*Vermivora cyanoptera*) was the result of a source/sink dynamic between swamp forests and uplands of southern New York (Confer et al. 2010). Clearly, the research by Confer et al. (2010), though limited in scope, provided important insight regarding potential differences in Golden-winged Warbler reproductive success between upland and wetland communities. However, no published studies have compared Golden-winged Warbler habitat relationships between natural wetlands and upland timber harvests that meet the structural criteria presented in species-specific habitat management guidelines (i.e., Bakermans et al. 2011, 2015) and none have occurred within Appalachia where the species is most imperiled.

Wetlands constitute one of the only naturally occurring habitats used by Golden-winged Warblers today (Confer et al. 2011). This, coupled with the findings of Confer et al. (2010), suggest wetlands as a logical reference system for evaluating efforts to implement habitat management guidelines that target this at-risk species. Although we understand patterns of Golden-winged Warbler habitat use within anthropogenic upland communities quite well, such information within wetlands are scant, especially within Appalachia. As such, we collected avian and habitat data with two primary objectives in mind: (1) to compare the density of Golden-winged Warbler territories within timber harvests that met the species-specific criteria to that within a natural wetland reference system and (2) to describe patterns of Golden-winged Warbler habitat use within natural Appalachian shrub wetlands. Evaluation of Golden-winged Warbler use of shrub wetland and timber harvests in northeastern Pennsylvania will elucidate the relative contributions each system provides toward meeting Golden-winged Warbler habitat and population goals for the Appalachian Mountains presented in the species' conservation plan (Roth et al. 2012).

METHODS

Study area

We studied Golden-winged Warblers in the Poconos region of Pennsylvania (PA) where the species occurs at its highest statewide density (Larkin and Bakermans 2012). In addition to supporting many Golden-winged Warblers, the Poconos is known to support few Blue-winged Warblers and hybrid phenotypes are infrequent (Larkin and Bakermans 2012). The Poconos region of northeastern Pennsylvania is characterized by many rounded hills and low valleys (White and Chance 1882). The soils of the Poconos region are largely undeveloped inceptisols that are thin, acidic, and have even been described as "inhospitable to plant growth" (Oplinger and Halma 2006:14). Such soils are thus of little use to agriculture (White and Chance 1882) and the region is now almost completely forested with minimal contemporary agricultural influence (McCaskill et al. 2009). This forested landscape, although managed in part for timber production, remains dominated by mature mixed-oak and northern hardwood forests (80–110 yr), woody wetlands, and suburban areas scattered throughout (McCaskill et al. 2009). We studied Golden-winged Warblers within the largest expanse (> 32,000 ha) of public land within the Poconos region, the Delaware State Forest (DSF). The upland forest types within DSF vary with dry-oak (*Quercus* spp.) heath, scrub oak (*Q. ilicifolia*) barrens, and northern hardwood forests constituting the majority (Wherry et al. 1979). A diverse array of wetland types also occurred within DSF with hardwood swamps, coniferous bogs, sedge marshes, and alder swamps among the most common. In fact, this region of PA hosts the highest density of wetlands in the state (Majumdar et al. 1989). Many of these wetlands, while hosting significantly different plant communities than uplands, still maintain the vegetative structure that is attractive to nesting Golden-winged Warblers: herbaceous nesting substrate punctuated by abundant woody cover, mature forest edge, and tall, interspersed song perches, e.g., snags, trees.

Site selection

During 2014, we conducted avian point counts within DSF of which $n = 32$ points were within 31 natural shrub-wetlands and $n = 10$ points were within 7 upland timber harvests. In 2015, we surveyed 26 additional point count locations within 24 timber harvests. Thus, across both years of our study we conducted surveys at 32 wetland points (within 31 wetland patches) and 36 timber harvest points (within 31 stands). Because our goal was to evaluate the efficacy of Golden-winged Warbler best management practices (BMP) guidelines, we only selected harvests that conformed to the Golden-winged Warbler BMP guidelines (Bakermans et al. 2011). Specifically, timber harvests included in our study met all of the following criteria: (i) > 4 ha in area, (ii) had residual basal areas ranging between 2.2–8.9 m^2/ha, (iii) abundance of regenerating woody stems, and (iv) were 1–10 yr postharvest. The 36 timber harvests monitored were all regenerating timber harvests with a mean area of 26.4 ha (range: 7.3–75.1 ha), mean basal area of 4.04 m^2/ha (range: 2.2–8.9 m^2/ha), and mean age of 3.1 yr postharvest (range: 2–7 yr). Though a variety of timber management prescriptions are used across northern Pennsylvania, overstory removals with scattered residuals (basal area: 2.3–4.6 m^2/ha) like those examined here are among the most common practices used to diversify forest age classes in the region. Timber harvests each had 1–2 surveys placed within them in a stratified random manner with five stands each containing two surveys and the remaining 26 stands each containing one survey.

Although Golden-winged Warblers nest in a variety of wetland types including high-canopy wetland types (Confer et al. 2010, 2011), we focused sampling within a single wetland type: early-successional palustrine wetlands. To select early-successional palustrine wetlands, we used ArcGIS version 10.2 (Environmental Systems Research Institute 2011) incorporating a combination of data (i.e., 2013 National Agriculture Imagery Program; USDA 2008, http://datagateway.nrcs.usda.gov; and the National Wetlands Inventory 2009 shapefile of Pennsylvania wetlands, http://www.fws.gov/wetlands/) to define candidate shrub-wetlands. Wetlands were selected as candidate locations if they were either freshwater emergent or shrub-wetland (Cowardin et al. 1979). Shallow, palustrine-type wetlands were further considered if they appeared (based upon visual examination of areal imagery) to be plant communities that were relatively open and dominated by shrubs and saplings (i.e., potential warbler habitat; Rossell et al. 2003). We used this same approach to delineate the boundaries of each shrub-wetland. We selected all wetlands that met these defined criteria within DSF. From this final list, we selected 31 continuous shrub-wetlands (i.e., uninterrupted by mature forest; range: 3–61 ha) that were in close proximity of our timber harvests. We placed two surveys within the largest wetland patch because of its large size while all other wetland patches contained a single point count each.

Avian surveys

To sample Golden-winged Warbler abundance within wetland and timber harvest, we placed point count stations within wetland and timber harvest interiors across DSF using a stratified-random sampling scheme. To generate stratified random points, we used the "create random points" tool in ArcGIS. We attempted to place all survey locations ≥ 80 m from an intact forest edge. We elected to ensure a distance of ≥ 80 m from mature forest edges when possible to maximize the area of target habitat (timber harvests and shrub wetlands) sampled because locations close to forest-target habitat edge would have included nonfocal vegetation communities, e.g., mature forest, within the radius of detectability for Golden-winged Warblers. All timber harvests were large enough to keep points ≥ 80 m from the intact forest edge. Because of the size/shape of some wetlands, survey locations were necessarily < 80 m from a forest edge and placed at the center of the wetland. As a consequence, our mean distance from forest edge within wetlands was 79 m. We identified wetland centers using ArcMap and the "calculate geometry" tool. We ensured that points were > 250 m apart to avoid double-counting Golden-winged Warblers (Ralph et. al 1995). The mean distance between points within the same habitat patch footprint was 431 m. Although the species is known to be occasionally detectable to 150 m (Kubel and Yahner 2007), we were unaware of any detections of the same GWWA at multiple points. Ultimately, this sampling scheme allowed us to survey an even number of point locations between wetlands and timber harvests.

To sample warblers at each point, we conducted standard point count surveys from 15 May to 15 June with two replicates each ($n = 136$ surveys across 68 points; Ralph et al. 1995). Each point count replicate occurred approximately 14 days apart. This one-month survey window encompassed most of the Golden-winged Warbler breeding season while including minimal overlap with migration/postbreeding dispersal periods (Highsmith 1989). All avian surveys began each day at sunrise and concluded four hours postsunrise. Before each survey, we recorded weather conditions including the (1) Beaufort wind index (0–5) and (2) sky condition (% cloud cover) in addition to (3) time, and (4) date. Each point count lasted a total of 10 minutes and consisted of passive observation of the number of singing Golden-winged Warbler males. We also recorded the distance (m from observer) at which each male was first detected. Recent work by Toews et al. (2016) suggested that Golden-winged and Blue-winged Warblers may be two color morphs of the same species. With this in mind, it is the Golden-winged Warbler phenotype that is being considered for listing under the Endangered Species Act (Sewell 2009) and for which best management practices have been developed (Bakermans et al. 2011, Roth et al. 2012). As such, this study focused only on the Golden-winged Warblers. Although we noted all *Vermivora* sp. of both sexes, the focus of this study was phenotypically pure Golden-winged Warblers and only males were recorded. Although subtle hints of plumage introgression could not be discerned in the field (because this typically requires handling of birds), we considered "phenotypically pure Golden-winged Warblers" (hereafter, Golden-winged Warblers) to be individuals with gray contour plumage, yellow secondary coverts, black throat/auriculars, and white malar/supercillium (Gill and Murray 1972). We attempted to visually confirm the phenotype of all singing *Vermivora* to allow exclusion of Blue-winged Warblers and phenotypic hybrids. This was done for the purpose of simplicity though we acknowledge that this does not address abundance of cryptic *Vermivora* hybrids, females, or nonterritorial males.

Wetland microhabitat quantification

In order to quantify the microhabitat variables relevant to warbler abundance, we conducted a vegetation survey at each point count location. We surveyed vegetation from 15 June to 15 July 2015. Vegetation surveys quantified two variable types: woody stems and plant strata. All vegetation data were collected along three radial transects, 100 m in length and oriented at 0°, 120°, and 240° from the point count location. Along each transect, both woody stems and plant strata measurements were taken at 10 "stops" (10 m apart; n = 30/point count location). Woody stem data consisted of a presence/absence for each of three size classes within a 1 m radius plot at each of 30 stops: "short" (0–1 m), "medium" (1–2 m), and "tall" (> 2 m).

Vegetation strata recorded at each stop consisted of the presence/absence of the following: tree canopy, sapling, shrub, fern, forb, sedge, moss, leaf litter, and bare ground. Trees > 10 cm in diameter-at-breast-height were classified as "canopy" and those ≤ 10 cm were considered saplings. Shrubs were woody plants with multiple primary stems (in contrast to single-stemmed saplings). Ferns were seedless vascular plants with compound fronds, e.g., sensitive fern, *Onoclea sensibilis*. Forbs were broad-leafed dicotyledonous plants, e.g., *Viola* spp. The plant category "sedge" included any monocotyledonous plant, however, was almost exclusively *Carex* spp. Plant strata were recorded with an ocular tube such that only strata that intersected with crosshairs in the ocular tube were considered present (modified from James and Shugart 1970, Thomas et al. 1996). Although a single stop could include multiple strata types, each stratum could only be represented once/stop and thus each point count location could have a maximum of n = 30 occurrences for each stratum. Both woody regeneration and plant strata values were analyzed as percentages, i.e., % cover, because some sites had outer portions of transects truncated because of irregularly-shaped wetland boundaries.

Broad-scale wetland quantification

We used remotely sensed data to examine wetland communities at three spatial scales relevant to the species' life history and ecology: 150, 250, and 500 m radius. The 150 m radius was chosen because it aligns with the maximum distance within which 90% of our warbler detections were made (Buckland et al. 2005). The 250 m scale was chosen to represent the territory + immediate surrounding area, approximating the male home-range (Frantz et al. 2016, Wood et al. 2016). Finally, we included 500 m because several other studies have suggested forest cover type at the scale is important to Golden-winged Warblers (Streby et al. 2012, 2015, Wood et al. 2016). Around each point count location, we created 150, 250, and 500 m radius buffers in ArcGIS. Within each buffer, we quantified four features: (1) upland forest composition; (2) wetland composition; (3) early-successional edge; and (4) habitat structure, derived from remotely sensed imagery, i.e., image texture (Wood et al. 2012). To quantify upland forest cover, we used the 2011 National Land Cover Data set (NLCD; Fry et al. 2011). Land cover covariates at each of the three spatial extents consisted of the percent cover of deciduous forest and mixed (coniferous/deciduous) forest. To quantify wetland composition, we used the National Wetlands Inventory shapefile (USFWS 2014) to delineate wetland boundaries and types. We used these data and further classified all wetlands into five analysis categories (i) shrub wetland (class: scrub/shrub), (ii) emergent wetland (class: emergent), (iii) deciduous forested wetland (class: forested, subclass: 1), (iv) coniferous forested wetland (class: forested, subclass: 4), and (v) open water. For sites with both scrub/shrub wetland and either "forested" or "emergent," the wetland fragment was classified as shrub wetland.

A previous study in the southern Appalachians found that Golden-winged Warblers nesting within a heavily managed wetland frequently incorporated wetland edges into their territories (Rossell et al. 2003). As such, we wanted to examine if Golden-winged Warblers exhibited a similar affinity for forest-wetland edge in our study area. To assess the influence of edge on Golden-winged Warbler abundance in our wetlands, we created a 75 m wide buffer around the interior-edge of the wetland that extended away from the forest edge into the shrub wetland. We selected 75 m radius because it approximates the defended territory of Golden-winged Warbler within a wetland community (Rossell et al. 2003, Frantz et al. 2016). We used ArcGIS to create the 75 m edge buffer by visually digitizing the shrub wetland and intact forest boundary on National Agriculture Imagery Program (NAIP) orthophotographs (2013, Pike County, Pennsylvania). The proportion of the 250 m and 500 m spatial extents that consisted of 75 m edge buffer was categorized as "shrub wetland edge."

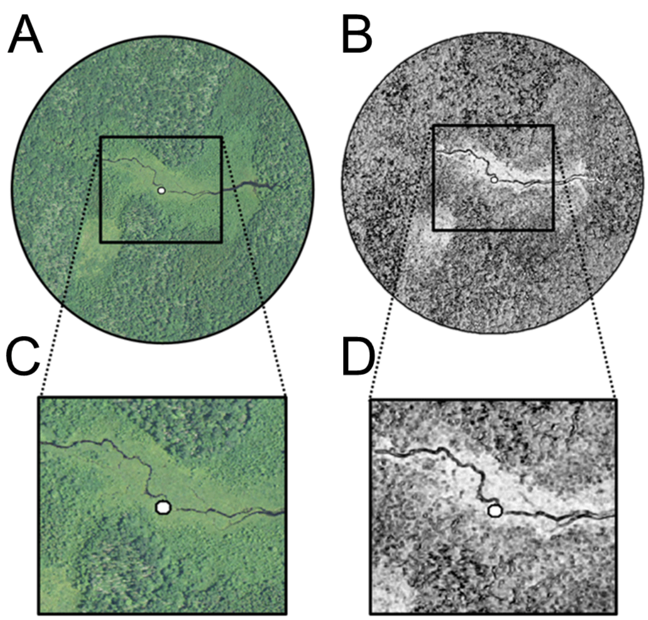
We calculated image texture for each spatial extent (St-Louis et al. 2006) to model the effects of structural heterogeneity on Golden-winged Warbler abundance (Confer et al. 2011, Wood et al. 2016). Image texture captures the variability in vertical and horizontal vegetation structure (Wood et al. 2012), and has been successfully employed to characterize habitat, at both fine- and broad-extents, for Golden-winged Warblers in New York and Pennsylvania (Wood et al. 2016). We used raster images from the NAIP orthophoto 2013 for Pike County as a base with which to calculate the texture (St-Louis et al. 2006; Fig. 1). To calculate the image texture at the three spatial scales, we used the "focal statistics" tool in ArcGIS to calculate attributes of the NAIP image raster values. By doing this for a neighborhood of 5x5 cells (1 m resolution), we used ArcGIS to estimate the raster value means and standard deviations around each location. Using these two values, we calculated the average coefficient of variation, i.e., structural heterogeneity, for the entire 150, 250, and 500 m spatial extent for each survey point.

Density estimation and comparison

To compare Golden-winged Warbler territory densities between natural shrub wetlands and managed timber harvests, we used distance sampling (Thomas et al. 2010). Distance sampling allowed us to generate easily interpreted estimates of density in territories/hectare. We generated density estimates using program DISTANCE version 6.2 (Thomas et al. 2010). DISTANCE uses object, e.g., animal, observation data in the form of distances to generate densities across a given level of resolution (Thomas et al. 2010, Marques et al. 2011). DISTANCE models a detection function for the dataset to generate density estimates based on the distances at which animals were observed from the survey location (Thomas et al. 2010). Prior to the final analysis of this dataset, we ran a set of models in program DISTANCE using appropriate combinations of key function and series expansion and ultimately selected the model with the lowest AIC value

(Buckland et al. 2005). The model with the lowest AIC for our dataset was a detection function with a hazard rate key function, and was thus selected for the data analysis (Buckland et al. 2005). Prior to DISTANCE analyses, we truncated the outer 10% of detections from our dataset as is recommended for distance-sampling analyses (Buckland et al. 2005). For the remaining observations, we ran a model with stratum-level, i.e., point, resolution estimates for both density and encounter rate but a global detection function.

Fig. 1. An example of macro-extent image texture (500 m radius) for a wetland point count location in northeastern Pennsylvania. The image texture used National Agriculture Imagery Program (NAIP) ortho rasters (A), which were converted to an image “texture” (B). Although superficially the image texture looks like a color conversion of the original NAIP raster, closer inspection reveals that the NAIP image shows photographic habitat characteristics (C), while the image texture characterizes the structural complexity (D).



Wetland habitat modeling

In addition to density, we also examined how abundance varied as a function of habitat covariates. To accomplish this, we created N-mixture models using the “unmarked” package in R (Kéry and Royle 2015, R Core Team 2016). N-mixture models allowed us to model variation in abundance across wetlands while simultaneously accounting for imperfect detection probability (Thompson 2002, Royle et al. 2005). Detection probability () is modeled within N-mixture models using repeated counts via a binomial distribution (Royle 2004). The latent abundance state (λ), in contrast, was modeled with a Poisson distribution (Royle 2004, Kéry and Royle 2015) using a logit link function. To evaluate and account for overdispersion, we estimated for our most parameterized model and adjusted within models. For each model, we calculated Quasi Akaike’s Information Criterion adjusted for small sample size and > 1.0 ($QAIC_c$), models were ranked by descending $QAIC_c$ and compared to a null (intercept-only) model. Prior to habitat modeling, we estimated pairwise Pearson’s correlation coefficients and ensured that there were no redundant variables within the dataset ($r > 0.70$; Sokal and Rohlf 1969). We found two variables (“> 2 m woody stems” and “open water”) to be redundant with “shrub cover” and “image texture,” respectively so these variables were not analyzed.

To model habitat relationships while accounting for detection probability, we modeled detection probability separately, then abundance separately at each spatial scale; in particular, we modeled habitat relationships using two submodels (and) where the best-performing detection model was incorporated into all consecutive abundance models. We modeled using four survey-specific covariates: wind index, sky condition, time since sunrise, and day of season. We then modeled using four suites of two data types; suite I varied warbler abundance as a function of microhabitat while suite II varied abundance as a function of 150, 250, and 500 m radius broad scale habitat covariates. Each model incorporated the best model as well as included an intercept + singular habitat covariates. Because of sample size limitations, we did not include quadratic terms within our models. We ranked models within each suite according to $QAIC_c$ and models < 2.0 $QAIC_c$ of a top model were considered competing models (Burnham and Anderson 2002). We assessed the biological significance of model effects by (1) evaluating whether each was ≤ 2.0 $\Delta QAIC_c$ of a null model and (2) whether 85% confidence intervals of model β terms overlapped with zero (suggesting weak covariate effects; Arnold 2010).

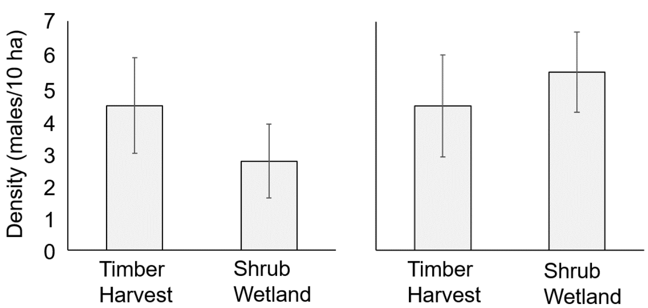
RESULTS

Density comparison

We made a total of 126 male *Vermivora* spp. detections of which 120 were phenotypic Golden-winged Warblers. These occurred between 6–250 m from observers. Of the 120 Golden-winged warblers, 70 and 50 were detected in timber harvests and wetlands, respectively. Of the 70 Golden-winged Warblers detected within timber harvests, $n = 29$ and $n = 41$ were detected in 2014 and 2015, respectively. When we truncated the outermost 10% ($n = 12$) of detections (Buckland et al. 2005), the remaining sample ($n = 108$; 66 within uplands and 42 within wetlands) excluded observer detections at distances 185–250 m. Based on the raw point count data, the naïve rate of occupancy for upland timber harvest surveys was 0.69 (25/36) while the wetlands, in contrast, had a naïve occupancy of 0.58 (18/32). The mean number of warblers observed per survey was 0.97 males/timber harvest survey and 0.78 males/wetland survey. When only sites with detections were considered, the average number of males detected/ survey increased in wetlands to 1.32 males/survey. Because timber harvests were all managed using Golden-winged Warbler - BMP and were all assumed to be suitable as habitat, analogous comparison was not made.

Estimated site-level density across all timber harvest and wetland sites combined was 3.57 (95%CI: ± 1.30) males/10 hectares. Density estimates across all surveyed locations were 4.41 (95%CI: ± 1.46) males/10 ha for managed upland timber harvests and 2.7 (95%CI: ± 1.1) males/10 ha for wetlands (Fig. 2). Because all upland timber harvests studied here conformed to Golden-winged Warbler habitat guidelines (Bakermans et al. 2011) whereas some of the wetlands we surveyed may have ultimately been unsuitable as habitat for nesting Golden-winged Warblers, we also examined densities between sites with confirmed occupancy between habitat types. When only considering sites where Golden-winged Warblers were observed, the density estimate for wetland sites increased to 5.5 (95%CI: ± 1.2) males/10 ha (Fig. 2). Between wetland sites with confirmed occupancy and all timber harvests, density estimates overlapped widely, and thus density was not different between the two community types (two-tailed t-test: $P = 0.38$).

Fig. 2. Densities of Golden-winged Warbler (*Vermivora chrysoptera*) males across all sites (left) and managed sites as compared only to shrub wetland sites with confirmed occupancy (right). Values generated in program DISTANCE and represent the density of males/10 ha of early-successional habitat. Error bars represent 95% confidence intervals.



Wetland habitat modeling

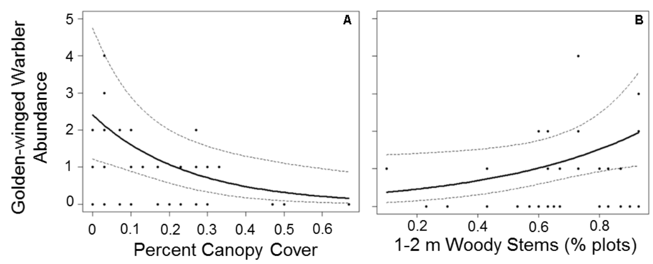
To model detection probability of Golden-winged Warbler males, we generated a set of five detection models within the N-mixture framework and ranked them according to their QAICc (Table 1). Because c-hat = 1.05 (slightly overdispersed), we adjusted in all of our N-mixture models (detection and abundance). We ranked all detection models, and, while all models were "plausible" ($\Delta QAIC_c < 4.0$), the null (intercept only) model for detection was ranked as the highest model. As such, this null detection model was used in consecutive abundance modeling (p[.], λ […]). $QAIC_c$ for p(.), λ(.) = 134.46.

Model suite I examined how warbler abundance varied as a function of microhabitat features within 100 m of survey locations. The best-ranked microhabitat model included a term for percent canopy cover (Table 2) describing a negative relationship with abundance (Fig. 3). Although this model had no competing models, a model including a term for density of medium height (1–2 m) woody stems was superior to the null model (> 2.0 $QAIC_c$) suggesting its positive relationship with warbler abundance (though weaker than λ [canopy]). A model including a term for sedge cover also ranked higher than the null, however, it was < 2.0 $QAIC_c$ of the null and therefore not a detectable relationship. Both the canopy model and the medium height woody stem model included covariate β estimates, which did not include zero in their 85% confidence intervals, and their effects were therefore biologically significant.

Table 1. Detection models used in N-mixture modeling that examined how wetland-breeding Golden-winged Warbler (*Vermivora chrysoptera*) detection probability varied as a function of survey covariates. For each model, we calculated Quasi Akaike's Information Criterion adjusted for small sample size ($QAIC_c$). $QAIC_c$ accounted for minor overdispersion within candidate sets (c-hat = 1.05). Models are shown in order of descending rank (> $QAIC_c$). Also reported are model weights w_i for model i, number of parameters (K), as well as the -2 Quasi Log(likelihood). The highest-ranking model as well as other statistically informative models are shown including parameter estimates and 95% confidence intervals. $QAIC_c$ for p(intercept only) = 134.46

Model parameters	$\Delta QAIC_c$	w_i	K	-2QLogLik
p (intercept only)	0.00	0.38	1	-66.99
p (int. + time since sunrise)	1.23	0.21	2	-66.26
p (int. + wind)	1.71	0.16	2	-66.51
p (int. + day of season)	2.15	0.13	2	-66.74
p (int. + sky condition)	2.31	0.12	2	-66.83

Fig. 3. Golden-winged Warbler (*Vermivora chrysoptera*) male abundance as a function of vegetation covariates explored in model suite I. Abundance varied as a function of canopy cover (the best ranked model, A) in a negative fashion. Golden-winged Warbler abundance also varied positively as a function of increasing density of medium (1-2 m tall) woody stems (i.e., shrubs and saplings, B)

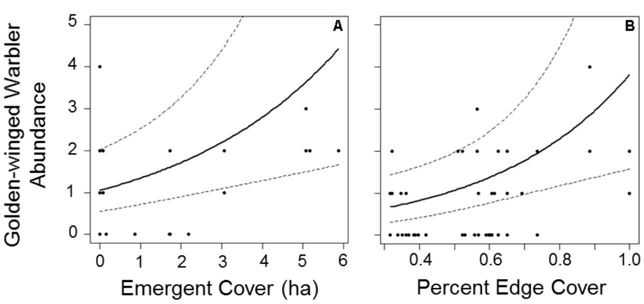


When we considered broad-scale habitat effects on abundance, we observed multiple patterns repeated across the three spatial extents examined (Table 3). The area (ha) of emergent wetland cover was a highly-ranked model at all three spatial extents and described a positive relationship with warbler abundance (Fig. 4A). Percent wetland shrub edge was also a highly ranked model (competing with emergent wetland cover) at both scales at which it was considered; wetland complexes comprising more wetland shrub edge hosted more Golden-winged Warblers than did larger complexes that comprised lower percentages of wetland shrub edge (Fig. 4B). The positive correlation of percent emergent wetland and percent wetland shrub edge with Golden-winged Warbler abundance was consistent across all three spatial scales. Although several other models (e.g., texture at 150 m and 500 m scales) ranked higher than the null model (p[.], λ [.]) at various scales (Table 3), $QAIC_c$ values for these models were always < 2.0 of the null and therefore its statistical equivalent.

Table 2. Model suite I: N-mixture model sets that examined how wetland-breeding Golden-winged Warbler (*Vermivora chrysoptera*) abundance varied as a function of vegetation covariates. For each model, we calculated Quasi Akaike's Information Criterion adjusted for small sample size ($QAIC_c$). $QAIC_c$ accounted for minor overdispersion within candidate sets (c-hat = 1.05). Models are shown in order of descending rank (delta $QAIC_c$). Complete models included both detection (p) and abundance (lambda) submodels. Also reported are model weights w_i for model i as well as the number of model parameters (K). The highest-ranking model as well as other statistically informative models are shown including parameter estimates and 95% confidence intervals. For relevant models, model beta estimates are also shown (85%CI)

Model parameters	$\Delta QAIC_c$	w_i	K	Beta coefficients
p (.), λ (int. + canopy)	0.00	0.75	2	β_1= 0.88 (0.19 - 1.56), β_2= -4.04 (-6.93 - -1.14)
p (.), λ (int. + medium woody)	4.67	0.07	2	β_1= -1.17 (-2.65 - 0.3), β_2= 1.99 (0.11 - 3.87)
p (.), λ (int. + sedge)	5.36	0.05	2	
p (.), λ (intercept only)	6.73	0.03	1	
p (.), λ (int. + elevation)	7.06	0.02	2	
p (.), λ (int. + large woody)	7.74	0.02	2	
p (.), λ (int. + sapling)	8.11	0.01	2	
p (.), λ (int. + small woody)	8.68	0.01	2	
p (.), λ (int. + forb)	8.92	0.01	2	
p (.), λ (int. + moss)	8.92	0.01	2	
p (.), λ (int. + no woody)	9.11	0.01	2	
p (.), λ (int. + shrub)	9.26	0.01	2	
p (.), λ (int. + fern)	9.36	0.01	2	

Fig. 4. Golden-winged Warbler (*Vermivora chrysoptera*) male abundance as a function of the best-supported 250 m scale N-mixture models in suite II. The area (ha) of emergent wetland cover (A) was demonstrated to be positively associated with Golden-winged Warbler abundance. Similarly, the percent of wetland complex within a 75 m edge zone (shrub wetland edge) was also positively associated with warbler abundance (B). No other N-mixture models were found to be significantly related to abundance based on QAICc ranking or β values.



DISCUSSION

The use of reference systems to evaluate management actions constitutes a key tool at the disposal of conservation biologists and land managers (Kaufmann et al. 1994). That we observed the density of Golden-winged Warblers within timber harvests to be similar to the density within nearby natural shrub wetlands is promising. This is an encouraging finding because Golden-winged Warbler population declines are believed to be driven primarily by declines in the availability of nesting habitat (Buehler et al. 2007, Rohrbaugh et al. 2016), and timber harvest represents one of the most effective ways to restore habitat for the species (Hunter et al. 2001, Roth et al. 2012). Recent work by Rohrbaugh et al. (2016) and Rosenberg et al. (2016) highlight the importance of increased breeding grounds conservation for the long-term stability of Golden-winged Warbler populations. Although it has been demonstrated that nesting success for this species is similar across a variety of community types (Confer et al. 2003, Bulluck and Buehler 2008, Kubel and Yahner 2007, Aldinger et al. 2015), no study before ours has compared territory density between managed habitat and a natural reference system. This may be because wetlands are the only remaining naturally occurring community type available to nesting Golden-winged Warbler (Confer et al. 2011) because of the ubiquitous suppression of naturally occurring disturbance sources across forests of eastern North America (Hunter et al. 2001).

Studies of reference communities are also important because they can characterize the variability of conditions within management targets, i.e., the "natural" habitat (Kaufmann et al. 1994). For Golden-winged Warblers occurring within shrub wetlands, we found a strong negative relationship between warbler abundance and canopy cover. This finding is consistent with the findings of several past studies suggesting that the species requires habitat with fewer trees (Confer and Knapp 1981, Askins 1994, Hunter et al. 2001, Wood et al. 2016, Leuenberger et al. 2017). This is not to suggest that Golden-winged Warblers breeding in shrub wetlands do not use trees or high-canopy areas but rather establish defended territories in highest densities within shrub wetlands with fewer trees in their interiors; it seems likely that Golden-winged Warblers nesting within shrub wetlands may forage in mature canopy trees around the peripheries of these habitats. Furthermore, breeding in association with ecotonal habitat may not only provide quality foraging opportunities (Bellush et al. 2016, Frantz et al. 2016) but perhaps even improve lifetime fitness through high rates of nesting success and/or access to quality postfledging habitat (Streby et al. 2014). In contrast to the density-canopy relationship described here, studies of the species within managed uplands have found the opposite trend suggesting that

Table 3. Model suite II: N-mixture model sets that examined how wetland-breeding Golden-winged Warbler (*Vermivora chrysoptera*) abundance varied as a function of land cover categories and image texture. For each model, we calculated Quasi Akaike's Information Criterion adjusted for small sample size ($QAIC_c$). $QAIC_c$ accounted for minor overdispersion within candidate sets (c-hat = 1.05). Models are shown in order of descending rank (delta $QAIC_c$). Complete models included both detection (p) and abundance (lambda) submodels. Also reported are model weights w_i for model i as well as the number of model parameters (K). The highest-ranking model as well as other statistically informative models are shown including parameter estimates and 95% confidence intervals. For relevant models, model beta estimates are also shown (85%CI)

150 m radius	$\Delta QAIC_c$	w_i	K	Beta Coefficients
p (.), λ (int. + emergent wetland)	0.00	0.67	2	β_1= -0.08 (-0.58 - 0.75), β_2= 0.37 (0.14 - 0.60)
p (.), λ (int. + texture)	4.01	0.09	2	
p (.), λ (int. + wetland conifer. forest)	4.51	0.07	2	
p (.), λ (intercept only)	5.04	0.05	1	
p (.), λ (int. + upland decid. forest)	6.70	0.02	2	
p (.), λ (int. + open water)	6.75	0.02	2	
p (.), λ (int. + shrub wetland)	6.75	0.02	2	
p (.), λ (int. + wetland decid. forest)	6.75	0.02	2	
p (.), λ (int. + upland mixed forest)	6.83	0.02	2	
250 m radius				
p (.), λ (int. + percent edge)	0.00	0.41	2	β_1= -1.21 (-2.40 - -0.02), β_2= 2.55 (0.84 - 4.26)
p (.), λ (int. + emergent wetland)	0.30	0.35	2	β_1= 0.05 (-0.60 - 0.70), β_2= 0.24 (0.09 - 0.40)
p (.), λ (int. + wetland conifer. forest)	4.37	0.05	2	
p (.), λ (intercept only)	4.58	0.04	2	
p (.), λ (int. + upland decid. forest)	5.20	0.03	1	
p (.), λ (int. + upland mixed forest)	5.28	0.03	2	
p (.), λ (int. + texture)	5.72	0.02	2	
p (.), λ (int. + open water)	6.06	0.02	2	
p (.), λ (int. + shrub wetland)	6.06	0.02	2	
p (.), λ (int. + wetland decid. forest)	6.06	0.02	2	
500 m radius				
p (.), λ (int. + emergent wetland)	0.00	0.32	2	β_1= -0.66 (-1.54 - 0.22), β_2= 2.15 (0.61- 3.69)
p (.), λ (int. + % shrub wetland edge)	0.02	0.32	2	β_1= 1.21 (0.21 - 2.22), β_2= -3.80 (-7.33 - -0.27)
p (.), λ (int. + texture)	2.89	0.08	2	
p (.), λ (intercept only)	3.29	0.06	2	
p (.), λ (int. + upland mixed forest)	3.53	0.06	1	
p (.), λ (int. + upland decid. forest)	3.64	0.05	2	
p (.), λ (int. + open water)	4.81	0.03	2	
p (.), λ (int. + shrub wetland)	4.81	0.03	2	
p (.), λ (int. + wetland decid. forest)	4.81	0.03	2	
p (.), λ (int. + wetland conifer. forest)	5.33	0.02	2	

Golden-winged Warblers use areas with moderate canopy cover within those community types (Patton et al. 2010, Roth et al. 2014, Bakermans et al. 2015). Furthermore, within certain wetland types, i.e., hardwood swamps, Golden-winged Warblers nest in clumps of tussock sedge growing beneath canopy cover as high as 60–80% (Confer et al. 2010). Still, our results suggest that, within Appalachian shrub wetlands, the species seeks open shrubland habitat containing few trees while apparently using adjacent forest edges for canopy tree access (Confer et al. 2003, Rossell et al. 2003. Patton et al. 2010).

Our results also corroborate with the findings from past work conducted in upland community types in that Golden-winged Warbler abundance increased with the abundance of 1–2 m woody stems. Golden-winged Warblers are known to have high affinity for shrubs and saplings (Hunter et al. 2001, Buehler et al. 2007, Roth et al. 2012, Wood et al. 2016) because they likely provide important foraging substrate (Bellush et al. 2016) and nest sites (Confer et al. 2011). Woody stems 1–2 m tall within the wetlands we studied were typically large shrubs and moderate-sized saplings, a vegetation size class understood to be important by previous work (Roth and Lutz 2004). It seems likely that woody vegetation of this size class facilitates the co-occurrence of herbaceous and woody cover types, a combination of features known to be important for the species (Confer and Knapp 1981, Klaus and Buehler 2001, Leuenberger et al. 2017).

At macro-scales, we consistently observed the same pattern: positive associations with emergent wetland and shrub wetland-edge cover. Our study is not the first to observe that wetland-breeding Golden-winged Warblers require emergent vegetation (Rossell et al. 2003, Confer et al. 2010), however, to our knowledge, none before have empirically described this relationship. Though emergent cover, i.e., herbaceous vegetation like grasses or sedges, was an important predictor of warbler abundance, we note that emergent cover was generally uncommon (mean: 7.81% wetland area at 500 m radius) and usually concentrated around near the wettest portions of shrub wetlands, e.g., near open water. Moreover, Golden-winged Warbler affinity for edge habitat is also somewhat intuitive; Golden-winged

Warblers are known to often incorporate mature forest edges into their territories (Hunter et al. 2001, Patton et al. 2010), especially within shrub wetlands where they may actually require edges (Rossell et al. 2003). Although our study did not examine the drivers behind these patterns, Rossell et al. (2003) suggested that Golden-winged Warblers within shrub wetlands may place nests near edges and edges are known to be relevant to the nesting ecology of this species (Patton et al. 2010, Streby et al. 2014).

The relationship between Golden-winged Warblers and edges seems to be, like the relationship to canopy cover discussed above, context-specific. Golden-winged Warblers nesting within timber harvests with adequate residual deciduous trees do not require edges for their territories (Hunter et al. 2001, Roth and Lutz 2004, Roth et al. 2012), likely because residual canopy trees fulfil a similar ecological role. Wetland communities studied here, most of which were beaver meadows, support successional gradients beginning along the upland edge and shifting inward as anaerobic soil conditions inhibit the growth of larger, deep-rooted plants (Naiman et al. 1988). Under these circumstances, it is expected that areas located far from the forest edge would be increasingly affected by hydric soils, thus altering the structure and composition of the plant community. This same pattern would not be expected within upland timber harvests where soil conditions are not anoxic and largely independent of edge. In fact, because vegetation and hydrological conditions are consistent throughout upland timber harvests, the inclusion of residual canopy trees can facilitate Golden-winged Warbler use of the entire site without shading out the understory. We add a note of caution that necessarily arises from this result: if Golden-winged Warblers establish territories more densely near habitat edges, a sampling regime such as ours that emphasizes sampling habitat interiors could underestimate density within habitat types as a whole by undersampling the ecotone region. Because Golden-winged Warblers are detectable at distances > 100 m (Kubel and Yahner 2007), and our average distance from wetland edge was 79 m, we believe this effect was minimal in our study. Moreover, the focus of this study was wetland interiors; future work explicitly examining wetland density within ecotone habitat or other wetland features of various quality would be worthy.

Although warbler densities were the same within the managed sites and our reference system (Fig. 2), patch sizes within shrub wetlands and timber harvests were not equal. Shrub wetlands considered here had a mean size of 12.74 ha whereas timber harvests were more than double the size (mean: 26.4 ha). We propose that, because Golden-winged Warblers do not require edges within timber harvests containing adequate residual basal area (i.e., 2.3-9.2 m^2/ha) as they do within shrub wetlands, these anthropogenic communities can support a greater absolute number of males/unit area compared to nearby reference shrub wetland systems. Still, wetland communities are likely of critical importance to the persistence of this species within the Poconos region. The Poconos Mountains supports more wetlands/unit area than any other region in Pennsylvania (Majumdar et al. 1989). Although eastern landscapes have lost much of their early-successional bird habitat (Hunter et al. 2001), persistent beaver activity within the Poconos region has maintained these wetlands in a long-term state of early-succession (Naiman et al. 1988). We suggest that portions of these wetlands are long-term refugia where Golden-winged Warblers can persist on the landscape, even during early-successional dry spells such as within recent decades of limited forest disturbance. This pattern is interesting because it mirrors, to some extent, patterns of occupancy observed in the Upper Great Lakes region where populations have shifted over time toward portions of Michigan, Wisconsin, and Minnesota characterized by greater shrub-wetland cover (Rosenberg et al. 2016). Although Confer et al. (2010) suggested that wetlands may serve as source habitat for Golden-winged Warblers, Peterson et al. (2016) found shrub wetlands to be poor quality habitat for the species in Minnesota and Manitoba. It seems likely that the work by Confer et al. (2010) is highly applicable to this system because their study sites were ~ 75 km from ours while the work of Petersen et al. (2016) occurred > 1500 km from Delaware State Forest.

Golden-winged Warbler affinity for wetland habitats like those of the Poconos may also be important in light of Blue-winged Warbler range expansion through Appalachia and the Great Lakes (Confer et al. 2003, Naujokaitis-Lewis and Fortin 2016, Rohrbaugh et al. 2016). Our results corroborate previous studies that found Blue-winged Warblers and hybrid *Vermivora* to be generally rare in the wetlands of the Poconos region whereas Golden-winged Warblers remain fairly common (Larkin and Bakermans 2012). Because Golden-winged Warblers may avoid interacting with Blue-winged Warblers by breeding within such wetland habitats (Confer et al. 2010), landscapes punctuated by wetland communities may offer regionally important spatial segregation between these two species (Confer et al. 2010). With this in mind, climate change is predicted to threaten wetland ecosystems like those studied here (Erwin 2009), which may ultimately drive Golden-winged and Blue-winged Warblers back together (Confer et al. 2010), leading to the extirpation of the former and replacement by the latter (Gill 1980, Naujokaitis-Lewis and Fortin 2016).

Although our study marks an early exploration of how Golden-winged Warblers use wetlands, it raises numerous additional questions regarding the species' breeding season ecology within natural wetlands. Future studies examining Golden-winged Warbler nest survival and postfledging ecology within Appalachian shrub wetlands would be valuable. To this end, quantifying the potential source-sink dynamics of Golden-winged Warbler between wetlands and anthropogenic upland early successional communities would prove useful for land managers working in this region. This is especially true given the potential value of shrub-wetlands to Golden-winged warbler conservation in the Appalachians in contrast to those in the western Great Lakes studied by Peterson et al. (2016). Additionally, exploration of the species' density within other wetland types such as high-canopy hardwood swamps (see Confer et al. 2010) would provide a more complete understanding of wetland use by the species. Studies with larger sample sizes should also consider density-based analyses in addition to (or in lieu of) N-mixture models (Barker et al. 2018) such as Hierarchical Distance Models (see Kéry and Royle 2015). Although our study leans heavily on the use of N-mixture models, model rank and relative ΔAICc were almost identical to auxiliary analysis using generalized linear models. Moreover, larger sample sizes than those presented here would allow more intensive modeling and might describe subtler relationships missed by our study. Ultimately, we believe that the findings presented here attest to the value of both timber harvests and shrub wetlands as habitat for Appalachian Golden-winged Warblers, both likely playing a role in the long-term conservation and management of this species.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1193

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