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Legacy tree retention in young aspen forest improves nesting habitat quality for Golden-winged Warbler (*Vermivora chrysoptera*)

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ABSTRACT

Residual canopy trees as biological legacies in harvested aspen stands may mimic characteristics of naturally disturbed forests. We investigated the effects of legacy tree retention in young aspen (*Populus* spp.) forest stands on the quality of nesting habitat for the Golden-winged Warbler (*Vermivora chrysoptera*), a species of conservation concern that is dependent upon recently disturbed forest and shrub habitats. Habitat quality was assessed by evaluating male density, male pairing success, percent of successful nests, daily nest survival, and productivity in young aspen stands (4–7 years post-harvest) with retained conifer legacy trees ($n = 3$), with retained hardwood legacy trees ($n = 3$), and without legacy trees (also referred to as clearcuts; $n = 3$). Male pairing success was higher in stands with legacy trees (68% in stands with conifer legacy trees, 71% in stands with hardwood legacy trees) than in clearcuts (10%). Only one nest was found in clearcuts. The percent of successful nests, daily nest survival rate, and productivity did not vary between stands with conifer legacy trees and stands with hardwood legacy trees. Based on high pairing success (resulting in high levels of nesting activity), retention of legacy trees in young aspen stands provided higher quality nesting habitat than clearcuts. Male density was an excellent indicator of pairing success (pseudo $R^2 = 0.976$). Aspen stands harvested for nesting habitat should support a minimum density of 0.2 males/ha to have approximately 75% of males successfully paired. High male densities (>0.2 males/ha) were achieved by retaining at least 13 legacy trees/ha with at least nine of these comprising hardwood species with a mean diameter at breast height ≥ 16 cm.

1. Introduction

In post-disturbance environments, biological legacies such as scattered live trees fill important ecological roles, and their retention may allow silvicultural treatments to more closely emulate natural disturbances (Seymour et al., 2002; Lindenmayer et al., 2006; Manning et al., 2006). Legacy canopy trees as individuals or patches are known to increase bird diversity in managed aspen (*Populus* spp.) forests (Merrill et al., 1998), and can also benefit certain bird habitat-guilds or individual species in other forest communities (Hansen et al., 1995; Schieck and Hobson, 2000; Tittler et al., 2001; Lefort and Grove, 2009). The impact of legacy canopy trees on bird habitat quality has been investigated using proxies for quality such as nest success (Tittler and Hannon, 2000; Duguay et al., 2001; Stuart-Smith and Hayes, 2003) and body condition in the post-breeding season (McDermott and Wood, 2010). Such demographic traits are generally accepted as better indicators of habitat quality than abundance or density estimates alone (Van Horne, 1983). Most previous research suggests that bird nest predation rates in forest stands was not affected by green-tree retention harvests or by density of retained trees (Tittler and Hannon, 2000; Duguay et al., 2001; Stuart-Smith and Hayes, 2003). One of these studies (Duguay et al., 2001) reported species-specific nest success for five passerine species, with higher nest predation rates in harvested stands with retained trees versus unharvested stands for one species, Acadian Flycatcher (*Empidonax virescens*).

We investigated the impact of legacy canopy tree retention, also called green-tree retention, in young aspen stands on a high conservation priority migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*), during the breeding season. This species is dependent on disturbance events in forest ecosystems to create appropriate breeding habitat (Confer et al., 2011). The species' recent declines have been blamed in part on the maturation of forests in eastern North America (Confer et al., 2011). The Golden-winged Warbler, like other shrubland-dependent species, likely evolved to utilize forest openings regenerating with shrubs and young trees created by natural disturbances such as wind, fire, and beaver activity in forested landscapes (Hunter et al., 2001; Lorimer, 2001). These openings likely contained both live and dead legacy canopy trees in varying densities with scattered individuals and patches depending on the intensity of the disturbance (Foster and Boose, 1992; Frelich, 2002; Fig. 1a). Retention of legacy canopy

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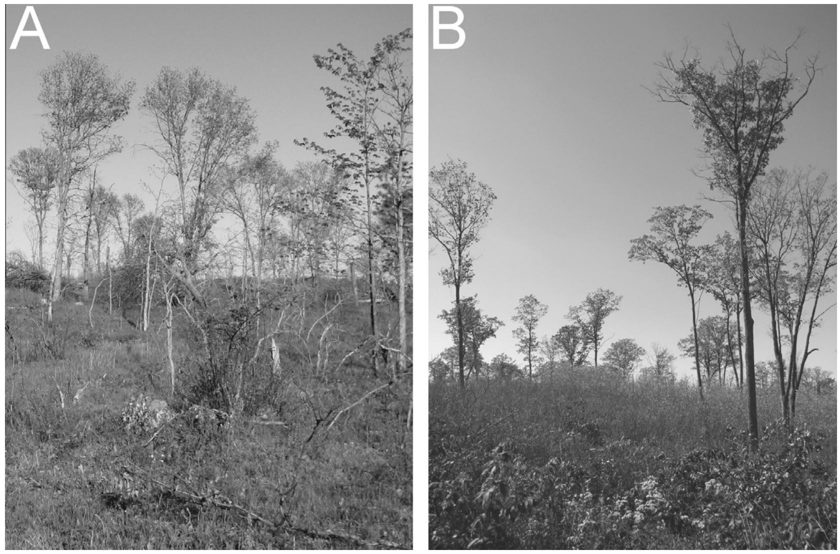

Fig. 1. Disturbed forests occupied by Golden-winged Warblers. (A) Blowdown caused by a straight-line windstorm in an aspen-oak stand in northwestern Wisconsin. The photo was taken one year after the storm following salvage removal of fallen trees. (B) Commercially-managed aspen stand with retention of hardwood legacy trees, primarily northern red oaks, three years post-harvest in north-central Wisconsin. Photos by Amber Roth.

trees in harvested even-aged forest stands has been proposed as a means of silviculturally mimicking this natural disturbance pattern (Seymour et al., 2002; Lindenmayer et al., 2006; Fig. 1b).

An estimated 76% of the global population of Golden-winged Warblers breeds in the Boreal-Hardwood Transition Bird Conservation Region (Blancher et al., 2007). Thus, management practices that create high quality breeding habitat in this region are critical to the species' future. Regenerating aspen forests supported the highest relative abundance of Golden-winged Warblers among several habitat types occupied by Golden-winged Warblers in northern Wisconsin (Martin et al., 2007). Among regenerating aspen stands, Golden-winged Warbler abundance or density was quite variable suggesting that not all stands are equally attractive and that stand characteristics may explain differences in use and quality (Roth and Lutz, 2004; Martin et al., 2007). Our objectives were to: (1) evaluate effects of legacy tree retention and legacy tree type on nesting habitat quality for Golden-winged Warblers in young aspen stands using male density, pairing success, nest survival, and productivity, (2) determine if male density reflects habitat quality based on demographic indicators, and (3) recommend aspen forest silvicultural guidelines for foresters and land managers interested in providing high quality nesting habitat for Golden-winged Warblers.

2. Methods

2.1. Study area

We selected nine young, aspen-dominated forest stands in Oneida and Vilas Counties, Wisconsin (45°43'N, 89°32'W) in an area defined by glacial moraines and outwash plains. Soils were characterized as sand, sandy loams, or loamy sands and ranged from moderately well-drained to excessively drained (Soil Survey Staff, 2010). Three stands were selected for each of three treatments: (1) aspen stands with no legacy tree retention, referred to hereafter as clearcuts, (2) aspen stands with conifer retention, and (3) aspen stands with hardwood retention. Stands ranged from 17 ha to 44 ha in area, and were commercially harvested using green-tree retention guidelines between 1997 and 2002. The regenerating aspen was therefore 4–7 years-old at the start of this study. Timber harvest prescriptions called for removal of all aspen and most tree species except trees to be retained. Retained trees included individuals marked by the forester and all large diameter pine (*Pinus* spp.) and oak (*Quercus* spp.; C. Dalton, pers. comm.). Aspen stands were dominated by *Populus tremuloides* and *Populus grandidentata* and included other abundant regenerating species, especially *Acer rubrum*, *Amelanchier* spp., *Prunus serotina*, *Quercus rubra* (northern red oak), and *Betula papyrifera* (paper birch). The dominant shrubs were *Rubus* spp. and *Corylus* spp. All sites were selected without prior knowledge of Golden-winged Warbler occupancy.

2.2. Field methods

Golden-winged Warbler territory and nest surveys were conducted 10 May–2 July 2007, 19 May–21 July 2008, 19 May–15 July 2009, and 16 May–3 July 2010. We captured and banded an estimated 88% of territorial adult males and 9% of adult females among all sites. Adults were targeted for capture using mistnets with tape playback (Kubel and Yahner, 2007) and then given a unique color band combination including an aluminum US Geological Survey Bird Banding Laboratory band for individual identification. In subsequent years, resighted birds were used to calculate annual return rates.

To determine territorial male densities in nesting habitat, we mapped locations for all territorial males using a modification of the protocol of Robbins (1970). Surveys for the same individual or stand were conducted at least three days apart. When possible, we used teams of two observers with one observer recording locations on a map and marking song perches while the second observer tracked the bird. Because of the dense vegetation, it was difficult to continually track a bird and thus considerable time was spent checking bands to make sure the same individual was resighted before resuming the survey. An identifiably unique individual was tracked until the observer(s) completed a full circuit of the bird's territory such that the bird primarily began using marked perch trees. Unbanded males prior to capture were identifiable by unique song characteristics, favorite song perches, discrimination from banded neighboring males, or other characteristic behaviors. We did not survey males into the fledging period. All perches were marked with flags and coordinates were collected later with a handheld Trimble XM Geographic Positioning

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System. From these locations, we used minimum convex polygons to delineate territorial boundaries, in order to accurately count the number of territorial males per aspen stand. Not all males were intensively mapped with each stand visit but, at a minimum, the presence–absence of each male was noted within previously known territorial boundaries. Territorial male densities were calculated based on the number of territories for males observed on at least eight visits per harvested stand area.

We considered males to have paired successfully when they were observed interacting with an adult female (e.g. copulating with or following a female) on at least two occasions or feeding nestlings or fledglings (Askins et al., 2007). Contrary to Askins et al. (2007), we deemed one observation of a female with a male as inadequate due to occasional "prospecting" behavior by females especially early in the breeding season or following nest failures. Pairing success was generally determined incidentally to nest searching which was conducted in every territory and represented dozens of person hours of observation per territory often with multiple observers present. Territorial males without females were visited on most site visits throughout the nesting season until nesting activity was largely completed for most other pairs, and thus we had high confidence that these males did not acquire mates. In stands with high male densities, we were conservative in our assignment of pairing success. We could not always differentiate unbanded females when they were sighted near territorial boundaries, when they left their mate's territory for extra-pair copulations (EPCs), or they switched mates following nest failure. EPCs are common in other Golden-winged Warbler populations (up to 55% of nests) so males without mates may have sired offspring (Vallender et al., 2007). We did not determine paternity for nestlings so we could only define pairing success based on behavioral observations.

Nests were located by searching the entire stand for females exhibiting nesting behavior, for adults feeding nestlings, and for good potential nest sites within male territories. After egg laying was completed, nests were monitored every three days or sooner if the predicted fledging date fell before the next routine visit. Fledging was considered successful based on observation of fledglings, banded adults carrying food, or substantial fecal material on the rim of the nest or on nearby perches.

To determine legacy tree basal area and density at the stand scale, we randomly established ten 1000-m^2 circular plots separated by at least 30 m in each stand using the Random Points tool in ArcGIS version 9.2 (ESRI, 2007). These plots were visited 19 May–14 August 2008. We defined legacy trees as trees that were retained during the most recent harvest rotation. Legacy trees were identified as live trees with diameter at breast height (DBH) at least 5 cm greater than the DBH of surrounding regenerating aspen trees and that were at least 1 m taller than surrounding regenerating aspen trees in order to be used as a song perch. For each tree with DBH > 10 cm, we recorded species, DBH, and whether it was alive or dead. To estimate regenerating tree stem density, a 100-m^{2-} nested plot was centered at the same point as the 1000-m^2 plot. All tree saplings $\geq$ 1.37 m tall and with DBH <10 cm were counted. Tree density and basal area estimates were calculated for each plot and averaged across each stand.

2.3. Data analysis

2.3.1. Aspen clearcut characteristics

Comparisons of legacy tree characteristics and regenerating aspen stem densities among legacy tree retention treatments were conducted using one-way Analysis of Variance (ANOVA) using SigmaStat version 3.5 (Systat, 2006). We used the Holm-Sidak test for multiple comparisons between treatments because it is more powerful than other tests such as Tukey and Bonferroni (Systat, 2006). A simple linear regression was performed in SigmaStat to relate legacy tree density to legacy tree basal area. Both variables were log transformed to meet normality and equal variance assumptions for the residual errors.

2.3.2. Golden-winged Warbler demographic characteristics and legacy tree retention effects

Differences in territorial male numbers and densities between legacy tree retention treatments and survey years were determined using two-way repeated measures ANOVA for normally distributed datasets using SigmaStat (Systat, 2006). The Holm-Sidak test was used for post hoc comparisons because it is a more conservative approach than other tests such as the Student–Newman–Keuls test (Systat, 2006). The difference in male pairing success among legacy tree retention treatments was evaluated using a Chi-square test. The nest success (i.e. percent of successful nests) difference among legacy tree retention treatments by year and pooled across years was evaluated using Fisher's Exact Test due to at least one cell in the contingency table having an expected value less than five.

To determine if daily nest survival rate (DSR) varied by year and legacy tree retention treatment, we used Program MARK version 5.1 (White and Burnham, 1999). We compared six *a priori* models to evaluate whether daily nest survival varied by: (1) year, (2) site, (3) legacy tree retention treatment, (4) year and legacy tree retention treatment, and (5) year and site as compared to (6) an intercept only model. All models were constructed using constant survival through the nesting season. Independent variables were coded as dummy variables. We used MARK to apply an information theoretic approach to evaluate the models using Akaike Information Criterion for small sample sizes (AICc). Models with an AICc difference of two or less of the best model were considered equivalent (Anderson, 2008). Models with AICc differences between four and seven of the best model were given considerably less support for inference of results (Burnham and Anderson, 2002). Model deviance was calculated in MARK.

Productivity was calculated as the number of fledglings per nesting territory based on procedures in Kubel and Yahner (2008). A nesting territory was defined as a territory for which we found at least one active nest during the course of a nesting season. We did not find more than one successful nest per territory. In SigmaStat (Systat, 2006), the difference in productivity between legacy tree retention treatments was determined using Kruskal–Wallis Analysis of Variance on Ranks due to a non-normal distribution.

2.3.3. Male density as an indicator of habitat quality

To evaluate whether territorial male density was a good measure of habitat quality in aspen forest stands, we correlated territorial male Golden-winged Warbler density with pairing success among stands. We explored a variety of regression functions to fit these data by year and by the mean across years in SigmaPlot 9.0 (Systat, 2004). For the yearly datasets, an exponential transformation of pairing success and a square root transformation of male density were required to meet normality and equal variance assumptions for the regression errors. A three-parameter sigmoid function consistently provided the best fit of the data among datasets and was used in a nonlinear regression procedure (NLMIXED) in SAS. We used a Newton–Raphson fitting algorithm, which is a derivative dependent method, as recommended by SAS (Schabenberger, 2011). Parameter start values were based on the fitted line parameters produced by SigmaPlot. Individual males were treated as a random effect. Pseudo-R^2 values were calculated using the following formula recommended by Schabenberger (2011): pseudo-$R^2 = 1 - \text{Sum of Squares(Residual)}/\text{Sum of Squares}(\text{Total}_{\text{Uncorrected}})$.

2.3.4. Male density and aspen clearcut characteristics

We used the findings of past studies to inform an *a priori* selection of variables that might influence Golden-winged Warbler habitat use or male densities. Stand age (i.e., regenerating aspen age) was selected as a proxy for stand development stage given that peak Golden-winged Warbler use is thought to occur between 2 years and 10 years post-clearcutting in aspen forests (Roth and Lutz, 2004; Martin et al., 2007). Regenerating aspen stem density has been found to be among the most important variables differentiating aspen stand use and preference among different early successional community types in Wisconsin (Roth and Lutz, 2004; Martin et al., 2007).

Given our prediction that the presence of legacy trees has a positive effect on Golden-winged Warbler densities, we included variables that would describe stand-scale legacy tree characteristics such as mean basal area of legacy trees by group (hardwood species, coniferous species, and all species) and mean stem density of legacy trees by the same groups.

The Golden-winged Warbler's propensity to probe, particularly by inserting its bill into curled leaves, leaf clusters, buds, and flowers, suggests that hardwood species may offer greater foraging opportunities than conifers (Ficken and Ficken, 1968). In general, Airola and Barrett (1985) found that migrant species in mixed-conifer forests were more likely to forage in deciduous trees than in coniferous trees. Thus the proportion of hardwood to conifer legacy trees might be important in evaluating habitat quality. We selected tree size based on mean DBH as a variable given males' frequent use of tall, canopy trees for song perches and foraging (Ficken and Ficken, 1968; Rossell, 2001).

We eliminated collinear variables based on a Pearson correlation coefficient $\geqslant 0.60$. The final set of variables included survey year, stand age, stand area, and mean values of regenerating aspen density, legacy tree stem density, conifer legacy tree size, hardwood legacy tree size, and proportion of hardwood to conifer legacy tree stem density. Ten models were developed to explain differences in male density across the aspen stands based on the reduced set of variables.

To account for repeated use of the same sites among years, year was treated as a random effect in our linear mixed effect models. Linear mixed effects candidate models were evaluated using program R (R Core Team, 2011) and package nlme (Pinheiro et al., 2011). For model-selection we used AIC_c (using package AICcmodavg (Mazerolle, 2011) in R version 2.13.2) to rank the candidate models. We fitted the models using the maximum likelihood procedure to generate the AIC_c rankings. We refitted the models using the restricted maximum likelihood procedure to estimate parameter values. For nested models considered competitive based on the differences in AIC_c, package AICcmodavg was used to estimate final parameter values and confidence intervals via model averaging (Burnham and Anderson, 2002).

To determine the minimum values or thresholds for legacy tree characteristics needed to achieve high male densities, we explored the correlation of each independent variable with mean male density in SigmaPlot. A three-parameter sigmoidal function consistently provided the best fit of the data among datasets and was used in a nonlinear regression procedure (NLIN) in SAS. Parameter start values were based on the fitted line parameters produced by SigmaPlot. Individual males were treated as a random effect. Pseudo-R^2 values were calculated as described above.

3. Results

3.1. Aspen stand characteristics

In the conifer legacy tree retention treatment, the legacy trees were primarily *Pinus strobus* (eastern white pine, 55%), *Pinus resinosa* (red pine, 23%), *Quercus rubra* (13%), and *Abies balsamea* (5%). In the hardwood legacy tree retention treatment, the legacy trees were primarily *Quercus rubra* (93%), *Pinus resinosa* (3%), and *Pinus strobus* (2%). Legacy trees in clearcuts were rare (Table 1) and comprised of *Quercus rubra* (31%), *Pinus resinosa* (23%), and *Abies balsamea* (23%).

Legacy tree density was significantly higher in stands with conifer retention, lowest in clearcuts, and intermediate in stands with hardwood retention (Table 1). Not surprisingly, conifer legacy tree density and basal area were highest in stands with conifer retention (Table 1). Legacy tree density and basal area were highly correlated (Adj. $R^2 = 0.916$, $F = 88.291$, $P \leqslant 0.001$) based on the following relationship: log (density) = 1.420 + (0.571*log(basal area)). Hardwood legacy tree size (mean DBH) was significantly smaller in clearcuts than in stands with hardwood retention (Table 1). Among all species, tree size was smaller in clearcuts than in stands with conifer retention (Table 1). Regenerating aspen stem density did not vary by treatment (Table 1). Most (97%) aspen saplings were $\leqslant$5.0 cm DBH.

3.2. Golden-winged Warbler demographic characteristics and legacy tree retention effects

We mapped territories for 36 males in 2007, 32 males in 2008, 31 males in 2009, and 32 males in 2010. Male return rates were 44% in 2008, 51% in 2009, and 51% in 2010. Only eight females were banded in 2007–10, and none were resighted during the study. No territorial male Blue-winged Warblers (*Vermivora cyanoptera*) were observed. We observed one territorial phenotypic hybrid in 2007, a male Brewster's Warbler (*V. chrysoptera x V. cyanoptera*) that returned in 2008 to defend the same territory. We did not include this individual in any analyses.

Among the four survey years, there were more territorial males in stands with conifer or hardwood retention than in clearcuts (Table 2). The number of territorial males was not affected by the survey year ($F_{3,35} = 0.373$, $p = 0.773$) or an interaction effect between year and treatment ($F_{6,35} = 0.533$, $p = 0.776$). Male density did not differ among legacy tree retention treatments (Table 2), and did not vary by year ($F_{3,35} = 0.209$, $p = 0.889$) or by interaction between year and treatment ($F_{6,35} = 0.367$, $p = 0.890$). Though the difference in male density between stands with legacy trees versus clearcuts was not statistically significant, the nearly 10-fold higher density of males in stands with legacy trees warranted a closer examination of the stand-scale legacy tree characteristics affecting male density and breeding success among retention treatments.

Male pairing success was relatively high in the conifer and hardwood retention treatments, with conservative estimates of 68% and 71% respectively (Table 2). Pairing success was low for males in the clearcuts, with only one male of eight individuals with 10 opportunities (10%) successfully acquiring a mate during four years. This particular male acquired a female during his third breeding season defending the same territory (i.e., one male with three opportunities for acquiring a mate).

We found 50 Golden-winged Warbler nests over four years (Table 2). Only one nest was found among clearcuts despite our dedicating a minimum of four search hours per visit and a minimum of eight visits per site searching for both females and nests spanning a minimum of 22 days following territory establishment. Eighty percent of nests were located by observing parental behavior (usually of the female) and 20% by investigating likely nest sites. Of the 25 nests that failed, 56% were depredated and 44% were abandoned. Four were likely abandoned due to research-related causes. No double-brooding was observed. The percentage of successful nests was similar between stands with hardwood legacy trees and stands with conifer legacy trees (Table 2). The one nest among clearcuts was successful.

Table 1
Legacy tree characteristics and regenerating aspen stem density (mean ± 1se) in young aspen forest stands in three legacy tree retention treatments in Oneida and Vilas Counties, Wisconsin, 2008. Significant differences based on $\alpha = 0.05$ between treatments in the post hoc test comparisons are indicated by different letters.

	Legacy Tree Treatment			$F_{2,6}$	*p*
	Clearcut (*n* = 3)	Conifer Retention (*n* = 3)	Hardwood Retention (*n* = 3)		
Legacy tree density (stems/ha)					
Conifers	2.67 ± 1.45A	86.00 ± 2.08B	2.33 ± 0.67A	1012.113	**<0.001**
Hardwoods	4.00 ± 2.00	16.33 ± 9.39	31.33 ± 9.82	2.981	0.126
All species	6.67 ± 2.60A	102.33 ± 10.48B	33.67 ± 9.62C	34.919	**<0.001**
Legacy tree basal area (m^2/ha)					
Conifers	0.18 ± 0.13A	6.10 ± 1.65B	0.23 ± 0.10A	28.292[a]	**<0.001**
Hardwoods	0.03 ± 0.02	0.57 ± 0.42	2.08 ± 1.08	2.506	0.162
All species	0.21 ± 0.15A	6.67 ± 2.06B	2.31 ± 1.02AB	6.077	**0.035**
Legacy tree size (dbh, cm)					
Conifers	26.72 ± 6.57	27.83 ± 3.82	34.31 ± 5.65	0.562	0.597
Hardwoods	9.80 ± 2.18A	16.71 ± 2.76AB	25.18 ± 3.60B	7.027	**0.027**
All species	12.17 ± 3.46A	26.15 ± 2.89B	26.34 ± 3.03AB	6.712	**0.029**
Mean regenerating aspen density (stems/ha)					
All species	12.803 ± 1.845	7.690 ± 1.115	10.053 ± 3.197	1.322	0.335

[a] Based on a square root transformation of conifer basal area.

Table 2
Demographic characteristics for Golden-winged Warblers (*Vermivora chrysoptera*) in young aspen forest stands without legacy tree retention (clearcuts), with conifer legacy tree retention, and with hardwood legacy tree retention in northern Wisconsin, 2007–2010. Significant differences based on $\alpha = 0.05$ between treatments in the post hoc test comparisons are indicated by different letters.

	Legacy tree retention treatment			Test Statistic$_{df}$		*p*
	Clearcut (*n* = 3)	Conifer retention (*n* = 3)	Hardwood retention (*n* = 3)			
Mean number of territorial males, mean ± 1se						
All years	0.8 ± 0.2A	4.7 ± 0.7B	5.5 ± 0.4B	$F_{2,35}$	6.933	**0.028**[a]
Mean territorial male density, individuals/ha; mean ± 1se						
All years	0.03 ± 0.01	0.22 ± 0.04	0.24 ± 0.03	$F_{2,35}$	3.028	0.123[a]
Male pairing success rate (total territorial males)						
All years	10% (10)	68% (56)	71% (66)	χ^2, *df* = 2	14.65	**0.001**
Number of nests (% successful)[b]						
2007	0 (0%)	7 (71%)	3 (67%)	Fisher's		1.000
2008	0 (0%)	6 (60%)	3 (67%)	Fisher's		1.000
2009	0 (0%)	6 (75%)	7 (57%)	Fisher's		1.000
2010	1 (100%)	6 (17%)	11 (40%)	Fisher's		0.273
All years	1 (100%)	25 (55%)	24 (52%)	Fisher's		0.671
Productivity, number of fledglings/nesting territory; mean ± 1se[b]						
All years[c]	5.0 ± 0.0	2.2 ± 0.5	2.2 ± 0.5	H_2	1.67	0.434

[a] Based on two-way repeated measures ANOVA.
[b] Calculation does not include four nests removed due to research-related abandonment.
[c] Kruskal–Wallis ANOVA on Ranks performed and Tukey Test used for post hoc pairwise multiple comparisons. Due to small sample sizes of successful nests by legacy tree treatment, data were pooled across years.

Nest DSR was 0.975 ± 0.015 in 2007, 0.977 ± 0.013 in 2008, 0.971 ± 0.014 in 2009, and 0.960 ± 0.012 in 2010. DSR was similar between the conifer (0.968 ± 0.010) and hardwood retention (0.967 ± 0.010) treatments. Based on a 24-day nest cycle, nest success was estimated at 0.46 for stands with conifer retention, 0.45 for stands with hardwood retention, and 1.00 for the clearcuts.

Of the models assessed to explore the effects of year, site, and legacy tree treatment on DSR, the site-only model was an improvement over the null (intercept-only) model though both the intercept-only model and legacy tree treatment model were competitive (Table 3). This suggests that nest survival did not vary by year and that site and legacy tree retention treatment explained as much DSR variation as the null model. Though DSR appeared to be lowest in 2010, this difference was not significant despite a 42% reduction in the percent of successful nests in 2010 (33%) compared to 2007–2009 (mean of 57%). Removal of the one nest in a clearcut still produced a competitive model ($\Delta AIC_c = 2.01$) suggesting that the slight difference in DSR (0.001) between stands with conifer retention and stands with hardwood retention may be important though it seems doubtful that this would produce important differences in nest productivity. In fact, productivity did not vary by legacy tree retention treatment and was 2.2 fledglings/nesting territory for the two treatments with legacy tree

Table 3
Model-selection results for models of nest survival (*S*) for Golden-winged Warbler daily nest survival rates in aspen forest stands without legacy tree retention (clearcuts; *n* = 3), with conifer legacy tree retention (*n* = 3), and with hardwood legacy tree retention (*n* = 3) in Oneida and Vilas Counties, Wisconsin, 2007–2010. Four nests that were abandoned due to research-related causes were removed from this analysis.

Model	K[a]	AIC_c	ΔAIC_c	w_i	Deviance
$S_{(site)}$	6	149.59	0.00	0.36	137.46
$S_{(intercept\text{-}only)}$	1	149.94	0.35	0.31	147.93
$S_{(legacy\ tree\ treatment)}$	2	150.50	0.91	0.23	146.49
$S_{(site\ +\ year)}$	8	153.53	3.93	0.05	137.30
$S_{(year)}$	4	154.90	5.31	0.03	146.84
$S_{(legacy\ tree\ treatment\ +\ year)}$	5	154.97	5.38	0.02	144.88

[a] Number of model parameters.

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retention, when four nests abandoned due to research-related causes were removed (Table 2).

3.3. Male density as an indicator of habitat quality

Of the demographic characteristics investigated, pairing success was the only one to vary by retention treatment and thus appeared to be the factor most likely to limit fledgling production. Pairing success related significantly to male density in all years (pseudo $R^2 = 0.948–0.980$, $P < 0.001$) and for mean values among years (pseudo $R^2 = 0.976$, $P < 0.001$) (Table 4 and Fig. 2). Pairing success was >40% when mean male density was above 0.1 individuals/ha, the inflection point in the sigmoid curve (Fig. 2), and consistently high (~75% on average) across years when mean male density was ⩾0.2 individuals/ha, the asymptote of the curve (Fig. 2).

3.4. Male density and aspen clearcut characteristics

The most parsimonious model explaining male densities in young aspen forest stands included legacy tree density and hardwood legacy tree size (Table 5). The second best model was considered competitive and included these variables with the addition of the proportion of legacy trees that were hardwood (Table 5). Male densities increased positively with legacy tree density, hardwood legacy tree size, and the proportion of legacy trees comprised of hardwood species (Table 6).

Mean male density reached an asymptote when hardwood legacy tree size was 16 cm DBH (Table 7). Mean male densities increased notably above a legacy tree density threshold of 13 stems/ha (Fig. 3), the point where the relationship reached an asymptote (Table 7). Similarly, the asymptote for the relationship between male density and hardwood legacy tree density was reached around nine stems/ha for hardwood legacy tree density (Table 7). There was a marginally significant ($P = 0.056$) positive relationship between male density and conifer legacy tree density with an asymptote at three stems/ha (Table 7). This suggests that Golden-winged Warblers were tolerant of conifer presence as long as a minimum density of hardwood legacy trees was retained. At relatively low legacy tree densities, a high proportion (>80%) of relatively large (⩾16 cm DBH) hardwood trees resulted in high male densities (Fig. 3). If stands have a high proportion of conifer legacy trees (>70%), retaining a minimum of nine hardwood trees/ha appeared to be adequate to produce similarly high male densities (Fig. 3).

4. Discussion

4.1. Male density indicates habitat quality

Because we expected that male density alone would be an inadequate indicator of habitat quality, we also examined male pairing success, nest survival, and nest productivity as part of our evaluation. Pairing success in our study was comparable to the 42–80% rate reported for a Golden-winged Warbler population in central Michigan (Will, 1986). For the closely related Blue-winged Warbler in a study in Connecticut (Askins et al., 2007), pairing success (54%) and nesting activity were higher in small habitat patches (supporting 1–2 territories) relative to large habitat patches (potentially supporting 2+ territories). However, the sites in this study were separated by as little as 10 m of forest. This suggests that nesting habitat may not be independent given that conspecific attraction could be occurring between sites and males could be moving between sites.

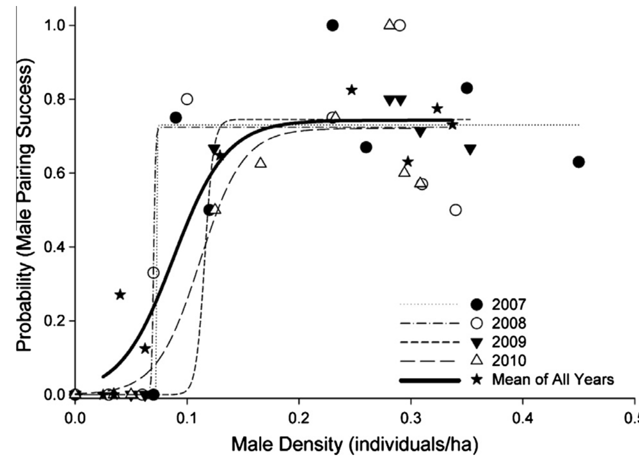

Fig. 2. Golden-winged Warbler male pairing success was a three-parameter sigmoid function of male density (See Table 4 for equations). Data were not transformed for easier interpretation and followed a similar pattern among years.

Contrary to our expectations, male density appeared to be an excellent indicator of pairing success. Perot and Villard (2009) found a similar relationship in a study of Ovenbirds (*Seiurus aurocapilla*), for which territory density was a good indicator of productivity. In our study, only one male occupying a clearcut acquired a mate, and then successfully reared fledglings. Thus, low male numbers and densities were indicative of low pairing success and low nesting probability. Male densities above 0.2 males/ha appear to indicate consistently high pairing success and nesting activity.

Male densities indicate habitat quality but defining optimal habitat quality for Golden-winged Warbler likely requires understanding the interactions of habitat characteristics and social behavior as suggested for other species (Ahlering and Faaborg, 2006). More research, especially with experimental manipulation, is needed to better understand the spatial and temporal interplay between habitat vegetation characteristics, conspecific attraction, and habitat quality. This should include an examination of the roles of site fidelity and annual adult survival relative to persistence of quality breeding habitat for this high conservation priority species.

4.2. Legacy tree retention improves habitat quality

The most striking result of this study was the overall poor habitat quality of large clearcuts (>16 ha). Low male densities and low

Table 4
Nonlinear models relating Golden-winged Warbler (*Vermivora chrysoptera*) territorial male pairing success to male density in aspen forest stands without legacy tree retention (clearcuts; $n = 3$), with conifer legacy tree retention ($n = 3$), and with hardwood legacy tree retention ($n = 3$) in Oneida and Vilas Counties, Wisconsin, 2007–2010. Both dependent and independent variables were transformed in the four yearly models to meet assumptions of normality and equal variances of the errors.

Year	Model	*F*	*p*	*Pseudo-R²*
2007	$\exp(\text{Male Pairing Success}_{2007}) = 2.390/(1 + \exp(-(\text{sqrt}(\text{Male Density}_{2007}) - 0.097)/0.215))$	47.64	<0.001	0.960
2008	$\exp(\text{Male Pairing Success}_{2008}) = 2.351/(1 + \exp(-(\text{sqrt}(\text{Male Density}_{2008}) - 0.151)/0.197))$	36.14	<0.001	0.948
2009	$\exp(\text{Male Pairing Success}_{2009}) = 5.273/(1 + \exp(-(\text{sqrt}(\text{Male Density}_{2009}) - 0.748)/0.466))$	99.53	<0.001	0.980
2010	$\exp(\text{Male Pairing Success}_{2010}) = 3.742/(1 + \exp(-(\text{sqrt}(\text{Male Density}_{2010}) - 0.449)/0.333))$	64.72	<0.001	0.970
Mean of all years	$\text{Male Pairing Success}_{\text{Mean}} = 0.743/(1 + \exp(-(\text{Male Density}_{\text{Mean}} - 0.088)/0.024))$	80.63	<0.001	0.976

Table 5
Selection results for linear mixed effects models of Golden-winged Warbler (*Vermivora chrysoptera*) territorial male density in aspen forest stands without legacy tree retention (clearcuts; $n = 3$), with conifer legacy tree retention ($n = 3$), and with hardwood legacy tree retention ($n = 3$) in Oneida and Vilas Counties, Wisconsin, 2007–2010. Survey year was the random effect in each model.

Model	K[a]	AIC_c	ΔAIC_c	w_i	Deviance
Density(Legacy Tree Stem Density + log(Hardwood Legacy Tree Size))	5	−59.259	0.000	0.563	35.629
Density(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees + log(Hardwood Legacy Tree Size))	6	−58.703	0.556	0.426	36.800
Density(Stand Area)	4	−50.230	9.028	0.006	29.760
Density(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees)	5	−48.438	10.821	0.003	30.219
Density(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees+ Conifer Legacy Tree Size)	6	−46.983	12.276	0.001	30.940
Density(Legacy Tree Stem Density + Conifer Legacy Tree Size)	5	−46.880	12.379	0.001	29.440
Density(Legacy Tree Stem Density)	4	−44.122	15.136	0.000	26.706
Density(Regenerating Aspen Density)	4	−39.515	19.744	0.000	24.402
Density(.)	3	−38.068	21.190	0.000	22.409
Density(Stand Age)	4	−35.586	23.672	0.000	22.438

[a] Number of model parameters.

Table 6
Average beta estimates and 95% confidence intervals for parameters based on the top models in Table 5 receiving AIC_c weights for Golden-winged Warbler densities in aspen forest stands with and without legacy tree retention ($n = 9$) in Oneida and Vilas Counties, Wisconsin, 2007–2010.

Parameter	β	95% Confidence interval	
		Lower	Upper
Intercept	−0.025	−0.627	0.576
log (Hardwood tree size)	0.160	0.090	0.231
Legacy tree stem density	0.001	0.000	0.002
Proportion of hardwood & conifer legacy trees	0.097	−0.033	0.226

Table 7
Nonlinear models relating Golden-winged Warbler (*Vermivora chrysoptera*) mean territorial male density to three legacy tree density characteristics in aspen forest stands without legacy tree retention (clearcuts; $n = 3$), with conifer legacy tree retention ($n = 3$), and with hardwood legacy tree retention ($n = 3$) in Oneida and Vilas Counties, Wisconsin, 2007–2010.

Model	F	p	Pseudo-R^2
Mean Male Density = 0.205/(1 + exp(−(LTD[a] − 11.164)/0.168))	14.39	0.001	0.753
Mean Male Density = 0.229/(1 + exp(−(HLTD[b] − 8.6941)/0.725))	17.09	0.002	0.832
Mean Male Density = 0.190/(1 + exp(−(CLTD[c] − 0.661)/0.406))	4.52	0.056	0.693
Mean Male Density = 0.267/(1 + exp(−(DBH[d] − 13.977)/0.278))	20.39	0.002	0.911

[a] Legacy tree density.
[b] Hardwood legacy tree density.
[c] Conifer legacy tree density.
[d] Hardwood legacy tree size.

pairing success resulted in little nesting activity. Aspen stands with retained legacy trees yielded higher pairing success (~70%). Nearly identical DSR and productivity for Golden-winged Warbler nests were found in small aspen clearcuts in Pennsylvania (Kubel and Yahner, 2008).

We have demonstrated the importance of legacy trees for improving habitat quality from the perspective of territorial male densities and pairing success. Other studies have documented the importance of scattered mature trees for Golden-winged Warbler occupancy (Huffman, 1997; Cumming, 1998). Patton et al. (2010) suggested that increasing scattered mature trees across large patches of open habitat potentially could improve occupancy, especially away from transitional edges between open and mature forest habitat.

Large hardwood trees appeared to be a particularly important characteristic of our aspen stands. Golden-winged Warblers preferred residual canopy trees (>6 m tall) over shrub-sapling layer song perches (<6 m tall) in Minnesota aspen forests (Back, 1982). This preference for large canopy trees as song perches was also documented for this species in mountain wetlands in North Carolina (Rossell, 2001). A majority of song perches (78%) in this study were in the upper 25% of the tree crown. This positioning was thought to optimize vocal display and attraction of a mate, an idea supported by acoustic research (Henwood and Fabrick, 1979; Mathevon and Aubin, 1997).

We speculate that retaining legacy trees in aspen stands mimics the appearance of forests disturbed by wind and other weather events that produce suitable nesting habitat for Golden-winged Warblers. Moderately severe natural disturbances often do not fell all canopy trees in the disturbed area and leave behind a combination of injured and healthy trees (Fig. 1). The newly opened canopy allows dense shrub development and the structural patchiness characteristic of Golden-winged Warbler territories. Clearcuts where no legacy trees are retained likely resemble rare, severe natural disturbances where no trees are left standing, and appear to be less attractive to Golden-winged Warblers.

Studies of other warbler species have found that pairing success increased as habitat patch area increased (Burke and Nol, 1998; Butcher, 2011). We did not find that nesting habitat area restricted pairing success given that much of the clearcut areas was unoccupied, as indicated by low male densities. When land managers have sites with low male densities (<0.2 males/ha), additional evidence of pairing and reproductive success should be documented when evaluating habitat quality.

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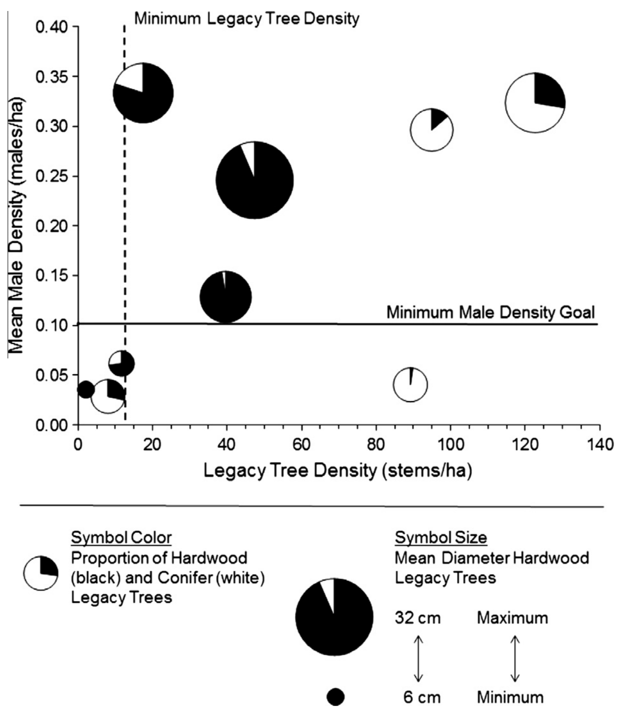

Fig. 3. Golden-winged Warbler territorial male densities in nine aspen forest stands were related to three legacy tree characteristics: legacy tree density, proportion of hardwood and conifer legacy trees, and size of hardwood legacy trees. Based in Fig. 2, a minimum density of 0.10 males/ha was needed to obtain >40% pairing success. Large, hardwood legacy trees were an important characteristic of aspen forest stands above the minimum male density goal, particularly at low legacy tree densities.

4.3. Recommendations for managing high quality habitat

Habitat management should be conducted with a specific Golden-winged Warbler population goal in mind. We suggest that an appropriate goal would be a breeding density of at least 0.2 territorial males/ha. Stands that support one or two territorial males at low densities (<0.2 males/ha) will not likely result in nesting activity. Though stand area was not an important variable in predicting male density, nesting habitat should be extensive enough to attain the population goal. The smallest area of nesting habitat required per territorial male among stands was 2.2 ha/male suggesting that at least 9 ha of nesting habitat was required to support a population of four pairs, the minimum observed among stands with legacy tree retention. Confer and Knapp (1981) found that most Golden-winged Warbler territories were located in 10–50 ha habitat patches. Confer (1992) suggested that 10–15 ha might be close to the optimal patch size in old field habitats. Thus a minimum of 9–10 hectares of nesting habitat seemed to be preferred by Golden-winged Warblers among these studies. However, at moderately low densities like our recommended minimum male density of 0.2 males/ha, at least 20 ha of suitable habitat may be necessary to support a breeding population. Land managers could assess male densities at other similarly managed sites in the area to determine the range of male densities that they can expect.

Kubel (2005) found that a minimum area of 1.0 ha was sufficient to attract breeding pairs. However, the clearcuts in that study were only 100 m apart with the result that males were likely able to detect one another (Kubel and Yahner, 2007). Similarly Roth and Lutz (2004) found that areas of habitat distributed as one large clearcut or two to three smaller clearcuts in close proximity attracted high densities of territorial males. Thus, managers have some flexibility in how they configure nesting habitat patches.

Land managers, especially foresters, have a great opportunity for creating high quality Golden-winged Warbler nesting habitat in aspen forests within the species' breeding range. For the Golden-winged Warbler, not all aspen clearcuts are created equal. When quantifying habitat for this species, it is important to also consider quality of habitat, in this case, the quality of the aspen forest. Retaining canopy trees can increase habitat quality in an even-aged harvest in aspen forest.

We acknowledge that the forest stands in this study may not be representative of all aspen forests across the Great Lakes states. Thus, the following recommendations should be viewed as approximate guidelines and not absolute rules to aid land managers with development of silvicultural prescriptions. We observed a lower Golden-winged Warbler density threshold around 13 trees/ha (or 0.9 m^2/ha), above which there was a notable increase in male density and pairing success. Huffman (1997) recommended a residual basal area of 4.6 m^2/ha, or approximately 20% residual canopy cover, in aspen forests in Minnesota. This suggests that optimal residual tree basal area and density for Golden-winged Warbler is likely higher than our 0.9 m^2/ha or 13 trees/ha minimum values.

At the range of legacy tree densities observed for the aspen stands in our study, we did not observe an upper Golden-winged Warbler density threshold as tree density increased. We expect that density should decline above a limit when canopy closure reduces shrub and grass/sedge density. Huffman (1997) observed that Golden-winged Warbler numbers declined and the composition of the bird community shifted at around 9.2 m^2/ha or approximately 40% residual canopy cover. Managers should also consider implications of potential reduction in aspen regeneration with increasing residual canopy cover (Huffman et al., 1999).

The high proportion of hardwood to coniferous legacy trees was likely only important where legacy tree density was low. Stands with a high proportion of conifer legacy trees seemed acceptable if a minimum of approximately nine hardwood legacy trees/ha (with average DBH $\geqslant$ 16 cm) was retained. The dominant hardwood legacy tree was northern red oak (93%) and it is unclear what role this species, as compared to other hardwood species, has in attracting Golden-winged Warblers to a site. We collected no data on the relative usage of oak to other species. Anecdotally, males spent much time singing and foraging in the canopies of large oak trees (personal observation). Wood et al. (2012) observed that Blue-winged Warbler and other migrant songbirds preferred northern red oak for foraging relative to other common dominant broad-leaved trees in Wisconsin. This may be due to relatively high arboreal caterpillar species richness and abundance in oaks of eastern deciduous forests (Summerville et al., 2003).

On sites where retention of oak is not an option, retention of other hardwood species may be adequate. In reclaimed mine habitat in Kentucky, black locust (*Robinia pseudoacacia*) was an important forage tree and planting new trees was recommended to improve habitat quality (Patton et al., 2010). In New York, Ficken and Ficken (1968) identified apple (*Pyrus malus*), black cherry (*Prunus serotina*), and hawthorn as the principal species utilized for foraging. Thus, it is likely that there are a variety of hardwood species that could be retained or planted in open, shrub-dominated habitats that Golden-winged Warblers would find attractive. Retention options will depend on which species are locally available, abundant, and tolerant of exposure following harvest.

For our study, the dominant legacy trees were northern red oak, eastern white pine, and red pine. Care should be taken when selecting trees for retention as some species will not tolerate the post-harvest exposure resulting in tree mortality within the first few years after the timber harvest. In our study, paper birch was occasionally retained but rarely survived the first years of post-harvest exposure (Roth, personal observation). Ideal legacy tree species are deep rooted, such as pines, and healthy dominant individuals that can withstand windthrow (Franklin et al., 1997). Based on research in British Columbia, managers should select trees with low height–diameter ratios and deep, sparse crowns (Scott and Mitchell, 2005).

Habitat management should be evaluated to determine if Golden-winged Warblers are responding as expected to specific silvicultural prescriptions. We found that male density was a good indicator of habitat quality when minimum thresholds for legacy tree characteristics were well understood. Given that nest searching or even establishing pairing success requires considerable time, personnel, and financial resources, it is fortunate that male density has the potential to be a reliable metric of habitat quality for this species in young aspen stands and possibly in other vegetation communities occupied by Golden-winged Warblers.

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