



## Original research article

## An evaluation and comparison of conservation guidelines for an at-risk migratory songbird



Darin J. McNeil<sup>a,i,\*</sup>, Kyle R. Aldinger<sup>b</sup>, Marja H. Bakermans<sup>c</sup>,  
Justin A. Lehman<sup>d</sup>, Anna C. Tisdale<sup>e</sup>, John A. Jones<sup>e</sup>, Petra B. Wood<sup>f</sup>,  
David A. Buehler<sup>d</sup>, Curtis G. Smalling<sup>g</sup>, Lynn Siefferman<sup>e</sup>, Jeffery L. Larkin<sup>a,h</sup>

<sup>a</sup> Department of Biology, Indiana University of Pennsylvania, PA, USA

<sup>b</sup> West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, WV, USA

<sup>c</sup> Department of Biology and Biotechnology, Worcester Polytechnic Institute, MA, USA

<sup>d</sup> Department of Forestry, Wildlife and Fisheries, University of Tennessee, TN, USA

<sup>e</sup> Department of Biology, Appalachian State University, NC, USA

<sup>f</sup> U.S. Geological Survey, West Virginia Cooperative Fish and Wildlife Research Unit, West Virginia University, WV, USA

<sup>g</sup> Audubon, NC, USA

<sup>h</sup> American Bird Conservancy, VA, USA

<sup>i</sup> Department of Natural Resources & Lab of Ornithology, Cornell University, NY, USA

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## ABSTRACT

For at-risk wildlife species, it is important to consider conservation within the process of adaptive management. Golden-winged Warblers (*Vermivora chrysoptera*) are Neotropical migratory songbirds that are experiencing long-term population declines due in part to the loss of early-successional nesting habitat. Recently-developed Golden-winged Warbler habitat management guidelines are being implemented by USDA: Natural Resource Conservation Service (2014) and its partners through the *Working Lands For Wildlife* (WLFW) program. During 2012–2014, we studied the nesting ecology of Golden-winged Warblers in managed habitats of the eastern US that conformed to WLFW conservation practices. We evaluated five NRCS “management scenarios” with respect to nesting success and attainment of recommended nest site vegetation conditions outlined in the Golden-winged Warbler breeding habitat guidelines. Using estimates of territory density, pairing rate, nest survival, and clutch size, we also estimated fledgling productivity (number of fledglings/ha) for each management scenario. In general, Golden-winged Warbler nest survival declined as each breeding season advanced, but nest survival was similar across management scenarios. Within each management scenario, vegetation variables had little influence on nest survival. Still, percent *Rubus* cover and density of >2 m tall shrubs were relevant in some management scenarios. All five management scenarios rarely attained recommended levels of nest site vegetation conditions for Golden-winged, yet nest survival was high. Fledgling productivity estimates for each management scenario ranged from 2.1 to 8.6 fledglings/10 hectares. Our results indicate that targeted habitat management for Golden-winged Warblers using a variety of management techniques on private lands has the capability to yield high nest survival and fledgling productivity, and thus have the potential to contribute to the species recovery.

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\* Correspondence to: Cornell University, 111A Fernow Hall, 226 Mann Dr., Ithaca, NY 14853, USA.

E-mail address: [djm462@cornell.edu](mailto:djm462@cornell.edu) (D.J. McNeil).

## 1. Introduction

Increasing anthropogenic stressors on at-risk wildlife populations present growing challenges for biologists and land managers worldwide (Madden, 2004; Heller and Zavaleta, 2009). Implementation of science-based management and subsequent evaluation efforts are critical steps for adaptive-based recovery programs (Bottrill et al., 2011). Although direct management is the primary pathway between scientific recommendations and a biological response by the target species, it has been argued that true conservation remains incomplete without monitoring to understand that response (Saterson et al., 2004; Ferraro and Pattanayak, 2006). Effective adaptive management processes involve compliance with recommendations (Ellefson et al., 2001), while allowing evaluation of successes and failures within management framework (Gibbs et al., 1999; Stem et al., 2005). Using data derived from monitoring, researchers can refine and improve management guidelines, thus making conservation strategies more efficient (Salafsky et al., 2002; Stem et al., 2005).

The Golden-winged Warbler (*Vermivora chrysoptera*) is a neotropical migrant songbird that has shown population declines since at least the 1960's (Sauer et al., 2014) or perhaps as early as the 1930's (Hill and Hagan, 1991). Although Golden-winged Warblers breed throughout both the Great Lakes and Appalachian regions, rates of decline are significantly more rapid in the Appalachian portion of the species' range. Golden-winged Warbler population declines are driven by a suite of population stressors (Roth et al., 2012), for example, Brown-headed Cowbirds (*Molothrus ater*) are a species of brood parasite which directly reduces the nesting success and fecundity of Golden-winged Warblers and other small passerines (Confer et al., 2003). Another challenge faced by Golden-winged Warbler populations is competition and hybridization with their closest congener, the Blue-winged Warbler (*V. cyanoptera*, Gill, 1980; Frech and Confer, 1987). Gill (1980) found that Golden-winged Warbler subpopulations become locally extirpated within 50 years of exposure to breeding Blue-winged Warblers. Moreover, conservation of the species' nonbreeding habitat in Central and South America remains imperative to this species conservation (Buehler et al., 2007). Even considering this diverse array of threats, it is thought that breeding habitat loss may be one of the primary drivers behind population declines (Hunter et al., 2001; Buehler et al., 2007; Roth et al., 2012). In fact, many species of shrubland birds are declining due to the loss of early-successional communities throughout eastern North America (Askins, 2001; Hunter et al., 2001).

Extensive management efforts are currently underway throughout much of the Golden-winged Warbler's range to stem the decline of this at-risk species. The losses of early-successional breeding habitat for Golden-winged Warblers are driven by human development, regeneration of forests on abandoned farmland, and changes in timber harvesting practices (Hunter et al., 2001; Buehler et al., 2007; Rosenberg et al., 2016). The Golden-winged Warbler Breeding Season Conservation Plan (hereafter, Conservation Plan; Roth et al., 2012), and guidelines by Bakermans et al. (2011) were developed as first steps to increase the availability of nesting habitat and to ultimately reverse population declines. These habitat guidelines provide detailed descriptions of a variety of context-specific management practices that can be used to create or maintain Golden-winged Warbler nesting habitat. Furthermore, some management agencies have adopted the habitat guidelines as direction for targeted conservation efforts across the species' two primary population segments: the Appalachian Mountain and Upper Great Lakes Regions.

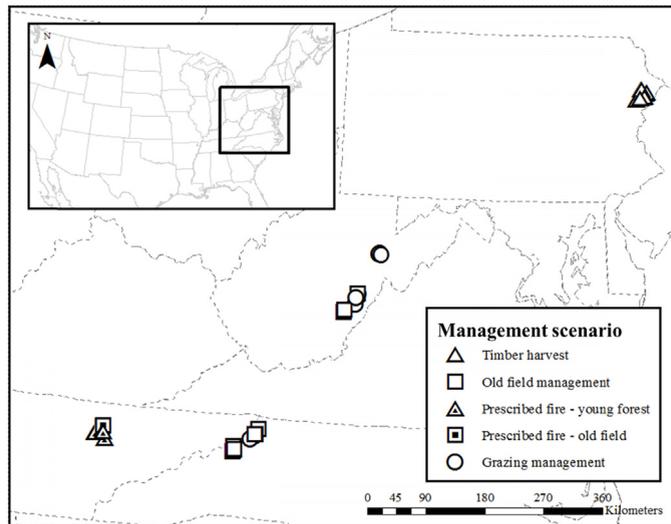
*Working Lands For Wildlife* (WLFW) is a conservation program that targets the implementation of Golden-winged Warbler habitat guidelines on private lands within the species' Appalachian Mountains breeding range (Ciuzio et al., 2013). This cost-share program was initiated in 2012 and is directed by USDA-Natural Resource Conservation Service (NRCS) in partnership with the US Fish and Wildlife Service. Private land management efforts like WLFW are a critical component of wildlife management in North America, as most manageable land area across the continent is privately owned (Scott et al., 2001). Because Golden-winged Warbler conservation is intimately tied to creating and maintaining nesting habitat through active land management, NRCS selected the Golden-winged Warbler as one of seven focal species targeted by WLFW (Ciuzio et al., 2013).

Pre-defined "conservation practices" are the foundational units of many NRCS conservation programs, including WLFW. NRCS conservation practices are individual activities (i.e., herbicide application, prescribed fire, forest stand improvement) that can be used singularly or in combination when developing conservation plans for landowners. As such, one of the first steps necessary for including Golden-winged Warbler as a focal species under WLFW was to identify those NRCS conservation practices that were likely to best achieve habitat conditions recommended in the habitat guidelines for Golden-winged Warblers (Bakermans et al., 2011; Roth et al., 2012). Herein, we evaluate what groups of NRCS conservation practices (hereafter termed "management scenarios") were most effective at creating high-quality Golden-winged Warbler nesting habitat. Specifically, we (1) evaluated the ability of five management scenarios to attain nest site vegetation conditions recommended in the Golden-winged Warbler habitat guidelines; (2) compared Golden-winged Warbler nest survival among five NRCS management scenarios; (3) quantified the effects of vegetation features on nest survival for each management scenario; and (4) estimated and compared production of young (fledglings/ha) for each management scenario.

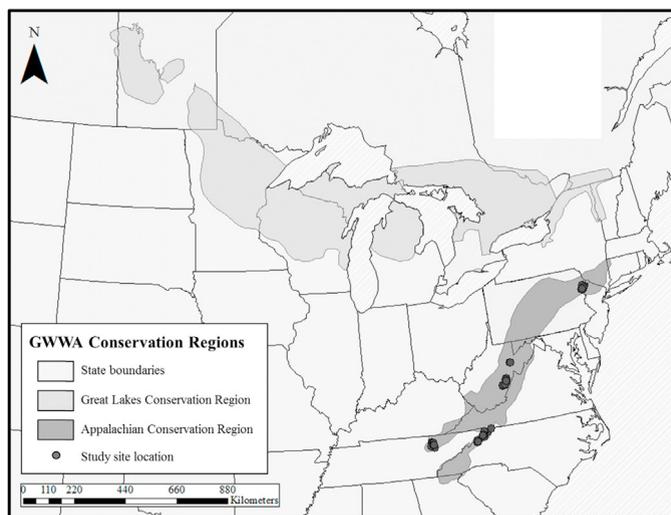
## 2. Methods

### 2.1. Study area

We examined Golden-winged Warbler nesting ecology across 45 study sites in North Carolina, Pennsylvania, Tennessee, and West Virginia (Fig. 1). All sites surveyed had recently been created or maintained using NRCS conservation practices and



**Fig. 1.** Locations of 45 study sites representing five management scenarios where Golden-winged Warbler (*V. chrysoptera*) breeding ecology was studied from 2012 to 2014. Sites each represented a general management type used by the Natural Resource Conservation Service –Working Lands For Wildlife program to create or maintain Golden-winged Warbler nesting habitat. All sites are each represented by a single point.



**Fig. 2.** Locations of 45 study sites representing five management scenarios where Golden-winged Warbler (*V. chrysoptera*) breeding ecology was studied from 2012 to 2014. Sites were all contained within the Appalachian Conservation Region as outlined by the Golden-winged Warbler Status Review and Conservation Plan (Roth et al., 2012).

were in areas that were known to consistently host populations of breeding Golden-winged Warblers. They also met the landscape level criteria provided in the Golden-winged Warbler Conservation Plan and management guidelines (Roth et al., 2012) and were within the Appalachian Golden-winged Warbler ‘Conservation Region’ (Fig. 2). As such, all study sites were located in heavily (>80%) forested landscapes at elevations that ranged 275–1645 m above mean sea level. Additionally, sites were in close proximity to existing populations of breeding Golden-winged Warblers and not in close proximity to existing populations of Blue-winged Warblers (Gill, 1980). Roth et al. (2012) recommend that habitat created for Golden-winged Warblers be isolated from sympatry with Blue-winged Warblers to reduce the likelihood of hybridization and competition between these two species. Forest communities in these landscapes were predominately mixed-oak and northern hardwood.

## 2.2. Management scenarios

Study sites were early successional forest or shrublands that were created or maintained through the implementation of one of five discrete management scenarios used by NRCS and its partners to create Golden-winged Warbler nesting habitat:



**Fig. 3.** Across 45 sites managed for Golden-winged Warblers, we monitored nests built within patches of managed early successional communities. Nests were considered “active” when observations with contents (i.e., eggs or young) were made (left). We focused our efforts on phenotypically “pure” Golden-winged Warblers (female shown, right), though hybrid phenotypes and Blue-winged Warblers (*V. cyanoptera*) did occur at very low frequencies.

grazing management, timber harvest, old field management, prescribed fire-old field, and prescribed fire-young forest. Grazing management sites ( $n = 11$ ) were located in NC and WV and ranged in area from 1.9 to 79.8 ha, totaling 343 ha. Grazing management is a method of maintaining existing Golden-winged Warbler habitat using domestic livestock and occasional mechanical maintenance (i.e., brush hogging) to limit natural succession of pasturelands. The result of this practice is a low intensity grazing system used to maintain an area in early successional habitat over extended periods of time. Timber harvest sites ( $n = 14$ ) were located in TN, WV, and PA. Sites ranged in size from 0.9 to 67.2 ha and totaled 345 ha. Timber harvest is a method that creates new Golden-winged Warbler nesting habitat via cutting of mature trees to revert the site to young forest with adequate residual basal area (2.3–9.2 m<sup>2</sup>/ha). Old field management sites ( $n = 12$ ) were located in NC and WV, and ranged in size from 1 to 125 ha, and totaled 566 ha. Old field management is generally used to create and maintain Golden-winged Warbler habitat by using mechanical methods to revert succession on fallow fields. The goal of this management strategy is to restrict the woody vegetation to 30%–60% shrub and sapling cover within a managed area. Prescribed fire – young forest ( $n = 5$ ) and prescribed fire-old field ( $n = 2$ ) sites were located in TN. Prescribed fire-young forest sites ranged in size from 3.5 to 20.5 ha and totaled 48 ha. Prescribed fire –old field sites ranged in size from 52.5 to 61.3 ha and totaled 116 ha. Both prescribed fire management scenarios use fire as an additional treatment on either timber harvest or old field management sites. Prescribed fire arrests succession in a manner that creates or maintains Golden-winged Warbler nesting habitat. Although fire creates habitat for this species, burning produces vegetation conditions that are sufficiently different from their initial management conditions (timber harvest and old field management) to warrant separate categories.

### 2.3. Nest searching and monitoring

During 2012–2014 spring breeding seasons, we searched for Golden-winged Warbler breeding pairs across 45 study sites. We attempted to locate nests of all pairs within treatment areas. To minimize any bias associated with nest location discovery, we consciously searched for nests (and parents) in all portions of each site to ensure that a representative sample of nests was obtained. We further minimized the potential bias of discovering a disproportionate number of nests in open vegetation types by following female behavioral cues (such as “tzip” calls (Ficken and Ficken, 1968)), nest material or food carries, and inconspicuous movements to areas with nesting cover) to locate nests rather than systematic searching (Martin and Geupel, 1993). Regardless of nest discovery cue, we focused our attention solely on nests built within the boundaries of each managed site.

For nests parented by phenotypic Golden-winged Warbler pairs, we monitored daily nest survival across sites using methods outlined in Martin and Geupel (1993, Fig. 3). We checked nests every 2–4 days initially and more frequently as fledging approached to maximize accuracy of nest fate determination while minimizing potential negative impacts of visiting nests. We classified a nest as “successful” if at least one Golden-winged Warbler nestling fledged. To decrease bias associated with misidentification of nest fate, we primarily used behavioral cues to determine nest fate as nest condition may be an unreliable gauge of nest success (Williams and Wood, 2002; Streby and Andersen, 2013). When nests were empty of chicks around the date fledging was anticipated, we carefully looked for behaviors such as adult alarm chips, adults carrying prey, and the visual/vocal cues produced by fledglings (Streby and Andersen, 2013, McNeil pers. obs.). We also found it helpful to have a partially-banded population of males which assisted in the identification of post-fledging families (see Fig. 3).

## 2.4. Territory delineation

To assist in the detection of females and the quantification of territory density, we mapped the territories of all male Golden-winged Warblers within each managed site. To accomplish this, we captured as many males at each site as possible using mist nets and Type I song audio lures (Swarthout et al., 2009). Each captured male was marked with a USGS aluminum band and 1–3 colored leg bands arranged to give each male a unique combination of colors so all males could be discerned from neighbors. We captured males such that territories of any non-banded males were flanked by color-banded males. After banding was complete (1–2 weeks in each study area, each season), technicians visited each site to map the territories every 2–3 days throughout the season. Technicians mapped each territory using a handheld GPS receiver to record the coordinates of all song perches and other sites where individual males were visually observed at least 5 min apart. We visited each male a minimum of eight times over the breeding season to collect 20–30 point locations used to delineate territory boundaries within each study site. Territory mapping provided a precise estimate of territory density for each site.

## 2.5. Vegetation sampling

We conducted vegetation surveys using a standardized sampling protocol at Golden-winged Warbler nests and at random locations. We conducted random vegetation plots at all sites where nest-monitoring occurred ( $n = 44$  sites) as well as an additional 28 sites for a total of 72 sites with vegetation sampling. Additional sites were those where territory delineation occurred and no warbler nests were located. We sampled one random location for every ha of treated area using systematic-random sampling which provided a representative sample of each site in its entirety, independent of warbler nest site selection. For nest locations, we measured vegetation characteristics after determining nest fate. We used a nested plot design (1-m, 5-m, and 11.3-m radius plots) centered on each nest and each random location. We visually estimated percent cover for six mutually-exclusive components of microhabitat: bare ground, leaf litter, grass, forbs, blackberry/raspberry (*Rubus* spp.), and woody plant species within the 1-m radius plot. To ensure that visual estimation of percent cover was consistent, technicians were trained using “dummy” locations until each crew could consistently arrive at consensus as to each location’s cover composition. We considered all grasses (family: Poaceae) and sedges (family: Cyperaceae) collectively as “grass”. Forbs were any herbaceous broadleaf plant (e.g., *Solidago* spp., *Aster* spp.) and any woody-stemmed plant (i.e., shrubs or saplings) was placed within the woody cover category. The plant category *Rubus* only included species from the genus *Rubus*.

Within the 5-m radius plots, we tallied 1–2 m tall shrubs (hereafter, short shrubs), >2 m tall shrubs (hereafter, tall shrubs), and saplings. We considered woody plants with multiple primary stems branching below the soil to be “shrubs”. Shrub species were typically those which remained small in size (generally <3 m) and thin in diameter (<10 cm at breast height). Common representative species within the shrub category were witch hazel (*Hamamelis virginiana*) or multiflora rose (*Rosa multiflora*). We considered “saplings” to be single stems that branched above the soil line, were <10 cm in diameter at breast height (DBH), and >0.5 m tall. Saplings were usually represented in the habitat and nearby landscape by mature tree counterparts. Within 11.3 m of plot center, we quantified basal area by measuring DBH of all trees (>10-cm DBH) using a standard diameter tape. We visually estimated the average shrub height (m), and average sapling height (m) across the entire 11.3-m plot. Distance-to-nearest edge was quantified using ArcGIS: ArcMap 10.3 and represented the Euclidean distance of the nest to the closest forest edge.

## 3. Data analysis

### 3.1. Nest survival models

We used an information theoretic approach to evaluate the effects of several variables of interest on Golden-winged Warbler nest survival (Burnham and Anderson, 2002). We began analyses by generating a set of ecologically plausible hypotheses and then constructed corresponding *a priori* models for each using the Nest Survival module in program MARK (ver. 7.1, Colorado State University, Ft. Collins, Colorado, USA). We modeled the binomially distributed data with the user-defined, logit-link function while simultaneously considering associations with ecologically plausible covariates. We did not standardize individual covariates, because the unstandardized covariates did not affect numerical optimization (Dinsmore et al., 2002; Rotella, 2007). However, we did standardize MARK nesting dates for each study area such that the earliest nest date across all years were defined as MARK “day 1” for each of the four study areas to account for latitudinal differences in nesting chronology (Aldinger et al., 2015).

We used Akaike’s Information Criterion adjusted for small sample bias ( $AIC_c$ ) for model selection (Burnham and Anderson, 2002). We considered the model with the lowest  $AIC_c$  value to be the best-supported model given the data and models with  $\Delta AIC_c \leq 2$  to be plausible, competing models (Burnham and Anderson, 2002). We assessed the relative plausibility of each model in the model suite by comparing individual model weights ( $w_i$ ). We used  $\beta$  coefficients and their standard errors (SE), and 95% confidence intervals (CI) for covariates in supported models to infer the biological importance of covariates. We included all nests that reached at least the egg-laying stage in our nest-survival analyses (i.e., active nests with contents). We split our analyses into two primary model suites. Model suite 1 included models that considered management scenario ( $n = 5$ ), study area (i.e., state), time-within-season (linear and quadratic), vegetation community type (i.e., agricultural

**Table 1**

Covariates, abbreviations, and units used in Golden-winged Warbler nest survival models for model suite II.

Covariate	Abbreviation	Units
Bare ground cover	bare	% cover/1 m
Leaf litter cover	litter	% cover/1 m
Non-vegetated (Bare + Litter) cover	non-veg	% cover/1 m
Grass cover	grass	% cover/1 m
Forb cover	forb	% cover/1 m
Herbaceous (Grass + Forb) cover	herb	% cover/1 m
<i>Rubus</i> spp. cover	<i>Rubus</i>	% cover/1 m
Woody	woody	% cover/1 m
Non-herbaceous ( <i>Rubus</i> + woody)	non-herb.	% cover/1 m
Short (1–2 m) shrub count	sh. shrub	count/5 m
Tall (>2 m) shrub count	tall shrub	count/5 m
Sapling count	sapling	count/5 m
All shrub count (short shrubs + tall shrubs)	all shrubs	count/5 m
Shrubs & saplings (all shrubs + sapling count)	shrubs & saps	count/5 m
Height of shrub layer	shrub hgt.	m (11.3 m radius)
Height of sapling layer	sap hgt.	m (11.3 m radius)
Basal area	basal	m <sup>2</sup> /ha (11.3 m radius)
Distance-to-nearest edge	DTNE	m

or silvicultural), and year. Model suite II included models that considered vegetation covariates we sampled at each nest site across all sites and then separately for each management scenario with appropriate sample sizes. Models within suite II included single-covariate models (e.g., grass), quadratic effects (e.g., grass<sup>2</sup>), and multiple-covariate models (e.g., *Rubus* + short shrub + forb) that we created by combining field-measured covariates (Table 1). For each model set within suite II, covariates from suite I were added if those covariates performed better than a constant model within the management scenario candidate set. The result was that some management scenario model sets included 'suite I' covariates (e.g., time + grass) and the equivalent model in a different management scenario lacking the suite I term (e.g., grass, no time effect).

### 3.2. Attainment of conditions recommended for nesting

We defined “recommended” nesting vegetation as the recommended vegetation characteristics for nest sites from the Conservation Plan. Recommended vegetation for Golden-winged Warbler nest sites includes 0%–10% bare ground, 2%–25% grass, 5%–40% *Rubus* (5%–40%), and 5%–50% woody vegetation (Roth et al., 2012). For forbs, the Conservation Plan recommends 4%–45% cover for “non-forest” sites (i.e., grazing management, old field management, and prescribed fire – old field) and 45%–100% for “silviculturally derived” sites (i.e., timber harvest, and prescribed fire – young forest). To evaluate the attainment of recommended nesting vegetation, we examined vegetation characteristics at stand-level plots. We defined “attainment” as the proportion of stand-level plots having vegetation characteristics that fell within ranges for recommended nesting vegetation. We then calculated the number of categories (of the five possible) that each plot attained.

### 3.3. Habitat-specific productivity

We estimated habitat-specific productivity for each management scenario as the number of fledglings produced per unit area (10 ha). Productivity was the product of four components: (1) territory density, (2) pairing rate, (3) probability of nest success given three nesting attempts ( $1 - [1 - \text{DSR}^{25}]^3$ ), and (4) number of fledglings produced per successful nest. Golden-winged Warblers typically require 25 days from onset of incubation to fledging (Confer et al., 2011). We chose to use three nesting attempts as the expended effort because this level of re-nesting is common among Appalachian *Vermivora* spp. (K. Aldinger, pers. obs.). We used a constant pairing rate (0.8) among management scenarios based on a compilation of pairing rates from Golden-winged Warbler populations across the Appalachian Mountain region (Confer et al., unpubl. data). We used the *propagate* package in program R (version 3.1.2, R Development Core Team 2014), a general function for the calculation of uncertainty propagation, to incorporate the uncertainty associated with each component into our final estimate of habitat-specific productivity. Finally, we also used the lowest and highest 95% confidence values for density, clutch size, and nest survival to calculate “worst case” and “best case” productivity for each management scenario.

## 4. Results

### 4.1. Attainment of recommended vegetation

We quantified vegetation at 2719 stratified random plots across 45 managed sites over the course of our study (746 in grazing management, 627 in old field management, 146 in prescribed fire – old field, 335 in prescribed fire – young forest, and 865 in timber harvest). Across all management scenarios, the attainment of individual vegetation conditions in random plots

**Table 2**

Attainment of five vegetation variables (bare ground, grass, forbs, *Rubus* and woody) as measured at stratified random ( $n = 2719$ , top) and nest locations ( $n = 288$ , bottom). Vegetation plots were sampled from 2012 to 2014 within sites managed in accordance to practices used by NRCS-WLFW to create Golden-winged Warbler habitat across the Appalachian Mountains. Plots were considered to have attained recommended levels of each habitat characteristic if the observed values fell within the recommended ranges by Roth et al. (2012). Values in parentheses represent standard error. Mode values for each management scenario are bolded.

Management scenario	Zero	One	Two	Three	Four	Five
Percent of attainment at random locations						
Grazing management	0.5 (0.2)	14.4 (2.8)	<b>36.88 (3.5)</b>	36.7 (3.5)	9.97 (1.7)	1.6 (0.6)
Old field management	0.9 (0.6)	26.1 (5.8)	29.94 (5.1)	<b>33 (6.3)</b>	9.2 (2.9)	0.8 (0.4)
Prescribed fire –old field	1.5 (1.5)	15.5 (0.9)	<b>46.3 (4.7)</b>	25.8 (5.4)	9.3 (1.1)	1.6 (0.5)
Prescribed fire –young forest	3.1 (0.9)	19.2 (4.5)	<b>41.9 (3.4)</b>	27.2 (3.6)	6.8 (1.9)	1.8 (0.7)
Timber harvest	6.4 (1.1)	33.6 (4.8)	<b>36.1 (3.9)</b>	15.3 (2.8)	8 (2.5)	0.6 (0.3)
All scenarios combined	3.2 (0.5)	25 (2.6)	<b>36 (2.1)</b>	26.3 (2.3)	8.5 (1.2)	1.1 (0.2)
Percent of attainment at Golden-winged Warbler nest locations						
Grazing management	0	10 (10)	6.3 (3.7)	<b>46.8 (8.5)</b>	28 (6.7)	8.8 (3.6)
Old field management	0	6.9 (2.6)	16.2 (4)	<b>46.4 (7.6)</b>	27.8 (5.2)	2.8 (2.1)
Prescribed fire –old field	0	9.1 (6.3)	37.4 (8.8)	<b>40.7 (2.2)</b>	10 (10)	2.9 (2.9)
Prescribed fire –young forest	0	22.2 (19.6)	18.9 (11.6)	<b>54.4 (20.2)</b>	4.4 (4.4)	0
Timber harvest	0	20.6 (8.2)	<b>37.9 (8.5)</b>	32.9 (8.5)	8.6 (3.9)	0
All scenarios combined	0	14.2 (4.3)	22.2 (3.9)	<b>42.8 (4.6)</b>	17.8 (3)	3 (1.2)

**Table 3**

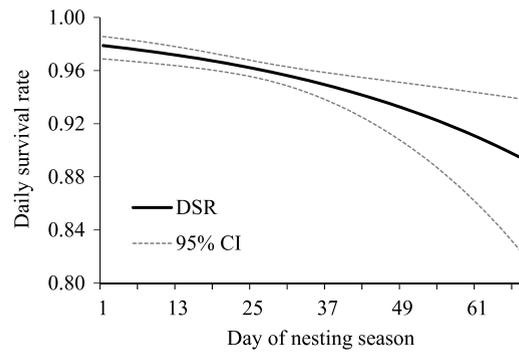
Model-selection results for daily survival rate (DSR) of nests of Golden-winged Warblers from model suite 1 using program MARK.  $AIC_c$  is Akaike's Information Criterion adjusted for small sample size,  $\Delta AIC_c$  is the difference in  $AIC_c$  values between individual models and the top model,  $w_i$  is the model weight, and  $K$  is the number of parameters in the model. We presented beta estimates for covariates in the plausible ( $\Delta AIC_c \leq 2$ ) models.

Model	$\Delta AIC_c$	$w_i$	$K$	Beta coefficients
int. + time	0.00	0.71	2	$\beta_1 = 3.86 (3.45-4.27)$ , $\beta_2 = -0.025(-0.04 - -0.01)$ ,
int. + time + time <sup>2</sup>	1.89	0.28	3	$\beta_1 = 3.98 (3.17-4.77)$ , $\beta_2 = -0.035(-0.09 - -0.02)$ , $\beta_3 = 0.00 (-0.001-0.001)$
intercept only (constant; int.)	10.28	0.00	1	
int. + management scenario	11.37	0.00	5	
int. + vegetation community type	11.62	0.00	2	
int. + study area	13.83	0.00	4	
int. + year	14.20	0.00	3	
int. + management scenario + year	15.02	0.00	7	
int. + vegetation community type + year	15.61	0.00	4	
int. + study area + year	17.77	0.00	6	

ranged from 30% (for grass) to 65% (bare ground). Among nests within each management scenario, the dominant vegetation immediately surrounding nests was forb (broadleaf herbaceous plants) with the exception of nests in timber harvest, which were dominated by woody vegetation. The attainment of recommended levels for all five nest vegetation variables occurred simultaneously in 39 of 2719 random plots (1.4%) and 12 of 288 nest site plots (4.2%) (Table 2). The average number of variables that were attained simultaneously in a single random plot ranged from 1.9 (SE = 0.12) in timber harvests to 2.5 (SE = 0.08) in grazing management sites. The average number of variables that were attained simultaneously in a single nest site plot ranged from 2.3 (SE = 0.10) in timber harvests to 3.4 (SE = 0.11) in grazing sites.

#### 4.2. Management scenario and temporal effects on nest survival (suite 1)

From 2012 to 2014, we located and monitored 288 nests that were parented by phenotypic Golden-winged Warbler pairs: 61 nests in grazing management, 86 nests in old field management, 48 nests in prescribed fire –old field, 14 nests in prescribed fire –young forest, and 79 nests in timber harvests. Raw nest success across all sites was 49.6% and mean clutch size was 4.4 eggs (site range: 4.14–4.57). Brown-headed Cowbird was rare (only 4.3% of nests) and therefore could not be included within models. Models that included management scenario as a covariate had nearly no support (all  $\Delta AIC_c \geq 10$ ; Table 3), suggesting that nest daily survival rate (DSR) was similar among the five management scenarios. Across management scenarios, DSR averaged  $0.96 \pm 0.003$ , which equates to an annual probability of  $0.77 \pm 0.035$  for a pair to produce a successful nest, given three attempts. The best-supported model contained a linear time-within-season covariate and was included in all subsequent models tested in model suite 2. A model containing linear and quadratic time-within season covariates also was plausible ( $\Delta AIC_c = 1.89$ ). Estimated DSR decreased over time with nests built later in the breeding season having lower success rates (Fig. 4).



**Fig. 4.** Daily survival rate (DSR) of Golden-winged Warbler (*V. chrysoptera*) nests as a function of the best-supported model from model suite I. The best-supported model within model suite I included only a covariate allowing daily survival rate (DSR) to vary as a function of time (i.e., day of nesting season).

#### 4.3. Vegetation effects on nest survival (suite II)

Prescribed fire –young forest was excluded from the model suite II analysis due to small sample size ( $n = 14$  nests). All other management scenarios were included in model suite II and each was also modeled separately. We observed a strong negative effect of date on nest survival within old field management and prescribed fire –old field but not for timber harvest and grazing management; a time effect was thus a component of old field management and prescribed fire –old field but not for timber harvest and grazing (which only included habitat covariates). Five models were competing among those generated for prescribed fire –old field nests, one of which was a time-only model ( $S(\text{intercept} + \text{time})$ ;  $\Delta\text{AIC}_c = 01.92$ ). Other plausible models ( $\Delta\text{AIC}_c < 2.0$ ) for prescribed fire –old field included an effect of 1–2 m shrub abundance and basal area (linear and quadratic for both), but the  $\beta$  estimates for all covariate terms overlapped zero suggesting weak relationships with nest survival. Nest survival in timber harvests also appeared to be largely independent of vegetation as the top model ( $S(\text{intercept} + \text{Rubus} + \text{Rubus}^2)$ ) had no competing models and covariate term  $\beta$  estimates overlapped zero (see Table 4).

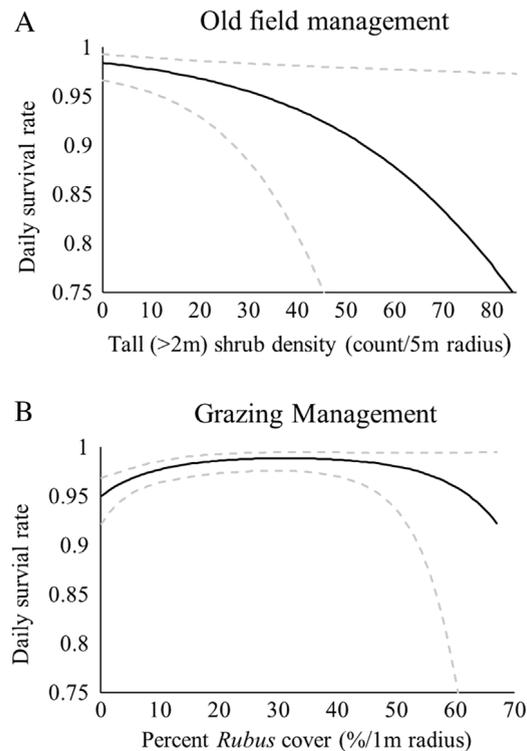
Old field management and grazing management sites showed stronger relationships between nest survival and vegetation. Nest survival in old field management sites appeared to be inversely related to the linear abundance of >2 m tall shrubs (Fig. 5A) although a quadratic relationship was also plausible ( $S(\text{intercept} + \text{time} + \text{tall shrub} + \text{tall shrub}^2)$ ;  $\Delta\text{AIC}_c = 0.59$ ). A third model which included a term for quadratic forb effects was also competing but the  $\beta$  estimates for the covariate terms overlapped zero suggesting a weak effect on nest survival. Grazing management models included only two competing models: a quadratic *Rubus* effect (Fig. 5B) and a linear *Rubus* effect with a combined model weight of 0.55.

#### 4.4. Management scenario-specific productivity

Across all management scenarios, Golden-winged Warbler nests produced 3.9 (95% CI: 3.7–4.1) fledglings/successful nest and management scenarios varied from 3.5 (95% CI: 2.4–4.6) in Prescribed fire–young forest sites to 4.1 (95% CI: 3.7–4.5) in grazed sites. Mean productivity varied considerably among management scenarios ranging from 2.1 fledglings/10 ha for prescribed fire – young forest to 8.6 fledglings/10 ha for prescribed fire – old field (Table 5). When we used the lowest 95% confidence bounds for male density, clutch size, and nest success for each management scenario, productivity of fledglings varied from 0 (prescribed fire – young forest) to 3.3 fledglings/10 ha (prescribed fire – old field). When we used the highest 95% confidence bounds for male density, clutch size, and nest success for each management scenario, productivity of fledglings varied from 6.9 in grazing management to 16.6 fledglings/10 ha in prescribed fire–old field (Table 5).

### 5. Discussion

Our study revealed that nesting success was comparable among the five NRCS-WLFW management scenarios we examined. Thus, although each management scenario produces or maintains habitat in different ways, they appear to have equal capability of producing conditions that support successfully-nesting Golden-winged Warblers. Past studies on other species have shown that various management alternatives produced varying levels of nesting success (Robertson, 1972; Suarez et al., 1997; Morse and Robinson, 1999; Gram et al., 2003; Remeš, 2003). These studies contrast with ours in that the plant communities we studied were created/maintained specifically for Golden-winged Warblers (via management scenarios) and the intended management result in all cases were conditions expected to benefit nesting Golden-winged Warblers (Bakermans et al., 2011; Roth et al., 2012). Other studies have also demonstrated that species-specific habitat management targeted toward creating nest site vegetation may support higher levels of nest survival than unmanaged sites (Beauchamp et al., 1996; Smith et al., 2002; Emery et al., 2005; Bakermans and Rodewald, 2009; Boves et al., 2013). The lack of among-scenario variation in nest success in our study further highlights the relatively consistent nesting success



**Fig. 5.** Among four nest survival model sets (timber harvest, old field management, grazing management, and prescribed fire — old field), two management scenarios (old field management and grazing management) exhibited significant relationships with habitat covariates. For old field management (A), the top model included a term for tall (> 2 m) shrubs. Sites maintained through grazing management (B) revealed a significant relationship between nest survival and the percent cover for *Rubus* spp.

rates these anthropogenic habitats provide to Golden-winged Warblers when species-specific, science-based guidelines are implemented.

The average daily nest survival rate as calculated by the top model in model suite I revealed that, not only was nesting success relatively high within managed habitats, but most Golden-winged Warbler pairs (76.7%) successfully fledged young each season when re-nesting was taken into account. Although our study did not observe the highest nest success rates ever reported for Golden-winged Warblers (72.5%; Klaus and Buehler, 2001), our observed rates of raw nesting success (49.6%) are consistent with or higher than many previously-reported rates (Confer et al., 2003; Bulluck and Buehler, 2008; Kubel and Yahner, 2008; Aldinger et al., 2015).

Our analyses also revealed how Golden-winged Warbler nesting success varied as a function of factors other than management scenario. Within model suite 1, we found that a linear time covariate best predicted daily survival of Golden-winged Warbler nests. Declining nest survival with advancing season has been reported previously for many species (Hochachka, 1990; Verhulst et al., 1995; Sperry et al., 2008), including Golden-winged Warblers (Bulluck and Buehler, 2008; Aldinger et al., 2015). Interestingly, when we conducted individual analyses for each management scenario, timber harvest ( $n = 83$  nests) and grazing management ( $n = 76$  nests) did not show the same time trend as observed within suite 1 ( $n = 288$  nests). Although the mechanisms behind this pattern remain unclear, it may be driven by differences in predator community dynamics or plant composition among the management scenarios. Plant communities derived via differing management actions could easily support different predation dynamics that might be realized as either a seasonally-constant or seasonally-increasing predation pressure (e.g., Sperry et al., 2008). Moreover, differences in leaf growth phenology among plant communities supported through different management scenarios could affect vertical and/or horizontal visibility of nests in a time-variant manner. Predator community dynamics may also vary among communities that are created using different management scenarios and thus exhibit differences in plant succession patterns (Kitchings and Levy, 1981; Carey and Johnson, 1995; Churchfield et al., 1997), something unexplored by our study.

Model suite 2 revealed few relationships between daily nest survival and the microhabitat features we quantified. Within grazing management sites, our results suggest that *Rubus* cover maintained at levels from 8%–55% appeared to achieve greater-than-average nest survival rates. *Rubus* cover was previously found to be an important feature that influenced female Golden-winged Warbler nest-site selection (Terhune et al., 2016), but may also contribute to lower nest success above 18% *Rubus* cover (Aldinger and Wood, 2014). We also found statistically significant negative relationships between tall-shrub count and daily nest survival within old field management sites, but the relationship was weak and confidence intervals

**Table 4**

Model-selection results for daily survival rate (DSR) of Golden-winged Warblers nests from model suite II using program MARK. Suite II included vegetation covariates and were modeled for prescribed fire–old field, old field management, grazing management, and timber harvest.  $AIC_c$  is Akaike's Information Criterion adjusted for small sample size,  $\Delta AIC_c$  is the difference in  $AIC_c$  values between individual models and the top model,  $w_i$  is the model weight, and  $K$  is the number of parameters in the model. We presented beta estimates for covariates in the plausible ( $\Delta AIC_c \leq 2$ ) models. All variables in Table 1 were included in models. We present top five models for each candidate set (no models ranked >5th had  $\Delta AIC_c \leq 2$  in any set).

Management scenario, model	$\Delta AIC_c$	$w_i$	K	Beta Coefficients
<b>Prescribed fire – old field</b>				
int. + time + sm. shrub	0.00	0.12	3	$\beta_1 = 3.95$ (3.01–4.90), $\beta_2 = -0.038$ (–0.07––0.01), $\beta_3 = 0.15$ (–0.08–0.37)
int. + time + basal area	1.41	0.06	3	$\beta_1 = 3.85$ (2.88–4.82), $\beta_2 = -0.042$ (–0.08 ––0.01), $\beta_3 = 0.05$ (–0.02–0.11)
int. + time + sm. shrub + sm. shrub <sup>2</sup>	1.56	0.06	4	$\beta_1 = 3.97$ (3.02–4.92), $\beta_2 = -0.038$ (–0.07––0.005), $\beta_3 = -0.04$ (–0.59–0.52), $\beta_4 = 0.02$ (–0.03–0.07)
int. + time + basal area + basal area <sup>2</sup>	1.84	0.05	4	$\beta_1 = 3.69$ (2.70–4.68), $\beta_2 = -0.05$ (–0.08––0.01), $\beta_3 = 0.16$ (–0.02–0.35), $\beta_4 = -0.01$ (–0.01–0.003)
int. + time	1.92	0.05	2	$\beta_1 = 4.02$ (3.06–4.98), $\beta_2 = -0.036$ (–0.07––0.003)
<b>Old field management</b>				
int. + time + tall shrub	0.00	0.15	3	$\beta_1 = 4.16$ (3.36–4.96), $\beta_2 = -0.03$ (–0.05––0.01), $\beta_3 = -0.04$ (–0.07––0.01)
int. + time + tall shrub + tall shrub <sup>2</sup>	0.59	0.11	4	$\beta_1 = 4.42$ (3.49–5.35), $\beta_2 = -0.04$ (–0.06––0.01), $\beta_3 = -0.07$ (–0.14––0.01), $\beta_4 = 0.001$ (–0.0001––0.001)
int. + time + forb + forb <sup>2</sup>	0.85	0.09	4	$\beta_1 = 6.11$ (4.04–8.17), $\beta_2 = -0.04$ (–0.06––0.01), $\beta_3 = -0.08$ (–0.16–0.01), $\beta_4 = 0.001$ (–0.0001–0.002)
int. + time + woody + woody <sup>2</sup>	2.03	0.05	4	
int. + time + bare	2.24	0.05	3	
<b>Timber harvest</b>				
int. + <i>Rubus</i> + <i>Rubus</i> <sup>2</sup>	0.00	0.41	3	$\beta_1 = 3.12$ (2.69–3.56), $\beta_2 = -0.12$ (–0.33–0.07), $\beta_3 = 0.01$ (–0.01–0.03)
int. + <i>Rubus</i>	2.15	0.14	2	
int. + woody	3.72	0.06	2	
intercept only (constant)	5.52	0.03	1	
int. + time + woody + woody <sup>2</sup>	5.63	0.03	3	
<b>Grazing management</b>				
int. + <i>Rubus</i> + <i>Rubus</i> <sup>2</sup>	0.00	0.32	3	$\beta_1 = 2.94$ (2.46–3.42), $\beta_2 = 0.10$ (0.03–0.16), $\beta_3 = -0.001$ (–0.003––0.159)
int. + <i>Rubus</i>	1.61	0.14	2	$\beta_1 = 3.11$ (2.63–3.54), $\beta_2 = 0.04$ (0.01–0.07)
int. + bare + bare <sup>2</sup>	3.01	0.07	3	
int. + basal area + basal area <sup>2</sup>	3.09	0.07	3	
int. + DTNE	4.31	0.04	2	

**Table 5**

Golden-winged Warbler demographics observed from 2012–14 among five habitat management scenarios across the Appalachians. Annual nesting success is scenario-specific daily survival rate (DSR) extrapolated to consider the possibility of up to three nesting attempts ( $1-[1-DSR^{25}]^3$ ). Brood size is the number of fledglings produced per successful nest. Male density is the number of male territories/10 ha as determined by territory mapping. Productivity is the number of fledglings produced/10 ha and is the product of annual nesting success, brood size, male density, and a constant pairing rate of 0.80. For annual nesting success, brood size, and male density, parentheses indicate 95% confidence intervals. For productivity, values shown within parenthesis represent “worst case” and “best case” extremes using the lower and upper 95% confidence intervals (respectively) for the values of annual nesting success, brood size, and male density.

Management scenario	Annual nesting success (annual likelihood)	Brood size (fledglings/nest)	Male density (males/10 ha)	Productivity (fledglings/10 ha)
Grazing management	0.88 (0.78–0.98)	4.1 (3.7–4.5)	1.4 (0.8–2.0)	4.0 (1.8–6.9)
Old field management	0.71 (0.57–0.86)	3.8 (3.5–4.1)	2.3 (1.7–2.8)	4.9 (2.7–7.9)
Prescribed fire–old field	0.70 (0.52–0.88)	4.1 (3.8–4.4)	3.7 (2.1–5.4)	8.6 (3.3–16.6)
Prescribed fire–young forest	0.39 (0–0.89)	3.5 (2.4–4.6)	1.9 (0.8–3.1)	2.1 (0–10.1)
Timber harvest	0.74 (0.6–0.87)	4.1 (3.7–4.4)	2.4 (1.7–3.0)	5.6 (3.1–9.1)
All scenarios combined	0.77 (0.7–0.84)	3.9 (3.7–4.1)	2.3 (1.6–3.1)	5.6 (3.2–8.6)

were wide. Finding few habitat covariates associated with daily nest survival is promising because it supports the idea that different management scenarios are similar in their ability to produce high nest survival.

Given that nest survival was quite high across all of our study sites, it was surprising that the attainment of recommended nest-site vegetation at random locations was low (1.1% of plots surveyed), regardless of management scenario. Although this seems somewhat paradoxical, this observation may be driven by the fact that Golden-winged Warbler territories

are structurally diverse and must support life history requisites other than nesting. Golden-winged Warblers are known to rely upon residual canopy trees for singing and foraging (Roth et al., 2014), saplings/shrubs for foraging (Bellush et al., 2016), mature forest for foraging and prospecting (Frantz et al., 2016), and forest understories for post-fledging (Streby et al., 2016). Indeed, despite the poor attainment of recommended nest-site conditions that we observed, the five management scenarios appear to result in a sufficient amount of high quality potential nest sites. Although conservation recommendations for Golden-winged Warblers often include those for non-nesting habitat attributes (e.g. residual trees, proximity to source patches; Roth et al., 2012; Bakermans et al., 2015), many avian conservation studies, including those for Golden-winged Warblers, focus heavily on ensuring the availability of nesting habitat (Brawn and Balda, 1988; Baillie and Peach, 1992; Newton, 1994; Holmes et al., 1996). Our study demonstrates that young forests and shrublands managed for passerine breeding habitat need not be composed entirely of “nesting” habitat. While our study sites appeared to have few areas that met the nesting habitat recommendations (Roth et al., 2012), we observed that female warblers often defied these recommendations with some nest sites in every management scenario, only adhering to a single habitat feature’s recommended range (Table 2).

Limited nest-site availability combined with consistently high nest survival observed during this study demonstrates a level of plasticity by Golden-winged Warblers to find quality nest sites. Because nest sites often failed to meet the conditions recommended by the Conservation Plan (Table 2), it appears that female Golden-winged Warblers are fairly flexible in their selection of vegetation features essential to successful nesting. Indeed, we anecdotally observed females apparently substituting *like* habitat features across plant classes. For example, warblers nesting in timber harvests regularly appeared to substitute forb cover for low-growing shrub cover (e.g. *Vaccinium* spp.), which may serve a similar function for nest survival. Because many young forest bird species, including the Golden-winged Warbler, exhibit high breeding site fidelity (Schlossberg, 2009; Confer et al., 2011), some plasticity in nest-site selection may represent an adaptation to breeding within rapidly-changing successional communities. Moreover, because early-successional communities are understood to have historically been derived from a variety of natural sources (i.e., beaver, wildfire, wind storms, etc.), successional specialists may be somewhat flexible with certain nest-site requirements (e.g., forbs vs woody vegetation). In addition to the results presented here on Golden-winged Warblers, it seems likely that these results would apply in some capacity across a variety of early-successional birds. For example, many other declining passerines also nest within Golden-winged Warbler habitat (e.g., Chestnut-sided Warbler *Setophaga pensylvanica*, Field Sparrow, *Spizella pusilla*). That the Golden-winged Warbler is considered a habitat specialist (even within early-successional habitats, see Confer and Knapp, 1981) yet remains tolerant of variation among management types suggests that different species with wider habitat niches may also be tolerant of a range of habitat conditions.

Production of fledglings (fledglings produced/10 ha) is arguably a more useful metric than nest survival alone when evaluating management success (Holmes et al., 1992; Flaspohler et al., 2001). Because maximizing the output of fledgling birds per unit of managed area is of key interest to managers, nest survival as a stand-alone demographic may be misleading when the true variable of interest may be reproductive output at the population level (Boves et al., 2013). It is thus important for land managers to collectively consider multiple components of species’ breeding ecology (e.g., territory density, clutch size, nest survival, and post-fledgling survival) when evaluating the relative values of different management actions (Boves et al., 2013). Among the three NRCS-WLFW management scenarios with sufficient sample sizes (grazing management, old field management, and timber harvest), fledgling productivity estimates were similar (4.0–5.6 fledglings/10 ha). This finding is important because not all management scenarios are equally-appropriate for implementation or favored by managers in all areas of the Golden-winged Warbler breeding range. Programs like NRCS-WLFW are often limited in the management options available, as implementation must not only adhere to species management guidelines, but also to funding constraints and private landowner objectives. While we believe fledgling productivity as we have quantified it is a better metric of management success compared to nesting success alone, we acknowledge that it still falls short of providing a complete evaluation and comparison of management scenarios. Consideration of fledgling survival to independence is an important demographic response to management that we did not examine in this study. While quantifying fledgling survival to independence is labor intensive and logistically challenging, incorporating it into future research would better evaluate the relative contribution of management actions to population recovery (Hostetler et al., 2015). Past studies have demonstrated that nest success and post-fledging survival can be independent parameters and both are important to consider (Cohen and Lindell, 2004; King et al., 2006; Schmidt et al., 2008). With this in mind, our study marks an important step in the evaluation of different management alternatives for Golden-winged Warblers, but we also recognize that any differences in post-fledging survival among management scenarios could alter outcomes.

## 6. Conclusions

To consider Golden-winged Warbler conservation within the iterative framework of adaptive management, we evaluated both the habitats produced through management as well as reproductive dynamics within those habitats. Although Golden-winged Warblers are generally regarded as habitat specialists, within early successional communities managed broadly under recently developed guidelines (Bakermans et al., 2011; Roth et al., 2012), the species appears to be quite flexible with respect to nest-site vegetation structure. Floristic composition within the various NRCS management scenarios was variable, yet Golden-winged Warbler nest survival did not differ and was only weakly associated with the vegetation features we quantified. Consideration of vegetation conditions alone might deem sites monitored in this study as management

failures. However, associated nesting data suggest the opposite. Because our nest survival rates were high and consistent with previously reported levels for this species, habitat created for nesting Golden-winged Warblers under NRCS-WLFW appears to have high potential to contribute to the maintenance or recovery of this species. Moreover, for those management scenarios for which we had sufficient sample sizes, we observed consistent rates of fledgling productivity when territory density, clutch size, pairing success, and nest survival were considered in combination. With this in mind, potential differences in post-fledgling survival would alter our recommendation that these management practices are equal in their benefits to the Golden-winged Warbler. Our study represents an accrual of evidence supporting the notion managed upland habitats (particularly timber harvest, old field management, and grazing management) host consistently high levels of Golden-winged Warbler nesting success and fledgling productivity. Thus the current habitat recommendations for Golden-winged Warblers, when met through NRCS management scenarios, are sufficient in producing a broad, but targeted range of habitat conditions that can be used successfully by breeding Golden-winged Warblers, which appear to be somewhat plastic in their nest-site requirements.

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## References

- Aldinger, K.R., Terhune II, T.M., Wood, P.B., Buehler, D.A., Bakermans, M.H., Confer, J.L., Flaspohler, D.J., Larkin, J.L., Loegering, J.P., Percy, K.L., Roth, A.M., Smalling, C.G., 2015. Variables associated with nest survival of Golden-winged Warblers (*Vermivora chrysoptera*) among vegetation communities commonly used for nesting. *Avian Conserv. Ecol.* 10 (6).
- Aldinger, K.R., Wood, P.B., 2014. Reproductive success and habitat characteristics of Golden-winged Warblers in high-elevation pasturelands. *Wilson J. Ornithol.* 126, 279–287.
- Askins, R.A., 2001. Sustaining biological diversity in early successional communities: The challenge of managing unpopular habitats. *Wildlife Soc. Bull.* 29, 407–412.
- Baillie, S.R., Peach, W.J., 1992. Population limitation in Palaearctic-African migrant passerines. *Ibis* 134, 120–132.
- Bakermans, M.H., Larkin, J.L., Smith, B.W., Fearer, T.M., Jones, B.C., 2011. Golden-winged Warbler Habitat Best Management Practices in Forestlands in Maryland and Pennsylvania. American Bird Conservancy. The Plains, Virginia. 26 pp.
- Bakermans, M.H., Rodewald, A.D., 2009. Think globally, manage locally: The importance of steady-state forest features for a declining songbird. *Forest Ecol. Manag.* 258, 224–232.
- Bakermans, M., Smith, B.W., Jones, B.C., Larkin, J.L., 2015. Stand and within-stand factors influencing Golden-winged Warbler use of regenerating stands in the central Appalachian Mountains. *Avian Conserv. Ecol.* 10 (1), 10. <http://dx.doi.org/10.5751/ACE-00747-100110>.
- Beauchamp, W.D., Nudds, T.D., Clark, R.G., 1996. Duck nest success declines with and without predator management. *J. Wildl. Manag.* 60, 258–264.
- Bellush, E.C., Duchamp, J., Confer, J.L., Larkin, J.L., 2016. Influence of plant species composition on Golden-winged Warbler foraging ecology in north-central Pennsylvania. In: Streby, H.M., Andersen, D.E., Buehler, D.A. (Eds.), *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*. In: *Studies in Avian Biology*, vol. 49, CRC Press, Boca Raton, FL, pp. 95–108.
- Bottrill, M.C., Walsh, J.C., Watson, J.E., Joseph, L.N., Ortega-Argueta, A., Possingham, H.P., 2011. Does recovery planning improve the status of threatened species? *Biol. Conserv.* 144, 1595–1601.
- Boves, T.J., Buehler, D.A., Sheehan, J., Wood, P.B., Rodewald, A.D., Larkin, J.L., Keyser, P.D., Newell, F.L., Evans, A., George, G.A., Wigley, T.B., 2013. Spatial variation in breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) throughout the Appalachian Mountains. *The Auk* 130, 46–59.
- Brawn, J.D., Balda, R.P., 1988. Population biology of cavity nesters in northern Arizona: Do nest sites limit breeding densities? *Condor* 90, 61–71.
- Buehler, D.A., Roth, A.M., Vallender, R., Will, T.C., Confer, J.L., Canterbury, R.A., Swarthout, S.B., Rosenberg, K.V., Bulluck, L.P., 2007. Status and conservation priorities of Golden-winged Warbler (*Vermivora chrysoptera*) in North America. *The Auk* 124, 1439–1445.
- Bulluck, L.P., Buehler, D.A., 2008. Factors influencing Golden-winged Warbler (*Vermivora chrysoptera*) nest-site selection and nest survival in the Cumberland Mountains of Tennessee. *The Auk* 125, 551–559.
- Burnham, P.K., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*, 2nd Edition. Springer Publications, Inc., New York, New York, USA.
- Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecol. Appl.* 5, 336–352.
- Churchfield, S., Hollier, J., Brown, V.K., 1997. Community structure and habitat use of small mammals in grasslands of different successional age. *J. Zool.* 242, 519–530.
- Ciuzio, E., Hohman, W.L., Martin, B., Smith, M.D., Stephens, S., Strong, A.M., Vercauteren, T., 2013. Opportunities and challenges to implementing bird conservation on private lands. *Wildl. Soc. Bull.* 37, 267–277.

- Cohen, E.B., Lindell, C.A., 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *The Auk* 121, 404–414.
- Confer, J.L., Hartman, P., Roth, A., 2011. Golden-winged Warbler (*Vermivora chrysoptera*). In: *The Birds of North America*, vol. 20, The Academy of Natural Sciences, The American Ornithologists Union, Washington D.C..
- Confer, J.L., Knapp, K., 1981. Golden-winged Warblers and Blue-winged Warblers: The relative success of a habitat specialist and a generalist. *The Auk* 98, 108–114.
- Confer, J.L., Larkin, J.L., Allen, P.E., 2003. Effects of vegetation, interspecific competition, and brood parasitism on Golden-winged Warbler (*Vermivora chrysoptera*) nesting success. *The Auk* 120, 138–144.
- Dinsmore, S.J., White, G.C., Knopf, F.L., 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83, 3476–3488.
- Ellefson, P.V., Kilgore, M.A., Phillips, M.J., 2001. Monitoring compliance with BMPs: the experience of state forestry agencies. *J. Forestry* 99, 11–17.
- Emery, R.B., Howerter, D.W., Armstrong, L.M., Anderson, M.G., Devries, J.H., Joynt, B.L., 2005. Seasonal variation in waterfowl nesting success and its relation to cover management in the Canadian prairies. *J. Wildl. Manage.* 69, 1181–1193.
- Ferraro, P.J., Pattanayak, S.K., 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biol.* 4, p. e105.
- Ficken, M.S., Ficken, R.W., 1968. Courtship of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. *Wilson Bull.* 80, 161–172.
- Flaspohler, D.J., Temple, S.A., Rosenfield, R.N., 2001. Effects of forest edges on Ovenbird demography in a managed forest landscape. *Conserv. Biol.* 15, 173–183.
- Frantz, M.W., Aldinger, K.R., Wood, P.B., Duchamp, J., Nuttle, T., Vitz, A., Larkin, J.L., 2016. Space and Habitat use of Breeding Golden-Winged Warblers in the Central Appalachian Mountains. In: Streby, H.M., Andersen, D.E., Buehler, D.A. (Eds.), *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*. In: *Studies in Avian Biology*, vol. 49, CRC Press, Boca Raton, FL, pp. 81–94.
- Frech, M.H., Confer, J.L., 1987. The Golden-winged warbler: Competition with the blue-winged warbler and habitat selection in portions of Southern, Central and Northern New York. *Kingbird* 2, 65–71.
- Gibbs, J.P., Snell, H.L., Causton, C.E., 1999. Effective monitoring for adaptive wildlife management: lessons from the Galapagos Islands. *J. Wildl. Manage.* 63, 1055–1065.
- Gill, F.B., 1980. Historical aspects of hybridization between Blue-winged and Golden-winged Warblers. *The Auk* 97, 1–18.
- Gram, W.K., Perneluzi, P.A., Clawson, R.L., Faaborg, J., Richter, S.C., 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conserv. Biol.* 17, 1324–1337.
- Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Cons.* 142, 14–32.
- Hill, N.P., Hagan III, J.M., 1991. Population trends of some northeastern North American landbirds: a half-century of data. *Wilson Bull.* 103, 165–182.
- Hochachka, W., 1990. Seasonal decline in reproductive performance of Song Sparrows. *Ecology* 71, 1279–1288.
- Holmes, R.T., Marra, P.P., Sherry, T.W., 1996. Habitat-specific demography of breeding black-throated blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *J. Anim. Ecol.* 65, 183–195.
- Holmes, R.T., Sherry, T.W., Marra, P.P., Petit, K.E., 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *The Auk* 109, 321–333.
- Hostetler, J.A., Sillett, T.S., Marra, P.P., 2015. Full-annual-cycle population models for migratory birds. *The Auk* 132, 433–449.
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Soc. Bull.* 29, 440–455.
- King, D.I., Degraaf, R.M., Smith, M.L., Buonaccorsi, J.P., 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J. Zool.* 269, 414–421.
- Kitchings, J.T., Levy, D.J., 1981. Habitat patterns in a small mammal community. *J. Mammal.* 62, 814–820.
- Klaus, N.A., Buehler, D.A., 2001. Golden-winged Warbler breeding habitat characteristics and nest success in clearcuts in the southern Appalachian Mountains. *Wilson Bull.* 113, 297–301.
- Kubel, J.E., Yahner, R.H., 2008. Quality of anthropogenic habitats for Golden-winged Warblers in central Pennsylvania. *Wilson J. Ornithol.* 120, 801–812.
- Madden, F., 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Hum. Dimens. Wildl.* 9, 247–257.
- Martin, T.E., Geupel, G.R., 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *J. Field Ornithol.* 64, 507–519.
- Morse, S.F., Robinson, S.K., 1999. Nesting success of a neotropical migrant in a multiple-use, forested landscape. *Conserv. Biol.* 13, 327–337.
- Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Cons.* 70, 265–276.
- Remeš, V., 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). *Conserv. Biol.* 17, 1127–1133.
- Robertson, R.J., 1972. Optimal niche space of the redwinged blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. *Can. J. Zool.* 50, 247–263.
- Rosenberg, K.V., Will, T., Buehler, D.A., Barker Swarthout, S., Thogmartin, W.E., Bennett, R.E., Chandler, R.B., 2016. Dynamic distributions and population declines of Golden-winged Warblers. In: Streby, H.M., Andersen, D.E., Buehler, D.A. (Eds.), *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*. In: *Studies in Avian Biology*, vol. 49, CRC Press, Boca Raton, FL, pp. 3–28.
- Rotella, J.J., 2007. Modeling nest-survival data: recent improvements and future directions. *Stud. Avian Biol.* 34, 145–148.
- Roth, A.M., Flaspohler, D.J., Webster, C.R., 2014. Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*). *Forest Ecol. Manag.* 321, 61–70.
- Roth, A.M., Rohrbaugh, R.W., Will, T., Buehler, D.A., 2012. Golden-Winged Warbler Status Review and Conservation Plan. <http://www.gwwa.org/plan>. (31 October 2015).
- Salafsky, N., Margoluis, R., Redford, K.H., Robinson, J.G., 2002. Improving the practice of conservation: a conceptual framework and research agenda for conservation science. *Conserv. Biol.* 16, 1469–1479.
- Saterson, K.A., Christensen, N.L., Jackson, R.B., Kramer, R.A., Pimm, S.L., Smith, M.D., Wiener, J.B., 2004. Disconnects in evaluating the relative effectiveness of conservation strategies. *Conserv. Biol.* 18, 597–599.
- Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski Jr., D.J., Link, W.A., 2014. The North American Breeding Bird Survey, Results and Analysis 1966–2013. Version 01.30.2015. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schlossberg, S., 2009. Site fidelity of shrubland and forest birds. *The Condor* 111, 238–246.
- Schmidt, K.A., Rush, S.A., Ostfeld, R.S., 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *J. Anim. Ecol.* 77, 830–837.
- Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C., Estes, J., 2001. Nature reserves: Do they capture the full range of America's biological diversity? *Ecol. Appl.* 11, 999–1007.
- Smith, D.G., Polhemus, J.T., VanderWerf, E.A., 2002. Comparison of managed and unmanaged Wedge-tailed Shearwater colonies on O'ahu: Effects of predation. *Pac. Sci.* 56, 451–457.
- Sperry, J.H., Peak, R.G., Cimprich, D.A., Weatherhead, P.J., 2008. Snake activity affects seasonal variation in nest predation risk for birds. *J. Avian Biol.* 39, 379–383.

- Stem, C., Margoluis, R., Salafsky, N., Brown, M., 2005. Monitoring and evaluation in conservation: a review of trends and approaches. *Conserv. Biol.* 19, 295–309.
- Streby, H.M., Andersen, D.E., 2013. Testing common assumptions in studies of songbird nest success. *Ibis* 155, 327–337.
- Streby, H.M., Peterson, S.M., Andersen, D.E., 2016. Survival and Habitat use of Fledgling Golden-Winged Warblers in the Western Great Lakes Region. In: Streby, H.M., Andersen, D.E., Buehler, D.A. (Eds.), *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*. In: *Studies in Avian Biology*, vol. 49, CRC Press, Boca Raton, FL, pp. 127–140.
- Suarez, A.V., Pfennig, K.S., Robinson, S.K., 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conserv. Biol.* 11, 928–935.
- Swarthout, S.B., Rosenberg, K.V., Rohrbaugh, R.W., Hames, R.S., 2009. Golden-Winged Warbler Atlas Project (US Fish and Wildlife Service Final Report). [http://www.nrcs.usda.gov/Internet/FSE\\_DOCUMENTS/nrcseprd331009.pdf](http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcseprd331009.pdf). (3 March 2016).
- Terhune II, T.M., Aldinger, K.R., Buehler, D.A., Flaspohler, D.J., Larkin, J.L., Loegering, J.P., Percy, K.L., Roth, A.M., Smalling, C., Wood, P.B., 2016. Golden-winged Warbler nest-site habitat selection. In: Streby, H.M., Andersen, D.E., Buehler, D.A. (Eds.), *Golden-Winged Warbler Ecology, Conservation, and Habitat Management*. In: *Studies in Avian Biology*, vol. 49, CRC Press, Boca Raton, FL, pp. 109–125.
- USDA: Natural Resource Conservation Service, [online] 2014. Working Lands For Wildlife 2014 Progress Report. <http://goo.gl/mE74va>. (Accessed 22 January 2016).
- Verhulst, S., Van Balen, J.H., Tinbergen, J.M., 1995. Seasonal decline in reproductive success of the great tit: Variation in time or quality? *Ecology* 76, 2392–2403.
- Williams, G.E., Wood, P.B., 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with Wood Thrushes (*Hylocichla mustelina*) using miniature video cameras. *The Auk* 119, 1126–1132.