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Cerulean Warbler (*Setophaga cerulea*) and Associated Species Response to Operational Silviculture in the Central Appalachian Region

Gretchen Emily Nareff
West Virginia University, genareff@mix.wvu.edu

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**Cerulean Warbler (*Setophaga cerulea*) and Associated Species Response to Operational
Silviculture in the Central Appalachian Region**

Gretchen E. Nareff

Dissertation submitted
to the Davis College of Agriculture, Natural Resources, and Design
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Doctor of Philosophy
in
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Petra B. Wood, Ph.D., Chair
Donald J. Brown, Ph.D.
James Rentch, Ph.D.
Michael Strager, Ph.D.
Adam Duerr, Ph.D.

Division of Forestry and Natural Resources

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ABSTRACT

Cerulean Warbler (*Setophaga cerulea*) and Associated Species Response to Operational Silviculture in the Central Appalachian Region

Gretchen E. Nareff

In this study, I assessed the response of Cerulean Warblers (*Setophaga cerulea*) and 5 additional songbird species to timber harvests prescribed through operational silviculture. The research took place in relatively contiguous mature deciduous forests in 4 states in the central Appalachian region—Kentucky, Pennsylvania, Virginia, and West Virginia, USA.

For the first part of the study, I collected Cerulean Warbler abundance and territory data through point counts and territory mapping, respectively. I used the point count data to model Cerulean Warbler abundance pre- and post-harvest at 5 study areas (Kentucky [n=1], Virginia [n=2], West Virginia [n=2]) and post-harvest at an additional 2 study areas (West Virginia [n=2]). I analyzed territory data from 2 of the 4 study areas in West Virginia. The primary objective was to determine Cerulean Warbler response to timber harvests, implemented based on the Management Guidelines for Enhancing Cerulean Warbler Breeding Habitat in Appalachian Hardwood Forests (“Guidelines”), published in 2013, but covering a broader range of topographic conditions than those described in the Guidelines. The harvests at my study areas encompassed all available slope positions (i.e., lower to ridge) and aspects (i.e., Beers aspects 0–2). Two of my study areas were within the Ridge and Valley physiographic region, not included in the original study. I used 3 point types—harvest interior, harvest edge, and reference—to assess Cerulean Warbler change in abundance pre- and post-harvest and by years-post-harvest. I used dynamic, open population *N*-mixture models with point count data from the 5 study areas sampled pre- and post-harvest to estimate modeled abundance and population growth and change in abundance pre- to post-harvest, while accounting for detection bias. Using only the post-harvest data from these 5 study areas and the count data from the 2 study areas sampled only post-harvest, I used static *N*-mixture models to estimate modeled abundance and change in abundance among years-post-harvest. The primary results of this analysis indicated that point type, basal area of their preferred tree species, and basal area of large diameter trees were the most important drivers of Cerulean Warbler abundance. Models including slope position and Beers aspect had limited support for the data, which is important in comparing my findings to the Guidelines in which harvests were implemented within Cerulean Warbler preferred habitat characteristics of north- to northeast-facing aspects and upper slopes and ridgelines. Territory density increased 100% between pre-harvest and 2 years post-harvest. The greatest increases in abundance and territory density occurred where pre-harvest numbers were low.

For the second part of my study, I used logistic regression and resource selection functions to assess male Cerulean Warbler territory habitat selection with matched used-available habitat data. I used vegetation points at male Cerulean Warbler singing locations as “used” locations, which I delineated from detections during 7–8 territory mapping visits, and systematically sampled vegetation points within the territory mapping plot grids as “available.” The basal area data were organized into 8 categories reflecting Cerulean Warbler preferred or avoided tree species and structure. I also compared territory size and territory clustering among

pre- and years-post-harvest. Territory size decreased post-harvest, suggesting an improvement in quality of breeding habitat. Territory size should increase when resources or quality are less than adequate and the bird must move around more to acquire resources. I did not observe territory clustering in any year. Pre-harvest, male Cerulean Warblers selected for increasing Beers aspect, whereas tree species composition was not important for territory habitat selection. Conversely, post-harvest, Beers aspect was the least important variable to cerulean habitat selection (largest $\Delta AICc$ value). Male Cerulean Warblers selected for increasing percentage of basal area that was trees intermediate to or overtopped by the canopy trees (i.e., midstory vegetation). Post-harvest, males selected breeding habitat across a wider range of available vegetation and topographic conditions than they did pre-harvest.

Finally, for the third part of my study, I analyzed the response of 5 additional focal species to the harvests at the same 7 study areas I used for Cerulean Warbler analysis, plus 2 additional study areas in Pennsylvania. The focal species are Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), Hooded Warbler (*S. citrina*), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*). I selected focal species that use the range of seral stages available in the central Appalachian region or that can be created and maintained through operational silviculture (i.e., early successional to mature forest). I again used static N -mixture models to estimate abundance and population growth of the 5 focal species, pre- and post-harvest, and among years post-harvest. I analyzed territory density for 4 of the 5 focal species. Eastern Towhee, Indigo Bunting, and Hooded Warbler increased post-harvest and continued to increase 2 and 3 years-post-harvest. Eastern Towhee and Indigo Bunting abundance increased most at harvest interior points followed by harvest edge points and both decreased in abundance at reference points. Hooded Warbler abundance increased at all 3 point types, indicating an overall positive response to the harvest mosaics rather than just to the reduction of basal area or opening of the canopy. Scarlet Tanager and Wood Thrush abundance initially decreased post-harvest, but subsequently increased at harvest edge and reference points or reference points, respectively. Although Wood Thrush remained on the study areas, their territory density declined by 50% during the first year post-harvest.

Within the third part of this study, I used the avian community data from 5 years of point counts to assess differences in community structure among point types within pre-harvest and each post-harvest year, and among pre- and the post-harvest years by point type. I used analysis of similarity and an ordination technique to evaluate the data. The avian community structure did not differ among point types pre-harvest nor did it differ among years at reference points, but the community structure did differ increasingly by year-post-harvest and among years at harvest interior and harvest edge points.

In summary, my findings corroborate the results of the Management Guidelines for Enhancing Cerulean Warbler Breeding Habitat in Appalachian Hardwood Forests, but show that harvests designed with Cerulean Warblers in mind can create breeding habitat on otherwise less desirable topographic conditions. Further, topographic conditions were not important influences on abundance of the five focal species from the third part of my study. Where mature forests are not available, silvicultural prescriptions can be used to enhance forest stands for Cerulean Warblers and a broad suite of other birds, particularly those that breed in shrubby early successional habitat, young forest, or mature forest gaps. Benefits to closed canopy, mature forest species may be limited, but my results show that they were not extirpated from harvest mosaics that retain reference stands or at least lighter harvests with higher basal area.

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TABLE OF CONTENTS.....	v
LIST OF TABLES.....	vii
LIST OF FIGURES	x
LIST OF APPENDICES.....	xiv
 CHAPTER 1: Introduction	 1
Study Areas.....	4
Literature Cited	8
CHAPTER 2: Cerulean Warbler (<i>Setophaga cerulea</i>) response to operational silviculture in the central Appalachian region	 22
Abstract.....	22
1.0 Introduction.....	23
2.0 Methods.....	25
2.1 Regional study area.....	25
2.2 Harvests.....	26
2.3 Vegetation sampling	28
2.4 Avian surveys.....	29
2.5 Statistical analyses	31
3.0 Results.....	36
3.1 Vegetation	36
3.2 Territory density.....	36
3.3 Pre-post-harvest abundance	36
3.4 Post-harvest-only abundance	38
4.0 Discussion	38
4.1 Overall changes in territory density and abundance	38
4.2 Response to topographic metrics	40
4.3 Response to vegetation	40
4.4 Response to years-post-harvest.....	41
5.0 Conclusions.....	42
Literature Cited	43

CHAPTER 3: Breeding habitat selection by male Cerulean Warblers (<i>Setophaga cerulea</i>) in response to operational silvicultural prescriptions in the central Appalachian region	62
Abstract	62
1.0 Introduction	63
2.0 Methods	65
2.1 Regional study area	65
2.2 Harvests	66
2.3 Territory mapping	66
2.4 Vegetation sampling	68
2.5 Topographic metrics	69
2.6 Statistical analyses	70
3.0 Results	71
3.1 Territory size	71
3.2 Territory clustering	72
3.3 Habitat selection	72
4.0 Discussion	72
4.1 Overall changes in territory size	72
4.2 Territory clustering	74
4.3 Habitat selection	74
5.0 Conclusions	75
Literature Cited	76

CHAPTER 4: Avian community response to forest management in the central Appalachian region: Effects of operational silviculture for the Cerulean Warbler (<i>Setophaga cerulea</i>)	98
Abstract	98
1.0 Introduction	99
1.1 Natural history of focal species	100
2.0 Methods	103
2.1 Regional study area	103
2.2 Harvests	103
2.3 Vegetation sampling	105
2.4 Avian surveys	106
2.5 Statistical analyses	108
3.0 Results	114
3.1 Vegetation	114

3.2 Territory density.....	114
3.3 Detection probability	114
3.4 Point count analysis	115
3.5 Community structure	116
4.0 Discussion	117
5.0 Conclusions	120
Literature Cited	121

LIST OF TABLES

CHAPTER 2.

Table 1. Summary of study areas sampled to evaluate Cerulean Warbler (<i>Setophaga cerulea</i>) response to harvests at 7 study areas in the central Appalachian region during 2013–2017. Point count surveys (n=5 study areas) and territory mapping (n=2 study areas, SJ and WC) were conducted pre- and post-harvest and point count surveys for 3 years post-harvest at 2 additional study areas harvested prior to the initiation of our study. Point counts were surveyed up to 3 years post-harvest	50
--	----

Table 2. Survey and study area variables used to model detection probability and abundance, respectively, of Cerulean Warblers (<i>Setophaga cerulea</i>) in the central Appalachian region at seven harvested study areas 2013–2017	51
--	----

Table 3. Model selection process to determine the most parsimonious N-mixture models that explain change in Cerulean Warbler (<i>Setophaga cerulea</i>) abundance from pre- to post-harvest at five study areas in Kentucky, Virginia, and West Virginia 2013–2017. N-mixture models for 114 sample points with 1 year pre-harvest and 1 year post-harvest data are shown. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. K is the number of parameters in a model, AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model's AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables are defined in Table 2	52
--	----

Table 4. Model selection process to determine the most parsimonious N-mixture models that explain change in Cerulean Warbler (<i>Setophaga cerulea</i>) abundance from 1 year post-harvest to 3 years post-harvest at seven study areas in Kentucky, Virginia, and West Virginia 2013–2017. Static N-mixture models for 187 points with post-harvest data are shown. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. K is the number of parameters in a model, AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model's AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables in models are defined in Table 2.....	53
---	----

Table 5. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked N-mixture models (see Table 3) estimating population growth of Cerulean Warblers (*Setophaga cerulea*) at 114 points at five harvested study areas in Kentucky, Virginia, and West Virginia 2013–201753

Table 6. Parameter estimates, standard errors (SE), 95% lower and upper confidence intervals (CI), and P-values from the top ranked N-mixture model estimating population growth of Cerulean Warblers (*Setophaga cerulea*) at 187 points at seven harvested study areas in Kentucky, Virginia, and West Virginia 2013–201754

CHAPTER 3.

Table 1. Topographic and vegetation variables used to model breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) in the central Appalachian region at 4 harvested study areas 2013–201681

Table 2. Means $\pm$ standard error of vegetation (above) and topographic (below) variables used to calculate resource selection functions for male Cerulean Warbler (*Setophaga cerulea*) habitat selection in 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. Variables are defined in Table 182

Table 3. Models to calculate resource selection functions (rsf) to assess pre-harvest breeding habitat selection by male Cerulean Warblers (*Setophaga cerulea*) within 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. “rsf” is the resource selection function, “use” is a binomial variable for used or available habitat, B is the number of bootstrap iterations, and m is the argument describing the matching of use-availability data by mapping plot, which required a long string of characters, not shown here. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. AICc is the Akaike’s Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, Δ AICc is the difference between each model’s AICc value and the lowest AICc value in the candidate set, and wi is the Akaike weight of each model in relation to the entire candidate set. Variable codes are defined in Table 183

Table 4. Models to calculate resource selection functions (rsf) to assess post-harvest breeding habitat selection by male Cerulean Warblers (*Setophaga cerulea*) within 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. “rsf” is the resource selection function, “use” is a binomial variable describing either used or available habitat data, B is the number of bootstrap iterations, and m is the argument describing the matching of use-availability data by mapping plot, which required a long string of characters, not shown here. AICc is the Akaike’s Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, Δ AICc is the difference between each model’s AICc value and the lowest AICc value in the candidate set, and wi is the Akaike weight of each model in relation to the entire candidate set. Variable codes are defined in Table 1.....84

CHAPTER 4.

Table 7. Summary of study areas sampled to evaluate avian response to harvests at 9 study areas in the central Appalachian region during 2013–2017. Point count surveys and territory mapping were conducted pre- and post-harvest at 7 study areas and point count surveys for 3 years post-harvest at 2 additional study areas harvested prior to the initiation of our study. Point counts were surveyed up to 3 years post-harvest.....129

Table 2. Survey and study area variables used to model detection probability and abundance, respectively, of 5 songbird species in the central Appalachian region at 9 harvested study areas 2013–2017130

Table 3. Variables used to model response in abundance of 5 songbird species to timber harvests in the central Appalachian region at 9 harvested study areas 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH). Variables were tested individually or in simple additive models. Model set 1 includes variables that were important to Cerulean Warbler abundance post-harvest at the same study areas (Nareff et al. 2019). Model set 2 includes variables to assess the response to timber harvests over years-post-harvest. Model set 3 includes variables that may be important to the individual focal species based on their breeding habitat preferences. Codes for variables are defined in Table 2. Modeling results are reported in Table 4.....131

Table 4. Model selection process to determine the most parsimonious N -mixture models that explain change in 5 focal species' abundances from pre- to post-harvest and among years-post-harvest at 9 study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Modeling was based on 795 samples from 207 sample points (pre-harvest $n=134$, 1 year post-harvest $n=207$, 2 years post-harvest $n=184$, 3 years post-harvest $n=123$). K is the number of parameters in a model, $AICc$ is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model's $AICc$ value and the lowest $AICc$ value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables are defined in Table 2132

Table 5. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from mixed effects models examining change in territory density from pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 4 harvested study areas in West Virginia 2013–2016.....137

Table 6. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked (i.e., $\Delta AICc < 2$) N -mixture models estimating abundance pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia,

and West Virginia 2013–2017. Variables tested were from the top ranked models explaining Cerulean Warbler (*Setophaga cerulea*) abundance in 2013–2017 (Nareff et al. 2019). Codes for variables in models are defined in Table 2138

Table 7. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked *N*-mixture models estimating abundance by years-post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2.....139

Table 8. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked *N*-mixture models estimating abundance pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2140

Table 9. Fits of variables tested on avian community data by point type (top) and years-post-harvest (bottom; YPH) using non-metric multidimensional scaling (NMDS) ordinations. Models using data from 2 years post-harvest did not converge. Ordinations incorporate the songbird community represented by detections of birds sampled well by point counts (Appendix A) within 50 m of 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2. Bolded values indicated the strongest fits (highest R^2 values).....141

LIST OF FIGURES

CHAPTER 1.

Figure 1. Location of the nine study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Rabbit Hole (RH) and Clear Creek State Forest (CCSF) in Pennsylvania; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia10

Figure 2. Breeding Bird Survey abundance map for the Cerulean Warbler global population 1966–201511

CHAPTER 2.

Figure 1. Location of the regional study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia.....55

Figure 2. Wolf Creek harvest within the Elk River Wildlife Management Area in West Virginia shown as an example of our experimental design. Here, harvest interior, harvest edge, and reference point count locations and territory mapping plots were monitored during 2013–2016 for Cerulean Warbler (*Setophaga cerulea*) abundance and territory density across a timber harvest mosaic. Harvests (clear cut [CC], variable retention, single-tree selection, and group selection) are labeled as described by land managers and were not uniform across each harvest block.56

Figure 3. Cerulean Warbler territory density by territory mapping plot pre-harvest (Pre; 2013–2014), 1 year post-harvest (1 YPH; 2014–2015), and 2 years post-harvest (2 YPH; 2015–2016) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests implemented as operational silvicultural prescriptions. Study areas were Stonewall Jackson Lake Wildlife Management Area (SJ) and Wolf Creek (WC) at Elk River Wildlife Management Area in West Virginia.57

Figure 4. Percent change in estimated abundance of Cerulean Warblers (*Setophaga cerulea*) following tree harvest in forested stands in Kentucky, Virginia, and West Virginia during 2013–2017. The hierarchical model used to estimate abundance included study area as a covariate for initial abundance, point type as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise as covariates for detection probability. Estimated changes in abundance are based on abundance at 54 harvest interior and harvest edge points. Three points with change >300% (709%, 823% and 1260% at harvest interior points) were omitted from the graph to more clearly show the relationship with pre-harvest abundance.....57

Figure 5. Pre- and post-harvest Cerulean Warbler (*Setophaga cerulea*) modeled abundance by point type (harvest interior, harvest edge, reference) at 114 sample points at five harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Bars represent 95% confidence intervals. The hierarchical model used to estimate abundance included study area as a covariate for initial abundance, point type as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise for detection probability58

Figure 6. The three panels show Cerulean Warbler (*Setophaga cerulea*) modeled abundance or population growth rate (# birds/point) at 114 harvest interior, harvest edge, and reference sample points relative to the percentage of basal area that was preferred tree species ≥ 10 cm dbh at five harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Preferred tree species include sugar maple (*Acer saccharum*), white oaks (*Quercus* spp.), and hickories (*Carya* spp.). Post-harvest abundance relationship to

percent basal area that is preferred tree species (A), change in abundance pre- to post-harvest (B) and predicted population growth rate with 95% confidence intervals (C) are shown. The model used to estimate abundance included study area as a covariate for initial abundance, percentage of basal area that was preferred tree species as a covariate for population growth rate, and observer, ordinal date, noise and time-since-sunrise for detection probability59

Figure 7. The three panels show Cerulean Warbler (*Setophaga cerulea*) modeled abundance or population growth rate (# birds/point) at 114 harvest interior, harvest edge, and reference sample points relative to the percentage of basal area that was large diameter trees (≥ 40.6 cm dbh) at five harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Post-harvest abundance (A), change in abundance pre- to post-harvest (B), and predicted population growth rate with 95% confidence intervals (C) are shown. The model used to estimate abundance included study area as a covariate for initial abundance, percentage of basal area that was large diameter trees as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise for detection probability60

Figure 8. Mean Cerulean Warbler (*Setophaga cerulea*) modeled abundance (birds/point) at 187, 164, and 123 sample points at seven harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017, 1, 2, and 3 years-post-harvest, respectively. Bars represent 95% confidence intervals. The model used to estimate abundances post-harvest included study area, point type (harvest interior, harvest edge, reference), years-post-harvest, and calendar year as covariates for post-harvest abundance, and observer, ordinal date, and time-since-sunrise for detection probability. Two points were on the edge of a partial harvest in the first year post-harvest and then true harvest points two years post-harvest after the harvest was complete. This resulted in the numbers of harvest interior points to be the same for the first two years post-harvest.....61

CHAPTER 3.

Figure 1. Location of the 4 study areas within the Appalachian Mountains Bird Conservation Region for this investigation of Cerulean Warbler (*Setophaga cerulea*) habitat selection. Study areas are Coopers Rock State Forest (CR), Stonewall Jackson Lake WMA (SJ), and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA in West Virginia.85

Figure 2. Estimated locations of Cerulean Warblers (*Setophaga cerulea*) recorded over approximately 6 weeks during territory mapping sampling in 2016 at Stonewall Jackson Lake Wildlife Management Area, Lewis County, West Virginia. Observations are used to delineate territories and select vegetation sampling plots to assess habitat selection.....86

Figure 3. Example of territory vegetation point assignment at Cerulean Warbler (*Setophaga cerulea*) territories delineated at Stonewall Jackson Lake Wildlife Management Area, Lewis County, West Virginia in 2016. Vegetation was sampled at every-other mapping point and at all territory points (Terr_Veg)87

Figure 4. Cerulean Warbler (*Setophaga cerulea*) mean territory size $\pm$ standard error pre-harvest, 1 year post-harvest (1 YPH), 2 years post-harvest (2 YPH), and 3 years post-harvest (3 YPH) on 10 territory mapping plots at 4 study areas in West Virginia. The 4 study areas were Stonewall Jackson Lake Wildlife Management Area, Wolf Creek and Dynamite at Elk River Wildlife Management Area, and Coopers Rock State Forest.....88

Figure 5. Cerulean Warbler (*Setophaga cerulea*) selection of Beers aspect (x-axis), pre-harvest. Beers aspect (0–2) represents forest productivity with the least productive, xeric aspects approaching 0 and the most productive, mesic aspects having values approaching 2. Selection strength (y-axis) with median (gold line) 95% confidence intervals is shown. Selection strength increased as Beers aspect increased. Resource selection functions were calculated from logistic regression on used-available habitat data on 4 plots at 2 study areas with pre- and post-harvest data in West Virginia 2013–201689

Figure 6. Cerulean Warbler (*Setophaga cerulea*) selection of midstory vegetation (x-axis), post-harvest. Midstory vegetation, stems ≥ 10 cm dbh that were intermediate to or overtopped by the forest canopy, was assessed as a percentage of overall basal area at sampling points, shown here as a decimal rather than percentage (i.e., 1 = 100% of basal area was intermediate or overtopped by the canopy). Selection strength (y-axis) with median (gold line) and 95% confidence intervals is shown. Selection strength increased as % of midstory increased. Resource selection functions were calculated from logistic regression on used-available habitat data on 10 plots at 4 study areas in West Virginia 2013–2016.....90

CHAPTER 4.

Figure 1. Location of the 9 study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of avian response to harvest treatments. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Rabbit Hole (RH) and Clear Creek State Forest (CCSF) in Pennsylvania; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia.....142

Figure 2. Wolf Creek harvest within the Elk River Wildlife Management Area in West Virginia shown as an example of our experimental design and a harvest mosaic. Here, harvest interior, harvest edge, and reference point count locations and territory mapping plots were monitored during 2013–2016 for songbird abundance and territory density across a timber harvest mosaic. Harvests (clear cut [CC], variable retention, single-tree selection, and group selection) are labeled as described by land managers and were not uniform across each harvest block.....143

Figure 3. Mean territory density (territory/ha) and standard error of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 4 study areas (n=10 plots) in West Virginia, pre-harvest and 1, 2, and 3 years-post-harvest (YPH)144

Figure 4. Abundance (birds/point) of 5 focal songbird species pre-, 1 year (1YPH), 2 years (2YPH), and 3 years (3YPH) post-harvest at 9 study areas in Kentucky (n=1), Pennsylvania (n=2), Virginia (n=2), and West Virginia (n=4) 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*; WOTH). Modeled abundance is based on the top model examining response to years-post-harvest for each species (Table 4)145

Figure 5. Abundance (birds/point) of 4 focal songbird species at harvested point counts at 9 study areas in Kentucky (n=1), Pennsylvania (n=2), Virginia (n=2), and West Virginia (n=4) 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH). Modeled abundance is based on the top model examining response to species-specific variables for each species (Table 4)146

Figure 6. Figure 6. Analysis of similarity (ANOSIM) was used to test for differences in songbird community structure among point types (harvest interior [H], harvest edge [E], and reference [R]) among pre-harvest (PRE) and 1 year (1YPH), 2 years (2YPH), and 3 years (3YPH) post-harvest at 9 study areas in the central Appalachian region. The songbird community differed among point types all years post-harvest, but was similar pre-harvest. The y-axis shows the dissimilarity rank, calculated based on the species richness at each sample point.....147

Figure 7. Analysis of similarity (ANOSIM) was used to test for differences in songbird community structure among pre-harvest (0) and years-post-harvest (1–3) at harvest interior (HI), harvest edge (HE), and reference (Ref) point types at 9 study areas in the central Appalachian region. The songbird community differed among pre-harvest and the three years post-harvest at harvest interior and harvest edge points, but was similar at reference points. The y-axis shows the dissimilarity rank, calculated based on the species richness at each sample point.....148

Figure 8. Non-metric multidimensional scaling (NMDS) was used to ordinate the songbird community 3 years post-harvest at 9 study areas in the central Appalachian region. The ordination shows alpha codes for avian species (Appendix A) and the significant fit of the mean basal area ($\geq 10 \text{ m}^2/\text{ha}$) surface gradient. The avian community is grouped by point type: harvest interior (red), harvest edge (blue), and reference (black).149

LIST OF APPENDICES

CHAPTER 1.

Appendix A. Study area maps12

CHAPTER 3.

Appendix A. Cerulean Warbler territories on 10 territory mapping plots at 4 study areas in West Virginia during 2013–2016	91
Appendix B. FIA crown classifications	97

CHAPTER 4.

Appendix A. All avian species detected on unlimited radius point counts pre- and post-harvest, including their common and scientific names and American Ornithological Society (AOS) banding codes. Species in bold were included in one-way analysis of similarity on the avian community data to test for differences in the avian community structure among point types. Forest types describe where the species most commonly breeds: mature forest (mature), early successional (early), mid-successional (mid), gap specialist (gap)	150
Appendix B. Tree species common and scientific names sampled at point count stations pre- and post-harvest at 9 study areas	153

CHAPTER 1: Introduction

Much of the eastern United States was clearcut in the 19th and early 20th centuries (i.e., Bierman 2010, Johnson and Govatski 2013). Prior to large-scale clearing, eastern forests had remained relatively intact since the time of the last ice age, providing old-growth forests and their inherent structural diversity to native wildlife (Bierman 2010). Once the trees were gone, landowners often abandoned the remaining fields and left them to follow the path of succession without management. Subsequently, regeneration of the forests produced thousands of hectares of even-aged forests, with little heterogeneity in forest structure. This was likely detrimental to songbird species that rely on structural diversity within a forest stand to meet their daily and reproductive requirements, such as food sources, nesting substrate, and protective cover.

Subsequent to large-scale clearing, a conservation movement began, spurring forest management into action (Johnson and Govatski 2013). In more modern times, timber harvests often have multiple objectives, including wildlife management. Timber harvests provide structural heterogeneity, regeneration of mast producing trees, snags, and they may create early successional habitat. Harvests affect songbirds through all of these means, probably most importantly by altering forest structure. The extent and diversity of projects and scope of research on avian response to timber harvests is broad and, in some cases, well understood (Sallabanks et al. 2000).

The Cerulean Warbler (*Setophaga cerulea*; hereafter, “cerulean”) is a severely declining, late-successional songbird species whose core breeding range is in the hardwood forests of the Appalachian Mountains. The cerulean uses heavily forested landscapes with heterogeneous vegetation structure. Although not federally listed under the Endangered Species Act, it was petitioned for listing in 2000. The cerulean is considered a focal species of management concern by the U.S. Fish and Wildlife Service (USFWS), based on a range-wide population decline including a decline of 2.7% per year in the Appalachian Mountains between 1966 and 2015 and a decline of 1.6% per year between 2005 and 2015 (Sauer et al. 2017). The Partners in Flight (PIF) program indicates a 73% population decline within eastern forests since 1966 when the North American breeding bird surveys began (USGS 2018). Additionally, the cerulean is listed under the following international, federal, or state lists: USFWS’s Birds of Conservation Concern list for Bird Conservation Region (BCR) 28, Canada’s federal Species At Risk Act a Species of Special Concern, International Union for Conservation of Nature’s (IUCN) red list as

vulnerable, BirdLife International list as vulnerable to extinction, 5 state threatened and endangered species lists, and it is also identified as a species of greatest conservation need (SGCN) within the Wildlife Action Plans of 22 states.

As such, the cerulean is a species of conservation concern throughout its range. Because of its status, the cerulean has been a focus of research in the central Appalachian region where it reaches some of its highest abundances. In 2013, some of this research led to the production of the Cerulean Warbler Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests (Wood et al. 2013; hereafter, “Guidelines”). The Guidelines describe conditions for increasing or maintaining cerulean abundance and territory density within a limited range of conditions in Appalachian hardwood forests. This project was designed to assess cerulean response to harvests and the range of conditions recommended in the Guidelines, but implemented by means of more typical silvicultural prescriptions in the central Appalachian region (termed “operational silviculture” for the purpose of this research). Harvests for the Guidelines research were implemented only within preferred conditions of the cerulean (i.e., upper slopes and ridgelines and north- to northeast-facing aspects), whereas my harvests were implemented across the landscape at all available slope positions and aspects. Additionally, the Guidelines harvests were small, isolated, and each harvest block contained one level of canopy disturbance and residual basal area (i.e., light, moderate, and heavy). The harvests here were generally implemented as mosaics of a range of canopy disturbance within each study area (e.g., shelterwood adjacent to a single-tree selection). Where harvest mosaics were not designed, harvests were generally shelterwoods with a range of residual basal areas available throughout each study area. Reference areas were left uncut adjacent to and interspersed with harvested areas. The resulting conditions on the landscape were conditions that can be expected from harvests implemented by local land managers and thus I was able to assess cerulean response to available or future conditions created by harvests within the central Appalachian region.

The research contained in this dissertation centers on assessing cerulean response to timber harvests implemented as part of operational silvicultural prescriptions in the central Appalachian region. I organized my dissertation into 4 chapters, 3 of which cover my research and are intended for publication, and this first chapter explaining my general objectives, research justifications, and introduction to the study region. Chapter 2 was recently accepted for publication in *Forest Ecology and Management* and is available online at the time of this writing

(Nareff et. al. 2019). Chapter 2 addresses part of my overarching goal with this research, which was to evaluate response of ceruleans to harvests designed for their management, but placed on a broader range of topographic conditions than those used to produce the Guidelines. Results of my research can be used to refine the Guidelines and help land managers create and maintain habitat for this severely declining migratory songbird. Chapter 3 focuses on cerulean fine-scale habitat selection by comparing vegetation at points used by singing males to vegetation points within territory mapping plots, representing available habitat from which the birds could select breeding territories. The cerulean is well-studied in the central Appalachian region, but questions still remain about their habitat use and response to management. My results provide a better understanding of cerulean response to operational silviculture, at least within this region, which is the core of their breeding range. Chapter 4 turns to the songbird community response to the timber harvests at my study areas, with specific attention given to the response of Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), Hooded Warbler (*Setophaga citrina*), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*). I selected these species because they represent the range of seral stages available within the harvests, prior to the harvests, or within 3 years of the harvests. All were common at my study areas and I assessed their change in abundance and territory density between pre- and post-harvest conditions or relative to conditions in the 2–3 years following the harvests. The status of Wood Thrush is a growing concern among avian ecologists and I provide answers to questions about how timber harvesting affects their populations and how we might be able to manage breeding or post-breeding habitat for them within harvest mosaics.

One motivation for taking on this project was my interest in multi-use management of public lands. Many of the public land managers within our regional study area conduct timber harvests for reasons other than to produce songbird habitat. Most timber harvesting is used for oak regeneration, to sustain game species, and to sell for profit. However, these management goals can easily be achieved by implementing harvest mosaics that can also benefit a wide array of wildlife species with differing habitat requirements, and provide opportunities for hunting and non-consumptive recreation. The Guidelines are also being used by private landowners and this research will assist in providing far-reaching benefits for songbird species, particularly species of conservation concern.

Study Areas

A large team of technicians and researchers conducted this study. I did all of my field work at 4 study areas in West Virginia, while our partners were following the same protocols for bird and vegetation surveys in Kentucky, Pennsylvania, and Virginia. We collected data at 15 study areas among the 4 states; I present data from 9 study areas (Fig. 1; Appendix A). The 6 omitted study areas were either not harvested before the end of the project or harvested 10–20 years before initiation of the study and thus were not comparable to newly harvested areas. However, the data will be important for future studies or an extension of this research. The 15 study areas were located within the Appalachian Mountains BCR and 3 physiographic provinces: the Cumberland Plateau, Ridge and Valley, and the Allegheny Plateau. Most of the study areas fell within “Cerulean Warbler Focal Areas” delineated by the Appalachian Mountains Joint Venture (AMJV) partnership but all were within the core breeding range (Fig. 2). These areas were identified for their potential for sustaining or enhancing cerulean breeding habitat.

Kentucky

Six timber harvests totaling 32.4 ha were implemented on Grayson Lake Wildlife Management Area (WMA) (38°11'20.4"N, 83°0'36.72"W; Carter and Elliot counties) following the 2013 breeding season. The Grayson Lake WMA sits at approximately 906 m in elevation, on either side of Grayson Lake in eastern Kentucky. Kentucky Department of Fish and Wildlife Resources staff delineated, cruised, and marked 2 10.1-ha units, 2 4.0-ha units, and 2 2.0-ha units. Each unit was a shelterwood harvest. White oak (*Quercus alba*), tulip poplar (*Liriodendron tulipifera*), and hickory (*Carya* spp.) dominated the study area.

Pennsylvania

Clear Creek State Forest

The Clear Creek State Forest (CCSF) harvest (41°19'41.02" N 79°2'43.98"W) was located at 544 m elevation approximately 8.2 km northeast of the village of Sigel, Jefferson County, Pennsylvania. In 2002 the entire area was fenced in response to high deer predation on seedling trees. In 2010–2012 areas of dense mountain laurel (*Kalmia latifolia*) and black gum (*Nyssa sylvatica*) were treated with a combination of mechanical and chemical treatments to

promote oak regeneration and an early spring burn was conducted to reduce laurel and other competing plants. The 22.0-ha harvest included a larger shelterwood cut and a series of smaller group-selection openings (along the roadside of the area for aesthetic purposes). Mixed oaks and red maple (*Acer rubrum*) dominate the site. Harvesting occurred between the 2014 and 2015 breeding seasons.

State Game Land 86 Amoeba and Rabbit Hole

State Game Land (SGL) 86 (41°43'31.53" N 79°21'29.22"W) sits at a mean elevation of 531 m on the western bank of the Allegheny River in Warren County, Pennsylvania, within the Pennsylvania Game Commission's northwest region. The majority of SGL 86 was harvested in the early 1900s and part was harvested again in the early 2000s, including Amoeba, which is the reason for my exclusion of that data from my dissertation. Approximately 19.6 ha of the SGL, designated as Rabbit Hole, was harvested between the 2014 and 2015 breeding seasons and is included in the bird community chapter. Red maple, northern red oak (*Q. rubra*), and white oak were the dominant tree species.

Allegheny National Forest: Salmon Creek West Project

The Salmon Creek West Project (41°35'41.94" N 79°14'37.19" W) of the Allegheny National Forest was located approximately 11 km northwest of Marienville, Forest County, Pennsylvania, on a relatively flat plateau top averaging 535 m in elevation. Harvesting did not occur within the timeline of this study so the data were not included in analyses.

State Game Lands 35, 75, and 310

Three study areas at state game lands within the Pennsylvania Game Commission's northeast region were added for the 2015 and 2016 breeding seasons. State Game Land 37 (41°51'3.25" N 77°9'32.19"W) sits at a mean elevation of 497 m just west of the Tioga Reservoir in Tioga County, Pennsylvania. Part of SGL 37 was harvested in the early 2000s, which is the reason for my exclusion of those data from my dissertation. State Game Land 75 (41°26'7.65" N 77°19'54.26"W) sits at a mean elevation of 491 m in Lycoming County, Pennsylvania. State Game Land 310 (41°27'20.43" N 75°25'58.04"W) sits at a mean elevation of 460 m east of Lake Henry in Wayne County, Pennsylvania. I excluded the 3 point counts

surveyed at both SGL 75 and SGL 310 because the six points were either within or adjacent to a harvest or some type of canopy disturbance that resulted in conditions that precluded me from making appropriate comparisons to the other study areas.

Virginia

T. M. Gathright Wildlife Management Area

Three timber harvests totaling 35.5 ha were proposed for the T. M. Gathright Wildlife Management Area (37°58'36.64"N, 79°56'41.10"W; Gathright) in Bath County. One harvest totaling 14.8 ha was completed between the 2015 and 2016 breeding seasons and is included in my analyses. Gathright is approximately 11.3 km west of Warm Springs and about 16.1 km north of Covington, Virginia. The Gathright study area was located on the western slope of Coles Mountain above Lake Moomaw. The harvest site was along the ridge adjacent to the Coles Mountain Fire Road at an approximate elevation of 862 m; the most abundant tree species at the site were chestnut oak (*Q. montanus*) and northern red oak.

Highland Wildlife Management Area

Highland WMA (38°19'5.52"N, 79°34'39"W; Highland) in Highland County is approximately 48.3 km west of Staunton, Virginia. Four harvest sites within the Jack Mountain tract were selected for the study and while the tracts were harvested at different times during the study, I refer to Highland as 1 study area; I describe the tracts individually here and the data were analyzed accordingly, based on methods described in the following chapters. The 18.5 ha Jack Mountain Ridge Treatment 1 (HI1) harvest (38°18'41.10"N, 79°34'57.87"W) follows the contours of the eastern slope of Jack Mountain ridge at an approximate elevation of 961 m. The harvest occurred after the 2015 breeding season and the most abundant tree species were chestnut oak and red maple. Just south along Jack Mountain ridge is the 15.5 ha Jack Mountain Ridge Treatment 2 (HI2) harvest (38°18'36.73"N, 79°35'04.65"W) at an approximate elevation of 968 m. The most abundant tree species at HI2 were northern red oak and red maple and this harvest was completed following the 2014 breeding season. The third harvest site is the 8.8 ha Bear Mountain West Treatment 3 (HI3) (38°19'57.01"N, 79°34'06.61"W), north of treatments HI1 and HI2, along the eastern slope of Jack Mountain ridge at an approximate elevation of 932 m. The most abundant tree species at HI3 were chestnut oak and northern red oak. The fourth

harvest was the 14.2 ha Sounding Knob South Treatment 4 (HI4) (38°19'52.07"N, 79°34'59.57"W), west of HI3, just southeast of Sounding Knob at an approximate elevation of 1084 m. The most abundant tree species at HI4 were northern red oak and chestnut oak. Both HI3 and HI4 were harvested after the 2016 breeding season and were included in analyses.

West Virginia

Harvests at the 5 West Virginia study areas (Fig. 1) occurred as a mosaic at each study area, including shelterwood harvests, clearcuts, singletree selection, and group selection, with unharvested areas throughout (Appendix A). West Virginia Division of Natural Resources and Division of Forestry staff delineated, cruised, and marked all harvest areas.

Coopers Rock State Forest (CRSF)

Two study areas, Scotts Run II and Pisgah, were located within the CRSF, 21 km east of Morgantown, WV, which is cooperatively managed by the Division of Natural Resources and Division of Forestry. The Pisgah harvest area (39°39'3.83"N 79°46'21.67"W), in Preston County, was proposed to be 151.8 ha at a mean elevation of 652 m. The entire project area was last harvested in the 1930s. The pre-harvest data collected at Pisgah are not included in analyses here. Because I excluded Pisgah, I refer to the Scott's Run II harvest as CRSF throughout the remainder of my dissertation. The CRSF study area (39°38'54.40" N 79°48'23.63" W) is 77.2 ha at mean elevation 632 m and is contained primarily within Monongalia County, with a very small portion in Preston County. Most of the study area's current harvest, completed in 2012, is contained within the previous Scott Run harvest area, completed in early 1982, with the primary objectives to improve the overall quality of the stands for wildlife and to increase the health and vigor of residual trees. The primary objective of the CRSF harvest in 2012 was to improve oak regeneration and improve wildlife habitat. Prior to the harvest, the dominant tree was red maple. State foresters delineated two major timber types: tulip poplar and mixed-oak. Tulip poplar, chestnut oak, red maple, and northern red oak dominate the residual tree species composition.

The CRSF harvest incorporated a 4.7-ha regeneration harvest and a 2.8-ha savannah to provide large, mast producing-age oaks and some early successional habitat, the most limited habitat type at the state forest. Most trees above 15.2 cm dbh were removed in the regeneration harvest. Soft mast-producing trees and trees less than 15.2 cm dbh were left to provide food for

wildlife and vertical refuge for birds, respectively. Additionally, slash and treetops were left to reduce deer browse pressure and to provide refuge for wildlife.

Elk River Wildlife Management Area

Two study areas were located within the 7,375.4-ha Elk River WMA, approximately 8.0 km southeast of Sutton, West Virginia. By the end of May 2012, a harvest mosaic of approximately 39.8 ha was implemented at mean elevation of 481 m at the Dynamite site (38°38'31.05" N 80°36'25.26" W). Tulip poplar, oak, and hickory dominated the site, which had a red maple and cucumber magnolia (*Magnolia acuminata*) understory.

The Wolf Creek harvest (38°38'19.62" N 80°40'17.20" W) was approximately 5.6 km west of the Dynamite harvest. Approximately 6.1 ha were harvested during the winter in 2013 and the remaining 20.5 ha harvested immediately following the 2014 breeding season. Wolf Creek has a mean elevation of 398 m. Tulip poplar, oak, and hickory dominate the site. Wolf Creek was the steepest site with a ridgeline along the western edge of the harvest.

Stonewall Jackson Lake Wildlife Management Area

The Stonewall harvest (38°54'54.32" N 80°28'54.49" W) was approximately 13.7 km south of Weston, West Virginia. The harvest area was approximately 32.0 ha at a mean elevation of 408 m. Maples, ash (*Fraxinus* spp.), tulip poplar, and oaks dominated the site. Foresters retained patches of grapevines (*Vitis* sp.), specifically for ceruleans. The Division of Natural Resources killed small (<8 cm) red maple, American beech (*Fagus grandifolia*), and sourwood (*Oxydendrum arboreum*) in June 2014 using the hack-and-squirt method in preparation for the harvest. Harvesting was delayed at this study area and primarily occurred after August 2014, with a small portion harvested prior to the 2016 breeding season.

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Figure 1. Location of the 9 study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Rabbit Hole (RH) and Clear Creek State Forest (CCSF) in Pennsylvania; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia.

Figure 2. Breeding Bird Survey abundance map for the Cerulean Warbler global population 1966–2015.

Appendix A. Study area maps

Grayson Lake Wildlife Management Area, Kentucky.

Clear Creek State Forest, Pennsylvania.

SGL 86, Rabbit Hole, Pennsylvania.

Gathright Wildlife Management Area, Virginia.

Highland Wildlife Management Area, Virginia. Units 1–2. The reference point within the harvest boundary was a harvest edge point, but had the same basal area pre- and post-harvest and thus was analyzed as a reference point.

Highland Wildlife Management Area, Virginia. Units 3–4.

Coopers Rock State Forest, West Virginia.

Dynamite, Elk River Wildlife Management Area, West Virginia.

Stonewall Jackson Lake Wildlife Management Area, West Virginia.

Wolf Creek, Elk River Wildlife Management Area, West Virginia.

CHAPTER 2: Cerulean Warbler (*Setophaga cerulea*) response to operational silviculture in the central Appalachian region

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Abstract. The Cerulean Warbler (*Setophaga cerulea*) is a species of conservation need, with declines linked in part to forest habitat loss on its breeding grounds. Active management of forests benefit the Cerulean Warbler by creating the complex structural conditions preferred by the species, but further research is needed to determine optimal silvicultural strategies. We quantified and compared the broad-scale influence of timber harvests within central Appalachian hardwood forests on estimated abundance and territory density of Cerulean Warblers. We conducted point counts at 7 study areas across 3 states within the central Appalachian region (West Virginia [n=4], Kentucky [n=1], Virginia [n=2]) and territory mapping at 2 of the study areas in West Virginia, pre- and post-harvest, for up to 5 breeding seasons from 2013–2017. Our primary objective was to relate change in abundance to topographic and vegetation metrics to evaluate the effectiveness of current Cerulean Warbler habitat management guidelines. We used single-species hierarchical (*N*-mixture) models to estimate abundance while accounting for detection biases. Pre-harvest mean basal area among study areas was 29.3 m²/ha. Harvesting reduced mean basal area among study areas by 40% (mean 17.2 m²/ha) at harvest interior and harvest edge points. Territory density increased 100% ($P = 0.003$) from pre-harvest to 2 years post-harvest. Cerulean Warbler abundance increased with increasing percentage of basal area that comprised tree species preferred for foraging and nesting (i.e., white oak species [*Quercus* spp.], sugar maple [*Acer saccharum*], hickories [*Carya* spp.]) or of large diameter trees (≥ 40.6 cm diameter at breast height). Positive population growth was predicted to occur where these vegetation metrics were $>50\%$ of residual basal area. Post-harvest abundance at harvest interior points was greater than at reference points and when accounting for years-post-harvest in modeling abundance, Cerulean Warbler abundance increased at harvest interior and reference points 2 years post-harvest and subsequently decreased 3 years post-harvest. Modeled abundance remained the same at harvest edge points. Increases in abundance and territory density were

greater in stands with low pre-harvest densities (<2 birds/point or <0.40 territory/ha) of Cerulean Warblers, whereas populations within stands with higher densities pre-harvest had minimal changes in abundance and territory density. Overall, our results indicate that harvests based on the Cerulean Warbler Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests, at all available slope positions and aspects where pre-harvest densities are <0.40 territory/ha, may provide breeding habitat for Cerulean Warblers for at least 2 years post-harvest in the central Appalachian region.

Keywords: Cerulean Warbler, silviculture, *N*-mixture, forest bird management, upland hardwood forest

1. Introduction

The Cerulean Warbler (*Setophaga cerulea*) is a Nearctic-Neotropical migratory songbird with a steeply declining global population (Robbins et al. 1992, Sauer et al. 2017) whose core breeding range is within hardwood forests in the central Appalachian region of the eastern United States. Its decline has been linked to forest habitat loss on the breeding and wintering grounds (Robbins et al. 1992, Hamel et al. 2004) and lack of forest habitat management to provide needed structural complexity within mature forests on the breeding grounds (Boves et al. 2013b). Much of the eastern United States was clearcut in the 19th and early 20th centuries (e.g., Kelty and D'Amato 2005, Johnson and Govatski 2013, Thompson et al. 2013). Subsequent regeneration of forests and wildfire suppression following widespread clearcutting produced predominantly even-aged forests, with little heterogeneity in forest structure (Miller et al. 2004) that the birds require during the breeding season (Wood et al. 2013).

Because of its decreasing population size, the Cerulean Warbler is considered a species of conservation need throughout its range. The breeding range extends from its core in the central Appalachian region west to central Minnesota and easternmost Oklahoma and Kansas, east into parts of southern New England and north into southern Quebec and Ontario, Canada (Fig. 1; see Buehler et al. 2013 for detailed range description). The Partners in Flight (PIF) program indicates a 73% population decline within eastern forests since 1966 when the North American breeding bird surveys began (USGS 2018); eastern forests contain 72% of the overall population of Cerulean Warblers (Rosenberg et al. 2016). Further, PIF estimates that it will decrease another

50% within ca. 25 years if management remains at status quo (Rosenberg et al. 2016). Cerulean Warbler breeding habitat is characterized by large, tall trees within mature deciduous forests (Hamel 2000). In mountainous terrain, Cerulean Warblers are associated with steep, upper slopes and ridgetops, and north- to northeast-facing slopes (Weakland and Wood 2005, Hartman et al. 2009). They are also associated with canopy gaps (e.g., through windthrow), internal forest edges (e.g., partially closed-canopy roads), and topography that all provide opportunities for broadcasting their songs to defend territories and attract mates (Weakland and Wood 2005, Barg et al. 2006, Bakermans and Rodewald 2009, Wood and Perkins 2012, Perkins and Wood 2014).

Silviculture-based forest management can be an important tool to manipulate forest stand structure for gap-dependent mature-forest songbird species like the Cerulean Warbler (Buehler et al. 2008, Boves et al. 2013b, Sheehan et al. 2013, Wood et al. 2013, Hamel et al. 2016). Forest management techniques can be used in mid-seral stands, to mimic, in part, the more complex structural conditions found within late-seral stage forests (e.g., numerous and large canopy gaps, large canopy trees, multiple vegetation strata; Boves et al. 2013b). Canopy gaps allow sunlight to penetrate the overstory, increasing the vigor of desired seed trees, and to reach the forest floor where the sunlight aids in regeneration of multiple strata in the mid- and understories. The regeneration of this vegetation supports invertebrate prey species and thus spatially diverse foraging opportunities for insectivorous birds (Duguay et al. 2001, Newell and Rodewald 2012), and provides refuge for post-breeding adults and fledglings (Pagen et al. 2000, Vitz and Rodewald 2006, Porneluzi et al. 2014, Raybuck 2016, Ruhl et al. 2018). Waiting for natural succession to reach the late-seral stage is not ideal when managing for a species whose population is predicted to decline by another 50% within ca. 25 years (Rosenberg et al. 2016). Forest management can be used to provide the necessary structural diversity in a short period of time (Boves et al. 2013b, Sheehan et al. 2013).

Previously, a set of experimental forest harvests were used in the central Appalachian region to develop the Cerulean Warbler Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests (Wood et al. 2013; hereafter “Guidelines”). Three intensities of harvests were implemented on 10-ha forest stands isolated from other canopy disturbances on the landscape (Boves et al. 2013b). The harvests were within mature, mixed-mesophytic forests, on upper slopes and ridgelines, and on north- to northeast-facing slopes, preferred habitat for the Cerulean Warbler (Weakland and Wood 2005, Roth and Islam 2008, Perkins and Wood 2014).

Although the study determined the preferred range of basal area within these conditions (9.2–20.7 m²/ha; Wood et al. 2013), it is unknown if Cerulean Warblers would be attracted to similar harvests on less preferred slope positions and aspects. Thus, for our study, harvests were applied to a greater variability of contexts intended to expand upon the Guidelines. Harvests occurred on a broad range of available slope positions (lower to ridgetops) and aspects (Beers aspects 0–2; Beers et al. 1966) rather than being restricted to specific topographic characteristics. Total harvested area at each study area was larger (range 16.4–77.2 ha, mean 40.7 ± 7.7 ha) than in the original study, and harvests were not isolated from other disturbances in the landscape. Additionally, 2 of the study areas were in the Ridge and Valley physiographic region, which was not included in the original study.

Accordingly, our objective was to examine the response of Cerulean Warblers to a range of forest management treatments as part of operational silviculture prescriptions developed by land managers of state agencies, within the varied topographic conditions and forest types in the central Appalachian region. We addressed unanswered questions about the response in abundance and territory density of Cerulean Warblers by evaluating some conditions that are considered less preferred by the species (e.g., southwestern-facing slopes or lower slope positions). We also examined if species composition and size of residual trees within a harvested stand influenced response of Cerulean Warblers. We expected Cerulean Warbler abundance and territory density to increase where basal area was reduced in such a way that would open the canopy, but leave large diameter trees (≥ 40.6 cm diameter at breast height [dbh]), especially in stands where residual trees comprised white oaks (*Quercus* spp.), hickories (*Carya* spp.), and sugar maple (*Acer saccharum*). Based on the Guidelines, we expected greater increases to occur where basal area was reduced to 9.2–20.7 m²/ha on upper portions of north- to northeastern-facing slopes (Wood et al. 2013), but intended to determine if increases occurred where basal area was reduced to similar levels on less preferred slope positions and aspects.

2. Methods

2.1. Regional Study Area

We conducted fieldwork during 2013–2016 (Kentucky, West Virginia) and 2013–2017 (Virginia) in contiguous, mature forest landscapes at 7 study areas within the central Appalachian region and Appalachian Mountains Bird Conservation Region (NABCI 2000; Fig.

1). The region is characterized by a series of parallel, southwest- to northeast-trending narrow valleys and high ridges, and dry-mesic and mixed-mesophytic forest types dominated the study areas (USDA Forest Service 1994). Because all study areas were on Wildlife Management Areas (WMA) or State Forests (SF), they had been managed for a variety of objectives including experimental and teaching harvests, creation of wildlife food plots, or clearings for recreation and skid roads. The study areas (Fig. 1; Table 1) were Grayson Lake WMA, Kentucky (GL); T.M. Gathright WMA, Virginia (GA); Highland WMA, Virginia (HI); Wolf Creek (WC) and Dynamite (DY) within the Elk River WMA, West Virginia; Stonewall Jackson Lake WMA, West Virginia (SJ); and Coopers Rock SF, West Virginia (CR). They fell within 3 physiographic provinces: GL in the Cumberland Plateau, GA and HI in Ridge and Valley, and all West Virginia study areas in the Allegheny Plateau.

State partners identified areas for management, but all were within the core breeding range of the Cerulean Warbler (Sauer et al. 2017), represented a range of available slope positions, aspects, and elevations, and fell within “Cerulean Warbler Focal Areas” delineated by the Appalachian Mountains Joint Venture (AMJV) partnership (Fearer 2011). Focal Areas contain core populations of the Cerulean Warbler that are important for sustaining its current distribution or where additional active forest management will likely enhance the habitat for this bird. Tree species composition differed somewhat among study areas, but common overstory tree species included oaks (northern red oak [*Q. rubra*], scarlet oak [*Q. coccinea*], black oak [*Q. velutina*], white oak [*Q. alba*], chestnut oak [*Q. montanus*]), hickories, red maple (*A. rubrum*), sugar maple, black cherry (*Prunus serotina*), and tulip poplar (*Liriodendron tulipifera*). Elevation at the sampled points ranged from 214–1122 m (mean 586 m).

2.2. Harvests

The total area harvested at each study area for this project comprised a small proportion of each WMA or state forest (0.4–1.5%). The total area harvested at each study area (Table 1) was 16.4–77.2 ha (mean 40.7 ± 7.7 ha) and comprised small harvest blocks (0.4–6.9 ha), linear harvests (8.8–18.5 ha), or harvest mosaics (Fig. 2) encompassing a diversity of harvest types (i.e., shelterwood, group selection, clearcut with residuals) that resulted in a range of canopy openness. Many of the harvests were described by the local land managers as shelterwood systems, whereby the mature community is removed in two or more successive cuttings separated in time by 5–10 years, temporarily leaving mature seed trees and resulting in a new

even-aged system (Nyland 2007). However, our study ended before any overstory removal harvests were implemented. The other silvicultural systems used on the study areas included clearcuts with residuals and single-tree to group selection harvests. The ultimate goal of the harvests, outside of the intended use for our study, was to provide conditions where oaks and hickories would make up the bulk of the regenerating class, providing conditions that would allow desired, valuable saplings to outcompete less desirable species (e.g., red maple) (WVDOF 2006). We did not evaluate Cerulean Warbler response to specific harvest types, but to the resulting conditions in basal area and tree species composition. We designated 3 point types to make our assessments: harvest interior, harvest edge, and reference (detailed description in Section 2.4.2). We used unharvested areas around, and interspersed with harvests in order to compare Cerulean Warbler abundances between harvested and reference points (Fig. 2). The harvests and surrounding unharvested areas that contained sample points was considered a study area and they ranged 47–224 ha in size (Table 1).

Harvests were applied based on the Guidelines (Wood et al. 2013), but were placed on all available slope positions and aspects by state managers of each study area. Harvests were limited to the dormant season because the entire study region was within the range of the endangered Indiana bat (*Myotis sodalis*) that relies on trees and snags for day-roosts in the maternity season and therefore summer harvests were precluded (Silvis et al. 2016, Johnson and King 2018). Our original study design planned for 1 year of pre-harvest data collection followed by 3 years of post-harvest data collection at all study areas. However, poor winter weather and logistics related to harvest contracts delayed harvests at all but 1 of the study areas such that number of years sampled post-harvest varied from 1 to 3 years per study area (Table 1). Consequently, we sampled 2 additional study areas (DY and CR) that were harvested the winter before initiation of our study to increase post-harvest sample size (hereafter “post-only” study areas) to allow us to examine the influence of years-post-harvest on Cerulean Warbler abundance. Harvests were applied at DY and CR over the winter of 2012–2013 and were initially sampled during the 2013 breeding season (i.e., first year post-harvest). We sampled 5 study areas both pre- and post-harvest (hereafter “pre-post” study areas). Pre-harvest data were used for analyses only on the 5 pre-post study areas. However, post-harvest data from all 7 study areas were included in a separate post-only data analysis examining the relationship between Cerulean Warbler abundance to years-post-harvest.

2.3. *Vegetation Sampling*

We used standardized protocols across the study areas to quantify canopy tree basal area and tree species composition pre-harvest and the first year post-harvest because these metrics were important characteristics of Cerulean Warbler breeding habitat (Roth and Islam 2008, Perkins and Wood 2014). We placed four plots at each systematically placed point count location; one at the point center, one 35 m away from the center at magnetic north, and the remaining two at 120° intervals 35 m away from the center point (hereafter, “subplots”). We measured post-harvest basal area at 7 points at HI at only three subplots. We completed variable radius prism plots using a wedge prism (10-factor English or 2.5-factor metric) to tally live trees and snags at every subplot. Tree tallies from variable radius prism plots rely on the relationship between the diameter at breast height (dbh) of each tree and the distance between those trees and the observer. By holding the prism at a fixed distance from the eye over the plot center and rotating 360° around the prism, the observer tallies trees that are in the plot. For each snag, we recorded dbh. For each live tree, we recorded tree species or group (e.g., hickory group, red oak group) and dbh measured to the nearest centimeter (cm) using a Biltmore stick or dbh tape. Borderline live trees and snags were counted and included for tree composition values, but every other borderline live tree was removed to calculate total basal area. We sampled harvested subplots once pre-harvest and once post-harvest; we sampled unharvested subplots only once because vegetation did not change.

We calculated mean basal area of stems ≥ 10 cm dbh per point from the measured subplots at every point within the 3 point types (Boves et al. 2013b, Sheehan et al. 2013). We also calculated mean basal area of preferred and avoided tree species ≥ 10 cm dbh and of all sampled large diameter trees (≥ 40.6 cm dbh; Boves et al. 2013a). Preferred tree species for nesting and foraging included sugar maple, white oaks, and hickories whereas avoided tree species included red maple and red oaks (avoided tree species are used infrequently for foraging or nesting, but they are not uncommon in Cerulean Warbler territories; Barg et al. 2006, George 2009, Wood and Perkins 2012, Wood et al. 2013). We then summed the basal areas for each species or group in the subplots and calculated the percentage of basal area of preferred and avoided tree groups and all large diameter trees per point.

2.4. Avian Surveys

2.4.1. Territory mapping

For 2 of the 4 West Virginia study areas (SJ and WC), we quantified Cerulean Warbler territory density annually, pre- and post-harvest, using territory mapping (Bibby et al. 2000). We centered 2 16–17-ha plots over the harvest mosaics at each study area (Fig. 2) for a total of 4 territory mapping plots.

We situated plot boundaries so that each plot would encompass mostly harvested area, although each included a small amount of unharvested area (Fig. 2). We placed plots at least 100 m apart to avoid counting the same territory on more than one plot. We marked plot boundaries and an internal grid of 50-m intervals with plastic flagging before each field season. Unless a flagged tree was harvested, the flagging remained on the same trees for the duration of the study.

We initiated territory mapping surveys approximately 10 days after Cerulean Warblers first arrived at our study areas in West Virginia (19–23 April) and mapped territories during 7–8 visits per plot through early June 2013–2016. Surveys continued for 6 weeks with a minimum of 4 days between surveys (Bibby et al. 2000). One person surveyed an entire plot within a single morning from dawn to approximately 1100 hours. The same person sampled each plot within a season when logistically possible to maximize detections over repeated visits. We varied the starting points and routes taken through the plots between surveys to reduce time-of-day bias. We recorded singing, calling, and behavioral observations on topographic maps overlaid with the plot grids to accurately note slope position and aspect. We directed special attention to accurately noting multiple individuals that could be heard or seen concurrently (i.e., counter-singing, aggressive interactions) due to its importance in territory delineation. We delineated territory boundaries using detections and instances of counter-singing during the 7–8 visits annually. We estimated territory boundaries in a geographic information system (GIS; ArcMap 10.3, ESRI 2014). A territory can be delineated from a minimum of 2 territory mapping detections separated by 10 days over 8 territory mapping visits (Bibby et al. 2000, Haché et al. 2013). However, most of the individuals we mapped were reliable in their territorial behavior and once established, they were encountered during ≥ 3 territory mapping events. We used recurring locations of singing individuals as approximate territory locations, while locations of counter-singing and aggressive interactions likely represented actual territory boundaries.

Using the minimum convex polygon method (Sheehan et al. 2013, Wood and Perkins 2012), we drew lines in ArcMap to connect the outermost locations of singing males or other territorial cues (i.e., sightings of pairs), using knowledge of the habitat, locations of counter-singing males, and nests as guides. We used the connecting lines to form polygons that approximated territory boundaries. Because some territories extended beyond the boundaries of the territory mapping plots, we included in analyses territories with $\geq 50\%$ of their area within the territory mapping plot (Sheehan et al. 2013). We calculated annual territory density (# territory/ha) of individual territory mapping plots by summing the number of territories within a plot and dividing by the total area of the territory mapping plot.

2.4.2. Point Counts

We systematically placed point count locations (points) throughout the harvest and reference stands, spacing points ≥ 200 m from each other to avoid double counting birds. We placed harvest interior points within harvest units and ≥ 50 m from the closest edge of a harvest (mean distance 64.7 ± 4.5 m); harvest edge points could be inside or outside the harvest boundaries but all were < 50 m from the closest edge of a harvest (mean distance 5.8 ± 1.9 m); and reference points were ≥ 50 m, but generally ≥ 100 m from harvests (mean 319.8 ± 28.5 m; 84% of points ≥ 100 m). Edge effects for avian species are generally considered to occur within 50 m of forest edge (Paton 1994). We placed reference points in areas that were similar to pre-harvest conditions at the harvested points and where no harvests would take place for the duration of the project. Thus, reference points represented mature forest conditions generally available in our study landscape, and as such did not occur in mature forest conditions without internal edges (e.g., hiking trails, campgrounds, skid roads, water features).

We surveyed for Cerulean Warbler abundance at a total of 187 points including 114 pre-post points (28 harvest interior, 26 harvest edge, and 60 reference) and 73 post-only points (27 harvest interior, 11 harvest edge, and 35 reference). All points were sampled 2013–2016 except the post-only sites (CR and DY), which we dropped in 2016 because we had acquired data for 1–3 years post-harvest. In 2017, we sampled only the Virginia study areas (GA and HI; Table 1) to acquire the one-year post-harvest data for these study areas. We surveyed from 15 May to 29 June each year, which coincides with the peak breeding season for songbirds in the central Appalachian region (e.g., Newell and Rodewald 2012, Wood and Perkins 2012, Boves et al. 2013a, Sauer et al. 2017). Surveys were conducted on days without steady rain or sustained

winds >19 kilometers per hour (i.e., >3 on the Beaufort scale), between sunrise and 1100 hours. We recorded noise level, cloud cover, wind, and start time for each survey to incorporate into detection models (Table 2).

At each study area, a field crew of technicians or local biologists conducted the avian sampling. Most surveyors were experienced prior to the initiation of the study, but all were trained in bird identification, distance estimation, and sampling protocols before surveys began. We surveyed each point 3 times each year, with approximately 1 week between visits when possible. We attempted to survey points in a different order each visit to reduce time-of-day bias and by a different observer to reduce observer bias. We recorded detections within 5 distance bands indicating the distance of the bird from the observer (0–25 m, >25–50 m, >50–75 m, >75–100 m, and >100 m) but used only the first 2 distance bands in analyses (section 2.5.2)

2.4.3. *Topographic Metrics*

We used a 1:24,000 digital elevation model (DEM; USGS 2017) to calculate 2 topographic metrics (slope position and Beers aspect) within the 50-m radius for each point using the “Topography Tools for ArcGIS 10.3 and earlier” toolbox (version 10.3, Dilts 2015). We classified each point with 1 of 6 categories of slope position by obtaining the majority from the raster layer in GIS, using the “zonal statistic as table” tool, within the 50-m point count radius. Three categories were represented as the majority at our sample points: lower, middle, and ridge (Table 2). Beers aspect (0–2; Beers et al. 1966) represents forest productivity with the least productive, xeric aspects approaching 0 and the most productive, mesic aspects having values approaching 2. We assigned the mean Beers aspect within the 50-m point count radius for each point from the raster layer in GIS using the “zonal statistic as table” tool.

2.5. *Statistical Analyses*

2.5.1. *Territory density*

We used one-way repeated measures analysis of variance (ANOVA) and Tukey’s honestly significant difference (HSD) *post hoc* test to test for differences in our response variable, territory density, among levels of our predictor variable, years-post-harvest, with territory mapping plots as a random effect. We assigned the calculated territory densities to pre-harvest, 1 year post-harvest, and 2 years post-harvest. We tested the normal distribution and sphericity assumptions of ANOVA with a Shapiro Wilks test and Mauchly’s test, respectively. We considered results significant at $\alpha = 0.05$.

2.5.2. Point counts

We included bird detections within 50 m of the point count (point) center in our analyses to more closely relate abundance to vegetation and topographic characteristics measured within 50-m radius of each point. Cerulean Warblers have small territories (usually <1.0 ha; Oliarnyk and Robertson 1996, and Robbins et al. 2009, Kaminski and Islam 2013). Thus, any bird detected beyond 50 m of the point center will likely have little to no relationship with the vegetation and topographic characteristics at that point (Hutto 2016).

We used an *N*-mixture modeling approach to estimate abundance for the pre-post and post-only datasets separately. *N*-mixture models use spatially and temporally repeated counts to estimate abundance as a product of ecological processes and imperfect detection by linking two sub-models (Royle 2004, Dail and Madsen 2011, Kéry 2018). This is important because birds are likely not distributed randomly in space, as the landscape is heterogeneous, providing some patches of habitat suitable for breeding within an unsuitable matrix. Habitat and topographic covariates can be used to explain this distribution explicitly in the abundance estimation sub-model (Royle 2004), whereas survey-specific covariates (e.g., observer, weather) can be used to explain detection probability (Table 2). Using this approach, average abundance across points that share a spatial attribute (e.g., all harvest interior points, all points on ridges) can be estimated, as can temporal changes in abundance using dynamic models (Dail and Madsen 2011, Bellier et al. 2016).

N-mixture models are valuable to ecology, conservation, and monitoring wildlife populations because they provide an analysis method that is more efficient, less expensive, and can be applied to more easily attainable data, over a larger spatiotemporal extent than true mark-recapture studies (Kéry 2018). Use of *N*-mixture models to analyze count data (e.g., Barker et al. 2018) has been criticized because detection probability is assumed constant for all visits and auxiliary data are not used to estimate detection probability. However, *N*-mixture modeling is also considered a significant advancement in abundance modeling and some of the doubts projected on this method have been tested and determined unfounded (Joseph et al. 2009, Kéry 2018).

2.5.3. Hierarchical model configuration

We used package unmarked (version 0.11-0, Fiske and Chandler 2011) in program R (version 3.5.0, R Core Team 2018) for all hierarchical modeling. We specified the open

population model for pre-post data (section 2.5.5.) using the function “pcountOpen” with dynamics = trend, and the closed population model for post-only data (section 2.5.6.) using the function “pcount”. For both datasets, we used Poisson distribution and Akaike’s Information Criterion corrected for small sample size bias (AICc, Burnham and Anderson 2002). Model convergence was verified through sensitivity analysis by increasing K (the upper summation limit for the summation over the random effects in the integrated likelihood) and confirming no change in beta estimates (Kéry and Royle 2016).

2.5.4. *Detection probability covariates*

We used model selection to determine important detection probability covariates for inclusion in final analyses (Fuller et al. 2016). All candidate models included a covariate for observer proficiency, which was based on an observer’s previous experience as evaluated by team leaders in each state. The 36 observers were ranked as either low, moderate, or high proficiency, relative to all other observers that sampled birds during the study. We tested all combinations of observer with time-since-sunrise, ordinal date, and noise. Using AICc (Burnham and Anderson 2002), we selected the top pre-post-harvest and post-harvest-only detection probability models and used them for all subsequent analyses.

2.5.5. *Pre-post-harvest analyses*

We used open population *N*-mixture models to estimate abundance, population growth rate, changes in Cerulean Warbler abundance from pre- to post-harvest, and to quantify the influence of environmental variables on those parameters (Dail and Madsen 2011). Because pre-harvest abundance influences post-harvest abundance of songbirds (e.g., Wood et al. 2013, Porneluzi et al. 2014), inferences based on open population *N*-mixture models, which account for pre-harvest abundance, should be more robust than models that only examine post-harvest abundance patterns. Open population *N*-mixture models relax the closure assumption between primary sampling periods, allowing for estimation of population changes between breeding seasons for migratory songbirds. Closure is assumed among secondary sampling periods within a season (i.e., across the three visits). This is a reasonable assumption with songbirds during the breeding season when pairs have an established territory (Royle 2004), and when multiple visits are conducted within a short amount of time (here, 6 weeks).

For this analysis, we used the simplest open population dynamics structure:

$$N(i,t) = N(i,t-1) \times \Omega$$

where estimated abundance (N) at time t is based on N at time $t-1$ and the estimated population growth rate (Ω). This model does not separately estimate apparent survival and recruitment. We modeled point count data from the year immediately pre-harvest and the first year post-harvest for pre-post analyses (Nareff et al. 2019 dataset 1) to compare abundance immediately before and after harvesting.

We included study area as a covariate for initial abundance in every pre-post model to account for inherent differences in Cerulean Warbler abundance among study areas. To delineate important predictors of population growth rate, we tested vegetation and topographic variables that are relevant to Cerulean Warbler occurrence and abundance based on previous studies (Table 2; Boves et al. 2013b, Sheehan et al. 2013, Wood et al. 2013). We first used the 114 pre-post points to examine the influence of study area-level variables (i.e., slope position, Beers aspect, and point type) on abundance (Table 3). We developed 3 models to determine if slope position and aspect influence the Cerulean Warbler response to point type. To estimate changes between pre- and post-harvest abundance, we used the “ranef” unmarked function. This function estimates conditional abundance at each sample point, based on count data, covariates, and estimated detection probability. In a second model set, we examined the influence of basal area (Table 3), because basal area within and across point types was highly variable. Vegetation metrics from each harvest interior, harvest edge, and reference point included mean basal area of stems ≥ 10 cm dbh, percent mean basal area of preferred and avoided tree species (≥ 10 cm dbh), percent mean basal area of all large diameter trees (≥ 40.6 cm dbh), and the quadratic terms for these four basal area measurements (Table 3). For each model selection analysis, we used AICc to determine the most parsimonious model. Finally, we used the selected models to predict Cerulean Warbler abundance and population growth over a range of values for the most supported vegetation variables. We again used the “ranef” function as previously described and we also used the “predict” function to estimate abundance within a specified range of environmental variables (e.g., abundance at points with basal area between 5 and 50 m²/ha), based on our model input.

2.5.6. Post-harvest-only analyses

We developed 4 models using the point type and years-post-harvest variables to estimate the influence of years-post-harvest on Cerulean Warbler abundance (Table 4). Because point type had the most support of topographic variables for influencing population growth rate in the

pre-post dataset (section 2.8), we modeled the additive and interactive response to years-post-harvest and point type. We did not test vegetation variables because we sampled vegetation once post-harvest rather than each year post-harvest. Because some points were monitored post-harvest for 1 year while others were monitored for 2- or 3-years post-harvest, we modeled the multiple years of post-harvest abundance data in a single-season format. This approach required us to use a closed population N -mixture model (Royle 2004), which assumes closure among the 3 within-season visits, but the population is open across years. This approach achieves a larger effective sample size and is useful in cases with limited data or unequal sample sizes (Burnett and Roberts 2015, Fuller et al. 2016). While this modeling structure ignores some of the variability by assuming that abundance from each point count is independent across years, it is still reasonable for estimating temporal trends conditional on the explicit habitat covariates (Table 2; Linden and Roloff 2013, Kéry and Royle 2015, Ahlering and Merckford 2016, Fuller et al. 2016). As such, we added a years-post-harvest covariate for each point so that we could evaluate the post-only data according to our objectives. We had post-harvest data from 187 points across the 7 study areas (Nareff et al. 2019 dataset 2) resulting in 474 independent samples (1 year post-harvest $n=187$, 2 years post-harvest $n=164$, 3 years post-harvest $n=123$). Closed population N -mixture models estimate 3 parameters: abundance and detection probability. We included study area and calendar year in the abundance parameter for all models to account for inherent differences in Cerulean Warbler abundance among study areas and calendar years because harvests occurred in different years among study areas. We used the “ranef” function as described in section 2.5.5.

2.5.7. Assessing abundance-environmental variable relationships

For both datasets, we used abundance from supported models to graphically examine the change in pre- and post-harvest abundance or post-harvest abundance of Cerulean Warblers in relation to any variables that appeared within supported models. In doing so, we could examine confidence intervals and visually summarize results to aid forest managers in making management decisions. We evaluated the relationships between population growth and influential variables by assessing the sign and 95% confidence intervals of the slope (β coefficient).

3. Results

3.1. *Vegetation*

Within each harvest stand on each study area except GL, basal area was decreased substantially in relation to the unharvested reference stands. At pre-post study areas, basal area at harvested points was reduced by 13% at GL and by 35–60% (mean 44%) at the remaining study areas. At the 7 study areas, basal area in reference stands was 24.4–37.8 m²/ha. In harvested stands, post-harvest basal area was 7.0–25.3 m²/ha at harvest interior points and 18.1–27.0 m²/ha at harvest edge points. We recorded 33 tree species pre-harvest and 37 species post-harvest (Appendix B). Pre-harvest, the 5 tree species with greatest basal area, starting with the greatest, were northern red oak, red maple, chestnut oak, tulip poplar, and white oak. Post-harvest, the same 5 species were dominant, but chestnut oak accounted for the most stems, followed by red maple and northern red oak.

3.2. *Territory Density*

Pre-harvest, among the 4 territory mapping plots, we delineated 20 territories in 2013 (0.30 ± 0.06 territory/ha) and 14 territories in 2014 (0.28 ± 0.08 territory/ha). Post-harvest, we delineated 33 territories 1 year post-harvest (0.49 ± 0.10 territory/ha) and 44 territories 2 years post-harvest (0.66 ± 0.06 territory/ha). A Shapiro-Wilk test indicated the territory density data were normally distributed ($W = 0.93$, $P = 0.43$) and a Mauchly's test indicated the data did not violate the assumption of sphericity ($W = 0.77$, $P = 0.77$). Territory density differed significantly among the three pre-post-harvest year categories ($F_{2,9} = 4.3$, $P = 0.048$). *Post hoc* tests indicated the 51% change in territory density between pre-harvest and 1 year post-harvest ($P = 0.34$) and 32% change between 1 year and 2 years post-harvest ($P = 0.36$) were not significant, whereas the 100% increase between pre-harvest and 2 years post-harvest was statistically significant ($P = 0.04$). The change in territory densities by years-post-harvest was variable depending on pre-harvest density with lower densities increasing more than higher densities (Fig. 3).

3.3. *Pre-post-harvest abundance*

Pre-harvest abundance influenced post-harvest abundance at harvest interior and harvest edge points. Where increases in post-harvest modeled abundance did occur ($n=21$), the greatest increases occurred where pre-harvest abundance was <2.0 birds/point (Fig. 4). Of the 32 harvested points where modeled abundance decreased or did not change, 66% ($n=21$) were

harvest edge points and 34% (n=11) were harvest interior points. Some of these points (41%) had modeled pre-harvest abundance <1 and several close to 0.

All survey covariates were in the top detection probability model, and thus were included in final analyses (Table 3). For model set 1, the top model included point type as the only influence on abundance and resulted in 69% of model weight. Slopes of β coefficients from the top model were positive for harvest interior and harvest edge and negative for reference points, but 95% CIs overlapped zero for all point types (Table 5). Modeled abundance pre-harvest at harvest interior points (2.2 birds/point, 95% CI = 1.4–3.0), harvest edge points (1.8 birds/point 95% CI = 1.3–2.3), and reference points (1.8 birds/point 95% CI = 1.4–2.2) was similar. Post-harvest, abundance at harvest interior points (3.3 birds/point, 95% CI = 2.1–4.5) was greater than abundance at reference points (1.4 birds/point 95% CI = 1.0–1.8) and abundance at harvest edge points (1.7 birds/point, 95% CI = 1.1–2.3) remained similar to pre-harvest abundance (Fig. 5). The models testing the additive response of point type and Beers aspect ($\Delta AICc = 2.62$) and point type and slope position ($\Delta AICc = 3.40$) on population growth rate had less support for the pre-post data ($\Delta AICc = 2-7$; Burnham and Anderson 2011; Table 3). These models represented 19% and 13% of model weight, respectively, suggesting that population growth rate in response to harvest was less influenced by slope position and aspect than point type alone.

For vegetation covariates, 1 model with percent of basal area that was preferred tree species (bapref) and 1 model with percent of basal area that was large diameter trees (balarge) had the most support for explaining abundance (Table 3). These models had 37% and 20% of model weight, respectively. The positive slope of the β coefficient for bapref and a 95% confidence interval that did not include zero indicated a significant positive linear relationship between Cerulean Warbler abundance and increasing percent of bapref (Table 5; Fig. 6A). Positive change in abundance from pre- to post-harvest (Fig. 6B) and positive population growth (Fig. 6C) were predicted to occur where percent of bapref was generally >50%.

Cerulean Warbler abundance had a positive linear relationship with increasing percent of the basal area that was large diameter trees (Fig. 7A) indicated by the positive slope of the β coefficient for balarge; however, the 95% confidence interval overlapped zero (Table 5). Positive change in abundance at the point level, from pre- to post-harvest (Fig. 7B) and positive population growth (Fig. 7C) were predicted to occur where percent of balarge was generally >45% and >50%, respectively.

3.4. *Post-harvest-only abundance*

The top detection model for post-harvest only data, included observer, ordinal date, and time-since-sunrise covariates and thus were included in final analyses (Table 4). The model selection found the point type + years-post-harvest and point type models ($\Delta\text{AICc} = 0.89$) had the most support compared to the two other models (55% and 34% of Akaike weight, respectively; Table 4). We predicted slopes of harvest interior and harvest edge points relative to reference points and reference points relative to harvest interior points. Confidence intervals (95%) of β coefficients from the top model for harvest interior (positive slope) and reference (negative slope) points did not include zero, suggesting their significance in explaining population growth, whereas the confidence interval for harvest edge (positive slope) points did include zero (Table 6). Modeled abundance at harvest interior points increased slightly from 1 year post-harvest (mean = 0.9 birds/point, 95% CI = 0.6–1.2) to 2 years post-harvest (mean = 1.5 birds/point, 95% CI = 1.0–2.0), but decreased to 0.8 birds/point (95% CI = 0.5–1.1) 3 years post-harvest (Fig. 8). Modeled abundance at harvest edge points was relatively similar across years with mean = 0.7 birds/point (95% CI = 0.4–1.0) 1 year post-harvest, mean = 1.1 birds/point (95% CI = 0.6–1.6) 2 years post-harvest, and mean = 0.6 birds/point (95% CI = 0.3–0.9) 3 years post-harvest. Relative to harvest interior points, modeling indicated a significant negative slope at reference points; however, actual modeled abundance increased slightly between 1 (mean = 0.6 birds/point, 95% CI = 0.4–0.8) and 2 years post-harvest (mean = 1.0 birds/point, 95% CI = 0.8–1.2) and decreased 3 years post-harvest (mean = 0.7 birds/point, 95% CI = 0.5–0.9). Abundances among point types were similar 3 years post-harvest (Fig. 8).

4. Discussion

4.1. *Overall changes in territory density and abundance*

We observed that harvests on state lands that follow the Guidelines (Wood et al. 2013) for operational silviculture in support of Cerulean Warbler breeding habitat in the central Appalachian region had a positive effect on Cerulean Warbler territory density and abundance at our study areas, at least for the first 2 years post-harvest. Mean Cerulean Warbler territory density increased 100% from pre-harvest to 2 years post-harvest, which we posit is a result of mid- and understory regeneration. These results corroborate findings from the original experimental study (Sheehan et al. 2013). A diversity of habitat types is selected by the different

sexes and life stages of the species and different vegetative strata are used for different activities (e.g., Bakermans and Rodewald 2009, Boves et al. 2013a, Wood and Perkins 2012, Raybuck 2016). Accordingly, the full breeding and post-fledging season of the bird must be considered when managing for breeding habitat. Harvest mosaics with a range of canopy disturbances, such as the ones in our study, may provide this variety of habitat for the Cerulean Warbler (Boves et al. 2013a).

The previous regional study in the central Appalachian region determined that territory mapping plots with high pre-harvest territory density may have been at or near saturation and harvesting did not provide additional space for densities to increase (Boves et al. 2013b, Sheehan et al. 2013). The Guidelines suggested limited management where density is >5 territory/10 ha (0.50 territory/ha; Wood et al. 2013). Three of the 4 territory mapping plots in our study increased pre- to 1 year post-harvest, with 1 plot increasing substantially and 2 increasing moderately (Fig. 3). The plot with the highest pre-harvest territory density decreased in the first-year post-harvest and then returned to pre-harvest density 2 years post-harvest. This latter plot had moderate pre-harvest density (0.46 territory/ha), suggesting that it may have been close to saturation and harvesting did not improve habitat.

Some of the points with weak or negative responses in change in modeled abundance (Fig. 4) had modeled pre-harvest abundance <1.0 birds/point and close to 0. These points were all at GL and HI and may indicate these study areas and adjacent stands did not have enough birds to respond to the harvests. Grayson Lake and HI had the lowest proportions of points with Cerulean Warblers pre-harvest when summarizing raw data (29% and 11%, respectively, compared to $>55\%$ at GA, SJ, and WC). The Guidelines recommend implementing harvests where Cerulean Warblers are present, but not abundant, and our modeling supports this. Where there were increases in modeled abundance at our post-harvest points, the greatest increases occurred where Cerulean Warblers were present, but not abundant pre-harvest.

Although point type was included in the top model for explaining Cerulean Warbler abundance at our pre-post study areas, abundance did not change significantly by point type (it approached significance; $P = 0.08$; Fig. 5). However, when modeling years-post-harvest, change in abundance was significant and mean abundance was higher at harvest interior points than reference points (Fig. 8). Since we did observe a substantial increase in territory densities post-

harvest, the lack of significant changes in abundance at pre-post study areas is likely the result of high variability at the point level as indicated by the wide CI for harvest interior points.

4.2. Response to topographic metrics

Because our harvests were applied to a broad range of available topographic characteristics including coves, middle slope positions, and ridgelines, all available aspects, and harvests were applied to one physiographic region not included in the original study, we can update and expand the scope of inference for the Guidelines. Cerulean Warbler habitat selection varies throughout the breeding range (e.g., bottomland forests in the southeastern US), but in the central Appalachian region in mature forest stands, the species is typically more abundant on middle and upper slopes and ridgetops, at north- to northeast-facing aspects (Hamel 2000, Weakland and Wood 2005, Wood et al. 2006, Newell and Rodewald 2012). These topographic characteristics inherently result in canopy gaps particularly through windthrow. However, our study indicated that slope position and Beers aspect, when tested in models with point type, were not as influential as point type alone on post-harvest abundance of Cerulean Warblers (Tables 2 and 4). During early data exploration, we also tested interactive models of point type with slope position and point type with Beers aspect. However, these relationships were not important to change in Cerulean Warbler modeled abundance. This further supports our results, which indicated that timber harvests on less preferred slope positions and aspects can provide habitat for Cerulean Warblers, at least for 2 years post-harvest, during which time we saw increases in abundance and territory density. We observed that whereas harvests on the Cerulean Warbler's preferred slope positions and aspects provided breeding habitat for the birds, these same treatments on less preferred topographic characteristics also attracted Cerulean Warblers for multiple seasons. Thus, our study expands on the understanding of Cerulean Warbler response to forest harvesting.

4.3. Response to vegetation

Cerulean Warbler abundance showed a positive, albeit weak, relationship with percent basal area of preferred tree species (Fig. 6). The current Guidelines suggest retention of large diameter trees of preferred tree species because Boves et al. (2013a) found nests typically were in trees that averaged 35–48 cm dbh. Our results confirm that the presence of white oaks, sugar maple, and hickories is positively associated with Cerulean Warbler abundance and population growth rates in the central Appalachian region and provide management targets for percent

retention. While percentage of large diameter (≥ 40.6 cm dbh) trees was an important variable in our modeling (Table 3), the relationship with Cerulean Warbler abundance was not significant (Table 5). Cerulean Warbler selection of large diameter trees in the central Appalachian region is well-documented (e.g., Weakland and Wood 2005, Buehler et al. 2008, Hartman et al. 2009, Boves et al. 2013b). This relationship may be due to the structure of the tree itself, or the forest conditions where larger trees typically grow (i.e., old growth forests with canopy gaps). It is possible that harvests may have alleviated some of the dependence on large diameter trees for nesting by opening the canopy on a broader range of slope positions and aspects, without relying on large diameter trees for that to happen (i.e., windthrown trees creating gaps). Cerulean Warblers may select larger diameter trees because that is what tends to be available in mature forests (Hamel 2000). If the tree species is more important than the size of tree, you would expect to see the results we observed in our study.

4.4. Response to years-post-harvest

Years-post-harvest can be important in influencing Cerulean Warbler abundance because canopy closure over time limits the length of time a harvest is beneficial (Sheehan et al. 2013). We observed an overall increase in abundance and territory density 1 and 2 years post-harvest (although response varied among territory mapping plots and points). During the second year following harvest, regeneration of the understory likely provided higher quality foraging and refuge habitat for nesting females, post-breeding adults, and fledglings (Pagen et al. 2000, Vitz and Rodewald 2006, Boves et al. 2013a, Porneluzi et al. 2014, Raybuck 2016, Ruhl et al. 2018). Abundance subsequently decreased 3 years post-harvest. Previous research in the central Appalachian region observed higher post-harvest abundance up to 4 years post-harvest in moderate to heavy harvests, although the response to lighter harvests decreased across time more rapidly (Boves et al. 2013b, Sheehan et al. 2013). The increase of sunlight into the open canopy for 2 growing seasons may have allowed the canopy trees in the lighter harvests to grow enough to reduce the number and size of gaps (Perkey et al. 2011, Himes and Rentch 2013) such that the openings were no longer appropriate for Cerulean Warbler territories. The decline we observed 3 years post-harvest may have been driven by the small number of points sampled 3 years post-harvest, many of which were at our Kentucky (GL) study area. Basal area at GL was reduced by only 16% post-harvest, compared to 35–60% (mean 44%) at other study areas. By the third-year post-harvest, any harvest at GL was visually undetectable in the field because the canopy had

closed. Cerulean Warbler abundance at GL was the same pre-harvest through 2 years post-harvest after which it decreased in the third-year post-harvest. Despite the relatively short-term benefit to Cerulean Warblers indicated here and in other studies (Boves et al. 2013b, Sheehan et al. 2013), harvesting in a spatial and temporal mosaic may provide overall long-term benefits to Cerulean Warblers, as a variety of seral stages will be available across the landscape at any given time. Further, shelterwood harvests where the residual canopy is removed in a successive harvest 5–10 years after the initial cut, would not be expected to provide long-term benefits to the species.

5. Conclusions

As a species of conservation concern throughout its range, the Cerulean Warbler requires specific management strategies (Roth and Islam 2008, Boves et al. 2013a) and a better understanding of its response to forest management (Hamel 2000). Boves et al. (2013a) found that some preferred habitat features within territories actually led to a decrease in Cerulean Warbler nest success, indicating that local conditions need to be considered when managing for this species. In the absence of forests managed with harvesting practices that influence canopy structure, Cerulean Warblers in the central Appalachian region use older, heterogeneous forests, which provide appropriate conditions for breeding (Oliarnyk and Robertson 1996, Bakermans and Rodewald 2009, Boves et al. 2013a, Perkins and Wood 2014). Our harvests created appropriate Cerulean Warbler habitat in otherwise less preferred stands by decreasing the basal area to within the range recommended by the Guidelines, which opened the canopy while simultaneously retaining large specimens of tree species preferred by Cerulean Warblers.

Taking no forest management action in order to wait for the natural development of older, heterogeneous stands is not expedient when managing for a species of conservation concern, such as the Cerulean Warbler. Development of old growth forest conditions can take hundreds of years and in that time, this species could go extinct. The PIF predicts a 50% reduction in the Cerulean Warbler population within the Appalachian Mountains Bird Conservation Region, where our study areas occur, in fewer than 19 years (Rosenberg et al. 2016). Harvests with the conditions described here appear to be an effective management tool for creating the canopy structure and regeneration needed by breeding Cerulean Warblers for at least 2 years post-harvest. Based on our research, harvests appear most beneficial for increasing

abundance where Cerulean Warblers are present but not abundant pre-harvest (Fig. 4). Resources may be better directed towards enhancing habitat and increasing territory density in stands with low densities. Fortunately, managing breeding habitat for Cerulean Warblers simultaneously provides management opportunities for popular game species such as Wild Turkey (*Meleagris gallopavo*), Ruffed Grouse (*Bonasa umbellus*), and white-tailed deer (*Odocoileus virginianus*). These game species benefit from complex forest structure with mast-producing trees, interspersed with fields and young forests to satisfy habitat needs year-round and for all age classes and sexes (e.g., Thogmartin 2001, Tirpak et al. 2010). The results of our study also show that Wildlife Management Areas and State Forests, which are managed for multiple types of public use, may simultaneously be managed for declining species of conservation need.

Our study expands on the current knowledge of Cerulean Warbler breeding habitat in the central Appalachian region by broadening management opportunities within the landscape. Our results imply there are opportunities to create or manage Cerulean Warbler breeding habitat by implementing management practices throughout forest landscapes, and not limit management to specific topographic characteristics. We also identified management targets for size and composition of basal area. Changes in vegetation structure via timber harvesting appear to be more influential on Cerulean Warbler abundance and territory density and these needs could be incorporated into silvicultural prescriptions with objectives other than non-game species conservation.

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Table 8. Summary of study areas sampled to evaluate Cerulean Warbler (*Setophaga cerulea*) response to harvests at 7 study areas in the central Appalachian region during 2013–2017. Point count surveys (n=5 study areas) and territory mapping (n=2 study areas, SJ and WC) were conducted pre- and post-harvest and point count surveys for 3 years post-harvest at 2 additional study areas harvested prior to the initiation of our study. Point counts were surveyed up to 3 years post-harvest.

Point types (# points sampled)								
State	Study area ¹	Harvest interior	Harvest edge	Reference	Study area size (ha)	Harvested area (ha)	Harvest year ²	Years-post-harvest ³
Pre-post study areas								
KY	Grayson Lake WMA (GL)	7	7	7	92	16.4	2013	1–3 (n=14)
VA	Gathright WMA (GA)	4	1	6	47	35.5	2015	2 (n=5)
VA	Highland WMA (HI)	9	6	22	224	57.1	2015/ 2016	1 (n=15) 2 (n=8) 3 (n=3)
WV	Stonewall Jackson Lake WMA (SJ)	4	5	9	92	32.0	2014/ 2015	1 (n=9) 2 (n=7)
WV	Wolf Creek (WC)	4	7	16	111	26.6	2013/ 2014	1–2 (n=11) 3 (n=5)
Post-only study areas								
WV	Coopers Rock SF (CR)	16	5	18	186	77.2	2012	1–3 (n=21)
WV	Dynamite (DY)	7	10	17	163	39.8	2012	1–3 (n=17)

¹WMA=Wildlife Management Area; SF=State Forest

²Harvests occurred during the winter following the breeding season indicated (i.e., a 2013 harvest occurred during winter 2013–2014). At some study areas, harvests were completed over 2 winters.

³n = number of harvested points sampled within each year-post-harvest; all reference points were sampled every year post-harvest

Table 9. Survey and study area variables used to model detection probability and abundance, respectively, of Cerulean Warblers (*Setophaga cerulea*) in the central Appalachian region at seven harvested study areas 2013–2017.

Code	Covariate Type	Variable Description	Habitat Component or Use in Models
noise	Survey	Noise during visits (levels 0–4)	Detection probability
obsv	Survey	3 observer groups based on experience with bird ID and sampling methods	Detection probability
ord	Survey	Ordinal date	Detection probability
tssr	Survey	Time-since-sunrise	Detection probability
asp	Study area	Beers aspect (0–2; 0 is xeric and 2 is mesic)	Topography
SA	Study area	Study area; 5 pre-post, 2 post-only	Inherent regional differences
slope	Study area	Slope position (lower, middle, ridge)	Topography
pttype	Study area	Harvest interior, harvest edge, reference	Treatment
ba ¹	Vegetation	Mean basal area (m ² /ha) of tree stems ≥ 10 cm dbh	Canopy structure
baavoid ¹	Vegetation	% basal area (m ² /ha) composed of red maple, red oak group	Relationship to avoided tree species
balarge ¹	Vegetation	% basal area (m ² /ha) of large diameter trees (≥ 40.6 cm dbh)	Relationship to larger trees
bapref ¹	Vegetation	% of basal area (m ² /ha) composed of sugar maple, hickories, white oak group	Relationship to preferred tree species
year	Study area	Calendar year (2013–2017)	Inherent annual differences
ypb	Study area	Years-post-harvest (1–3 years)	Relationship to regeneration

¹Linear and quadratic terms were tested for the footnoted variables

Table 10. Model selection process to determine the most parsimonious N -mixture models that explain change in Cerulean Warbler (*Setophaga cerulea*) abundance from pre- to post-harvest at five study areas in Kentucky, Virginia, and West Virginia 2013–2017. N -mixture models for 114 sample points with 1 year pre-harvest and 1 year post-harvest data are shown. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. K is the number of parameters in a model, AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, Δ AICc is the difference between each model's AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables are defined in Table 2.

Model ¹	K	AICc	Δ AICc	w_i
<u>Model set 1: point type and topographic variables</u>				
λ (SA) Ω (pttype) p (obsv+ord+noise+tssr)	14	770.77	0.00	0.69
λ (SA) Ω (pttype+asp) p (obsv+ord+noise+tssr)	15	773.39	2.62	0.19
λ (SA) Ω (pttype+slope) p (obsv+ord+noise+tssr)	16	774.17	3.40	0.12
<u>Model set 2: vegetation variables</u>				
λ (SA) Ω (bapref) p (obsv+ord+noise+tssr)	13	767.25	0.00	0.39
λ (SA) Ω (balarge) p (obsv+ord+noise+tssr)	13	768.61	1.36	0.20
λ (SA) Ω (baavoid ²) p (obsv+ord+noise+tssr)	14	769.58	2.33	0.12
λ (SA) Ω (bapref ²) p (obsv+ord+noise+tssr)	14	769.62	2.37	0.12
λ (SA) Ω (balarge ²) p (obsv+ord+noise+tssr)	14	771.21	3.95	0.05
λ (SA) Ω (ba) p (obsv+ord+noise+tssr)	13	771.40	4.14	0.05
λ (SA) Ω (baavoid) p (obsv+ord+noise+tssr)	13	771.44	4.19	0.05
λ (SA) Ω (ba ²) p (obsv+ord+noise+tssr)	14	773.29	6.04	0.02

¹ λ = initial abundance, Ω = population growth rate, p = detection probability

Table 11. Model selection process to determine the most parsimonious *N*-mixture models that explain change in Cerulean Warbler (*Setophaga cerulea*) abundance from 1 year post-harvest to 3 years post-harvest at seven study areas in Kentucky, Virginia, and West Virginia 2013–2017. Static *N*-mixture models for 187 points with post-harvest data are shown. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. K is the number of parameters in a model, AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, Δ AICc is the difference between each model's AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables in models are defined in Table 2.

Model ¹	K	AICc	Δ AICc	w_i
p (obsv+ord+tssr) λ (SA+year+pttype+yph)	19	1451.55	0.00	0.55
p (obsv+ord+tssr) λ (SA+year+pttype)	18	1452.48	0.92	0.34
p (obsv+ord+tssr) λ (SA+year+pttype*yph)	21	1454.89	3.34	0.10
p (obsv+ord+tssr) λ (SA+year+yph)	<u>17</u>	<u>1460.35</u>	<u>8.80</u>	<u>0.01</u>

¹ p = detection probability, λ = abundance

Table 12. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked *N*-mixture models (see Table 3) estimating population growth of Cerulean Warblers (*Setophaga cerulea*) at 114 points at five harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017.

Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI
Model set 1: point type				
pttype				
Harvest interior	0.6	0.3	-0.1	1.2
Harvest edge	0.1	0.4	-0.6	0.8
Reference	-0.6	0.3	-1.2	0.1
Model set 2: vegetation variables¹				
bapref*	1.3	0.6	0.04	2.5
balarge	1.2	0.7	-0.2	2.6

¹bapref = percentage of basal area that was preferred tree species (white oak [*Quercus alba*], chestnut oak [*Q. prinus*], sugar maple [*Acer saccharum*], and hickories [*Carya* spp.]) and balarge = percentage of basal area that was ≥ 40.6 cm diameter at breast height

*Confidence intervals do not include zero, indicating significance

Table 13. Parameter estimates, standard errors (SE), 95% lower and upper confidence intervals (CI), and P-values from the top ranked N-mixture model estimating population growth of Cerulean Warblers (*Setophaga cerulea*) at 187 points at seven harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017.

Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI	P-value
pttype+yph					
Harvest interior*	0.5	0.2	0.2	0.8	<0.001
Harvest edge	0.2	0.2	-0.1	0.6	0.24
Reference*	-0.5	0.2	-0.8	-0.2	<0.001
yph	0.4	0.2	-0.1	0.8	0.09

*Confidence intervals do not include zero, indicating significance

Figure 1. Location of the regional study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Rabbit Hole (RH) and Clear Creek State Forest (CCSF) in Pennsylvania; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia.

Figure 2. Wolf Creek harvest within the Elk River Wildlife Management Area in West Virginia shown as an example of our experimental design. Here, harvest interior, harvest edge, and reference point count locations and territory mapping plots were monitored during 2013–2016 for Cerulean Warbler (*Setophaga cerulea*) abundance and territory density across a timber harvest mosaic. Harvests (clear cut [CC], variable retention, single-tree selection, and group selection) are labeled as described by land managers and were not uniform across each harvest block.

Figure 3. Cerulean Warbler territory density by territory mapping plot pre-harvest (Pre; 2013–2014), 1 year post-harvest (1 YPH; 2014–2015), and 2 years post-harvest (2 YPH; 2015–2016) for this investigation of Cerulean Warbler (*Setophaga cerulea*) response to harvests implemented as operational silvicultural prescriptions. Study areas were Stonewall Jackson Lake Wildlife Management Area (SJ) and Wolf Creek (WC) at Elk River Wildlife Management Area in West Virginia.

Figure 4. Percent change in estimated abundance of Cerulean Warblers (*Setophaga cerulea*) following tree harvest in forested stands in Kentucky, Virginia, and West Virginia during 2013–2017. The hierarchical model used to estimate abundance included study area as a covariate for initial abundance, point type as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise as covariates for detection probability. Estimated changes in abundance are based on abundance at 54 harvest interior and harvest edge points. Three points with change >300% (709%, 823% and 1260% at harvest interior points) were omitted from the graph to more clearly show the relationship with pre-harvest abundance.

Figure 5. Pre- and post-harvest Cerulean Warbler (*Setophaga cerulea*) modeled abundance by point type (harvest interior, harvest edge, reference) at 114 sample points at 5 harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Bars represent 95% confidence intervals. The hierarchical model used to estimate abundance included study area as a covariate for initial abundance, point type as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise for detection probability.

Figure 6. The 3 panels show Cerulean Warbler (*Setophaga cerulea*) modeled abundance or population growth rate (# birds/point) at 114 harvest interior, harvest edge, and reference sample points relative to the percentage of basal area that was preferred tree species ≥ 10 cm dbh at 5 harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Preferred tree species include sugar maple (*Acer saccharum*), white oaks (*Quercus* spp.), and hickories (*Carya* spp.). Post-harvest abundance relationship to percent basal area that is preferred tree species (A), change in abundance pre- to post-harvest (B) and predicted population growth rate with 95% confidence intervals (C) are shown. The model used to estimate abundance included study area as a covariate for initial abundance, percentage of basal area that was preferred tree species as a covariate for population growth rate, and observer, ordinal date, noise and time-since-sunrise for detection probability.

Figure 7. The three panels show Cerulean Warbler (*Setophaga cerulea*) modeled abundance or population growth rate (# birds/point) at 114 harvest interior, harvest edge, and reference sample points relative to the percentage of basal area that was large diameter trees (≥40.6 cm dbh) at 5 harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017. Post-harvest abundance (A), change in abundance pre- to post-harvest (B), and predicted population growth rate with 95% confidence intervals (C) are shown. The model used to estimate abundance included study area as a covariate for initial abundance, percentage of basal area that was large diameter trees as a covariate for population growth rate, and observer, ordinal date, noise, and time-since-sunrise for detection probability.

Figure 8. Mean Cerulean Warbler (*Setophaga cerulea*) modeled abundance (birds/point) at 187, 164, and 123 sample points at 7 harvested study areas in Kentucky, Virginia, and West Virginia 2013–2017, 1, 2, and 3 years-post-harvest, respectively. Bars represent 95% confidence intervals. The model used to estimate abundances post-harvest included study area, point type (harvest interior, harvest edge, reference), years-post-harvest, and calendar year as covariates for post-harvest abundance, and observer, ordinal date, and time-since-sunrise for detection probability.

CHAPTER 3: Breeding habitat selection by male Cerulean Warblers (*Setophaga cerulea*) in response to operational silvicultural prescriptions in the central Appalachian region.

Abstract. The Cerulean Warbler (*Setophaga cerulea*) is a species of conservation concern throughout its range. They require breeding habitat management where forests are not old enough or where specific habitat requirements are not available in mature forests because of historical management (or lack of management). To effectively manage breeding habitat for Cerulean Warblers, it is important to understand their habitat selection on a fine scale. We quantified breeding habitat selection of Cerulean Warblers and compared the influence of harvest treatments, pre- and post-harvest, within central Appalachian hardwood forests (i.e., oak [*Quercus* spp.]-hickory [*Carya* spp.] and mixed-mesophytic forests). We conducted territory mapping on 10 plots at 4 study areas in West Virginia for 4 breeding seasons during 2013–2016. Two study areas were sampled for 2 years pre-harvest (2013–2014) and 2 years post-harvest (2015–2016), while 2 others were sampled up to 3 years post-harvest (2013–2015). We compared mean territory size among pre-harvest and years-post-harvest and territory clustering per plot each year. Mean territory size decreased pre-harvest to 2 years post-harvest, but increased 3 years post-harvest. Territory clustering was not observed, with most territory mapping plots exhibiting dispersed territory placement. We used resource selection functions to assess Cerulean Warbler selection of vegetation and topographic metrics across territory mapping plots. We measured 173 points “used” by singing male Cerulean Warblers and 68 “available” points pre-harvest and 580 “used” and 170 “available” points post-harvest. Our primary objective was to assess Cerulean Warbler breeding habitat selection in relation to topographic and vegetation metrics, within harvest treatments that were applied based on current Cerulean Warbler habitat management guidelines. Male Cerulean Warblers selected for increasing Beers aspect pre-harvest, whereas post-harvest, they selected for increasing midstory structure. Post-harvest, they could select for habitat structure they require for foraging, mate attraction, and territory defense (i.e., singing) without being restricted by topographic conditions (i.e., Beers aspects approaching 2). Silvicultural prescriptions implemented based on the Guidelines improved habitat quality and provided more breeding habitat across the individual study areas.

Keywords: Breeding forest birds, operational silviculture, songbird habitat management, resource selection functions

1. Introduction

Understanding habitat selection is central to conservation biology and ecology and a necessity for wildlife habitat management and predicting animal distribution (e.g., Lele 2009, Jonzén 2013, Avgar et al. 2017). Extrinsic environmental and process patterns can influence the distribution of wildlife on the landscape (e.g., Lichstein et al. 2002, Mattsson et al. 2013). Demographic population processes such as territoriality and social behaviors can as well. Thus, individuals are not distributed randomly on the landscape; animals should cluster around resources, such as breeding habitat or a food source. Habitat selection happens on several scales (Johnson 1980). On the largest, coarsest scale, animals select a physical or geographical range. Then an animal selects its individual home range, or that of itself with its mate or social group. Third-order habitat selection pertains to selecting specific resources within that home range (Johnson 1980). Habitat selection on the finest scales include selecting specific food items or in the case of migratory songbirds, a nest site. Habitat selection requires an individual to predict future conditions based on assessments of what is available upon arrival in the spring. Being able to elucidate those predictors is the ultimate goal of any habitat selection study for breeding birds.

Nearctic-Neotropical migratory songbirds, such as the Cerulean Warbler (*Setophaga cerulea*; hereafter “cerulean”), take advantage of pulses of resources available for a short time within their breeding ranges in North America. Because of the hierarchical nature of habitat selection for breeding songbirds (Orians et al. 1991, Jones 2001, McGarigal et al. 2016), the estimation of specific habitat selection can be difficult. Migratory birds must select a breeding location within some landscape it is either familiar with from breeding attempts in previous years or from prospecting (Boulinier and Danchin 1997), or select an unfamiliar area based on perceived conditions of habitat. Once it has selected that area, for example a forest stand for a cerulean, the male then selects a territory location, which he will defend and advertise to potential mates. Within a territory, the female selects a nest patch and nest site with microtopographic or vegetation structure that may be unique relative to the entire territory, as can singing posts and foraging sites (Seagle 2005, Weakland and Wood 2005, Barg et al. 2006, Boves et al. 2013a, Carpenter and Wang 2016). Ceruleans do not use habitat within territories

uniformly; males use core areas for activities such as singing (Barg et al. 2006, Wood and Perkins 2012) and gap density may be higher in core areas of territories in West Virginia (Perkins and Wood 2014). There is some indication that males may be more plastic in their habitat selection than females (Boves et al. 2013a). Territories may also shift prior to the arrival of females (Barg et al. 2005, pers. obs.) as males engage in territorial disputes.

Birds should select breeding habitat that provides appropriate food resources, refuge, and a nest site and theoretically this should be the smallest space possible for effective territorial defense and mate guarding (Krebs 1971, Smith and Shugart 1987). Resource availability and habitat structure affect habitat quality and thus habitat size (Reitsma et al. 2008); higher quality habitat should provide a bird adequate resources in the smallest amount of space (Conner et al. 1986, Smith and Shugart 1987, Diemer and Nocera 2014).

Cerulean breeding habitat in the central Appalachian region is well-studied. The birds tend to nest on ridge tops and steep mid- to upper slopes where large trees dominate and canopy gaps provide ideal places for projecting songs and foraging (Weakland and Wood 2005, Boves et al. 2013a, Wood et al. 2013). The steep topography not only creates canopy gaps through natural disturbances, it influences productivity by creating microclimates with spatial variability of temperature, relative humidity, and plant water stress (Fekedulegn et al. 2004, Seagle 2005). This subsequently influences not only the tree species that grow there, but also how they grow. Aspect affects the amount and daily cycle of solar radiation received at different times of the year and has a strong influence on microclimate (Fekedulegn et al. 2003). Thus, aspect is a topographic cue that the cerulean and other mature-forest songbirds appear to use in selecting territories and one reason why the species may cluster its territories within stands (Roth and Islam 2007, Wood and Perkins 2012, Kaminski and Islam 2013). While several studies have examined how ceruleans respond to different silvicultural treatments, (e.g., Wood et al. 2005, Register and Islam 2008, Newell and Rodewald 2012, Sheehan et al. 2013, Wood et al. 2013, Nemes and Islam 2016), we know less about cerulean habitat selection within harvest mosaics and finer-scale habitat selection at the individual territory level relative to what is available.

In this study, we examine third-order breeding habitat selection (Johnson 1980) of male ceruleans. It is important to include spatial information when modeling wildlife habitat selection, particularly at small to medium spatial extents (Bahn et al. 2006), such as what we present here among 4 study areas in West Virginia. Using knowledge gained from the Cerulean Warbler

Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests (Wood et al. 2013; hereafter “Guidelines”), this study examines how male ceruleans select breeding habitat on a local-scale within harvest mosaics that offer structural diversity to the birds. We quantified basal area, tree species composition, and topographic metrics at vegetation points selected by estimating locations of singing male ceruleans at 10 territory mapping plots at 4 study areas in West Virginia. We used the data to examine cerulean breeding habitat selection by modeling used habitat features relative to those available. Based on our evaluation of abundance and territory density data at the same study areas (Nareff et al. 2019), we expected ceruleans to preferentially select territories where basal area comprised >50% large trees (≥ 40.6 cm dbh), particularly large white oaks (*Quercus* spp.), hickories (*Carya* spp.), and sugar maples (*Acer saccharum*). In this paper, we assessed the importance of large trees, tree species composition, and other vegetation variables that have been important in determining cerulean abundance, territory density, and habitat selection in other studies. We provide results on how ceruleans selected for or against certain attributes relative to what was available. These results add to the breadth of knowledge about cerulean breeding habitat selection on a fine scale and provide updated recommendations to landowners and land managers who are interested in providing habitat for ceruleans or multi-use forest stands.

2. Methods

2.1. Regional Study Area

We conducted fieldwork during 2013–2016 in contiguous, mature forest landscapes at 4 study areas within the central Appalachian region and Appalachian Mountains Bird Conservation Region (NABCI 2000; Fig. 1). The study areas are within the Allegheny Plateau, which is characterized by highly dissected terrain in a dendritic pattern with steep hills and narrow valleys, and dry-mesic and mixed-mesophytic forest types dominated the study areas (USDA Forest Service 1994). All study areas were on Wildlife Management Areas (WMA) or State Forests (SF) and included Coopers Rock SF (CR); Stonewall Jackson Lake WMA (SJ); and Wolf Creek (WC) and Dynamite (DY) within the Elk River WMA, West Virginia (Fig. 1).

All study areas were within the core breeding range of the cerulean (Sauer et al. 2017), represented a range of available topographic features, and fell within “Cerulean Warbler Focal Areas” delineated by the Appalachian Mountains Joint Venture (AMJV) partnership (Fearer

2011). Focal Areas contain core populations of the Cerulean Warbler that are important for sustaining its current distribution or where additional active forest management will likely enhance the habitat for this bird. Tree species composition differed somewhat among study areas, but common overstory tree species included oaks (northern red oak [*Quercus rubra*], black oak [*Q. velutina*], white oak [*Q. alba*], chestnut oak [*Q. montanus*]), hickories, red maple (*Acer rubrum*), sugar maple, black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), and tulip poplar (*Liriodendron tulipifera*). Elevation at the sampled points ranged from 291–675 m (mean 492 m).

2.2. Harvests

The total area harvested at each study area was 26.6–77.2 ha (mean 43.9 ± 9.9 ha) and comprised harvest mosaics encompassing a diversity of harvest types (i.e., shelterwood, group selection, clearcut with residuals) that resulted in a range of canopy openness. The ultimate goal of the harvests, outside of the intended use for our study, was to provide conditions where oaks and hickories would make up the bulk of the regenerating class, providing conditions that would allow desired, valuable saplings to outcompete less desirable species (e.g., red maple) (WVDOF 2006). Harvests were applied based primarily on the Guidelines (Wood et al. 2013), but were placed on all available slope positions and aspects by state managers of each study area. Various harvest types were placed in close proximity to each other resulting in harvest mosaics at each study area. See Nareff et al. (2019) for a detailed description.

2.3. Territory mapping

We used territory mapping (Bibby et al. 2000) to estimate locations of habitat use and delineate territories of ceruleans at our 4 study areas. For 2 of the study areas (SJ and WC), we quantified cerulean territory density annually, during 2 years of pre-harvest conditions, and up to 3 years post-harvest. For the other 2 study areas (CR and DY), we sampled territory density 1- and 3-years post-harvest (CR) or all 3 years-post-harvest (DY). We centered 2–3 plots each 16–17-ha in size over the harvest mosaics at each study area (Appendix A), depending on the size of the harvested area, for a total of 10 territory mapping plots. We situated plot boundaries so that each plot would encompass mostly harvested area, although each included a small amount of unharvested area. We placed plots at least 100 m apart to avoid counting the same territory on more than one plot. We marked plot boundaries and an internal grid of 50-m intervals (Fig. 2)

with plastic flagging before each field season. Unless a flagged tree was harvested, the flagging remained on the same trees for the duration of the study.

We initiated territory mapping surveys approximately 10 days after ceruleans first arrived at our study areas (mid-April) and mapped locations of ceruleans during 7–8 visits per plot for 6 weeks through early June 2013–2016 with a minimum of 4 days between surveys (Bibby et al. 2000). One person surveyed an entire plot within a single morning from dawn to approximately 1100 hours. The same person sampled each plot within a season when logistically possible to maximize detections over repeated visits. We varied the starting points and routes taken through the plots between surveys to reduce time-of-day bias. We recorded singing, calling, and behavioral observations on topographic maps overlaid with the plot grids (Fig. 2). We directed special attention to accurately noting multiple individuals that could be heard or seen concurrently (i.e., counter-singing, aggressive interactions) due to its importance in territory delineation. We estimated locations of birds when we first detected them relative to the grid flags and to topographic features rather than approaching a bird to mark its exact location (Bibby et al. 2000). Several grid flags could be seen at one time, assisting with accurately marking locations of birds on the mapping plots. Additionally, having plots assigned to individual surveyors for the duration of a season allowed us to become familiar with territories as they were forming and being defended.

Each day after surveys, we digitized our observations from the topo map into a geographic information system (GIS; ArcMap 10.3, ESRI 2014) by matching our estimated locations to features from the topographic layers. At the end of each season, we delineated territory boundaries using the digitized observations from the 7–8 annual visits. A territory can be delineated from a minimum of 2 territory mapping detections separated by 10 days over 8 territory mapping visits (Bibby et al. 2000, Haché et al. 2013). However, most of the individuals we mapped were reliable in their territorial behavior and once established, they were encountered during ≥ 3 territory mapping events (Fig. 2). We used recurring locations of singing individuals as approximate territory locations, while locations of counter-singing and aggressive interactions likely represented actual territory boundaries.

Using the minimum convex polygon method (MCP; Sheehan et al. 2013, Wood and Perkins 2012), we drew lines in ArcMap to connect the outermost locations of singing males or other territorial cues (i.e., sightings of pairs), using knowledge of the habitat, locations of

counter-singing males, and nests as guides. We used the connecting lines to form polygons that approximated territory boundaries (Appendix A). Bias is an inherent limitation with using MCP to define animal territories as it can overestimate the territory size by encompassing areas that were not actually used by the animal and it assumes that the delineated area is used uniformly (e.g., Burgman and Fox 2003, Börger et al. 2006, Nilsen et al. 2008). As such, we used MCP only for determining approximate territory boundaries to estimate territory size. We calculated the size of each territory with at least 1 registration within the territory mapping plot, or immediately adjacent to a plot, using the delineated polygons and the “calculate geometry” tool within ArcMap.

2.4. Vegetation Sampling

To represent habitat availability, we systematically sampled vegetation at every-other grid point on the territory mapping plot grid, but sampled adjacent points as needed to ensure coverage of the range of available habitat within each plot since harvest boundaries were not linear (Fig. 3). We sampled the selected mapping plot points once pre-harvest and once during the season immediately following harvest (SJ and WC) or once during the first year post-harvest (CR and DY) because we assumed that our vegetation metrics would not change during our study. This resulted in 16–18 vegetation points sampled per territory mapping plot, or approximately 1 vegetation plot/ha to represent habitat availability (pre-harvest $n=68$, post-harvest $n=170$).

We sampled vegetation on 2–7 (mode pre-harvest = 4, mode post-harvest = 3) of the cerulean detections used for delineating territories (section 2.3) to represent habitat use (Fig. 3). To ensure we were sampling habitat that was used as part of a territory, we only used locations of singing males for analysis. This resulted in 173 samples pre-harvest and 580 post-harvest. We sampled used habitat vegetation plots 1 time within the season the territory was active.

We used standardized protocols across the study areas to quantify tree basal area and tree species composition at every vegetation point. We completed variable radius prism plots using a wedge prism (10-factor English or 2.5-factor metric) to tally live trees and snags at sampling point. Tree tallies from variable radius prism plots rely on the relationship between the diameter at breast height (dbh) of each tree and the distance between those trees and the observer. By holding the prism at a fixed distance from the eye over the plot center and rotating 360° around the prism, the observer tallies trees that are in the plot. For each live tree and snag in a prism

plot, we measured dbh to the nearest centimeter (cm) using a Biltmore stick or dbh tape. For each live tree, we also recorded tree species or group (e.g., hickory group, red oak group). Borderline live trees and snags were counted and included for tree composition values, but every other borderline live tree was removed to calculate total basal area.

We calculated basal area of stems ≥ 10 cm dbh (Boves et al. 2013b, Sheehan et al. 2013) per vegetation point for 5 categories of stems (Table 1). They included snags, all live tree stems, all stems of preferred (bapref) and avoided (baavoid) tree species, and midstory trees. We also calculated large diameter trees (≥ 22.9 cm dbh; large), and “cerulean large” trees (≥ 40.6 cm dbh; cwlarge). The last size category was selected for nesting by ceruleans in the central/southern Appalachian region (Boves et al. 2013a). Preferred tree species in the central Appalachian region included white oaks, hickories, and sugar maples whereas avoided tree species included red maple and red oaks (George 2009, Wood and Perkins 2012, Wood et al. 2013). Based on observations of tree composition at study areas and at point counts with ceruleans detections within 50 m (Nareff et al. 2019), we added basal area of tulip poplar to the bapref and the cwlarge categories (see also George 2009). Snags can indicate some level of canopy or midstory openness, depending on the height, and may affect cerulean abundance (Weakland and Wood 2005). We also calculated basal area of preferred tree species in the cwlarge category to evaluate if the relationship with large trees is different if the category only includes those tree species preferred by ceruleans for nesting and foraging. Midstory trees were those placed into crown classes of intermediate or overtopped (USDA Forest Service Forest Inventory and Analysis classification system; Appendix B). Cerulean Warbler selection or avoidance of midstory vegetation may vary with sex (Boves et al. 2013a) and study region (Jones and Robertson 2001). We then summed the basal areas for each group at a sampling point and calculated its percentage of basal area per point, except snags, for which we used basal area (m^2/ha) per sampling point (Table 1).

2.5. Topographic Metrics

We determined point-level slope position and Beers aspect (section 2.2) for each sampled use and available vegetation point. We classified each point by 1 of 3 categories of slope position that represented the most frequently encountered categories at our sample points: lower, middle, and ridge (Table 1). Lower and flat were combined and upper was combined with ridge to assist with model convergence. Beers aspect (0–2; Beers et al. 1966) represents forest productivity

with the least productive, xeric aspects approaching 0 and the most productive, mesic aspects having values approaching 2. The 3 slope position categories were distributed similarly between used and available points with the majority classified as ridge, followed by lower (pre-harvest) or lower and middle equally (post-harvest). Because of this, we did not include slope position in our modeling, but evaluated cerulean selection of Beers aspect pre-harvest because we assumed it would be a more important habitat selection cue prior to harvesting (Nareff et al. 2019).

2.6. Statistical Analyses

2.6.1. Territory size

We used mixed effects modeling to test for differences in territory size among pre-harvest and all years-post-harvest using all delineated territories (2 years of pre-harvest data from SJ and WC and 2–3 years post-harvest from all 4 study areas). For mixed effects models, territory size was the response variable, pre-harvest (coded as 0) or year-post-harvest (coded 1–3) was the fixed effect, and territory mapping plot was the random effect. We used a Shapiro-Wilk test to test for normal distribution and used standard transformations as needed. We used visual exploratory methods to test for violations of assumptions on linearity, normal distribution of residuals, and homogeneity of variance, and a Bartlett test to test for homoscedasticity. We did this by plotting residuals vs observed values and plotting fitted values vs residuals (Zuur et al. 2009). We considered Bartlett test results significant at $\alpha = 0.05$.

2.6.2. Territory clustering

To evaluate territory clustering, we used the average nearest neighbor (ANN) function within the spatial statistics toolbox in ArcMap. This function returns z-scores and *P*-values to indicate if distribution of points is random or significantly dispersed or clustered. The function calculates the centroid of polygons to analyze the distance among neighboring polygons, here our territory polygons. The null hypothesis is that territories are distributed randomly on the landscape. We performed ANN tests for territory clustering each year pre-harvest at SJ and WC and each year post-harvest at all study areas. We used the individual territory mapping plots as the area parameter for each test because we mapped territories only within the mapping plots so analyzing clustering by study area would not be appropriate. The ANN function returns expected and observed mean distances and a nearest neighbor index, which is a measurement of the pattern (or lack of pattern) in points. Values >1 indicate dispersion whereas values <1 indicate clustering. The ANN function and subsequently the measures of significance are highly sensitive

to the area parameter value in that what is dispersed or random at a smaller extent may be clustered at a larger extent.

2.6.3. Habitat selection

To model habitat selection, we used a matched use-available design by sub-setting the data into batches of used and available points (Lele et al. 2019) from within their respective territory mapping plots. To batch the data, we gave each territory mapping plot a unique identifier (1–10) and gave the same identifier to each used or available sample point within its respective territory mapping plot. In doing so, the used habitat is assessed relative to the available habitat within the same territory mapping plot to avoid comparing a used point at one study area to an available point at a different study area. We used package *ResourceSelection* (version 0.3-4, Lele et al. 2019) in program R (version 3.5.0, R Core Team 2018), which allows this batching design for logistic regression. This modeling calculates resource selection functions (RSF) using weighted distributions of wildlife detections (i.e., use points). We modeled selection strength for each vegetation variable separately for pre- and post-harvest datasets. We modeled pre-harvest and post-harvest habitat selection separately. We used the singing-point samples (i.e., use) and systematically sampled territory mapping plot points (i.e., available) as the binomial dependent variable to test for selection of certain vegetation characteristics pre- and post-harvest or values of Beers aspect pre-harvest.

We used the *model.sel* function from package *MuMin* (version 1.43.6, Barton 2019) in program R (version 3.5.0, R Core Team 2018) to produce an AIC (Akaike's Information Criterion) table for model selection. We used the model selection results to determine the most important variables for cerulean breeding habitat selection and assigned selection or avoidance of habitat characteristics based on the slope of the β coefficient and 95% confidence intervals.

3. Results

3.1. Territory size

Mean territory size was 0.33 ± 0.03 ha ($n = 42$) pre-harvest, 0.25 ± 0.03 ha 1 year post-harvest ($n = 68$), 0.14 ± 0.01 ha 2 years post-harvest ($n = 65$), and 0.23 ± 0.03 ha 3 years post-harvest ($n = 34$; Fig. 4). A Shapiro-Wilk test indicated the territory size data were not normally distributed. We used Tukey's ladder of powers transformation to obtain a normal distribution. Territory size differed significantly among pre-harvest and the 3 years post-harvest ($F_{1,207} = 19.2$,

$P < 0.001$), declining from pre-harvest to 2 years post-harvest then increased 3 years post-harvest.

3.2. Territory clustering

Average nearest neighbor analysis indicated Cerulean Warbler territories were not significantly clustered on any territory mapping plot during any year (Appendix A). Territories exhibited either random (z-scores < 1 and P -values > 0.05) or significant dispersed (z-scores > 1 and P -values < 0.05) distribution. But for many of the ANN tests, territories exhibited a significant dispersed distribution (17 of 25 tests).

3.3. Habitat selection

3.3.1. Pre-harvest data

We analyzed 173 used and 68 available vegetation points pre-harvest. Mean values of most vegetation and topographic variables were similar between used and available sampling points (Table 2). However, the difference between mean Beers aspect at used and available sampling points was evident and model selection indicated that the most important variable for breeding habitat selection, pre-harvest, was Beers aspect (Table 3). Selection strength increased as Beers aspect increased ($\beta = 0.7$, 95% confidence interval: 0.05, 1.0; Fig. 5). The remaining variables did not influence cerulean breeding habitat selection pre-harvest.

3.3.2. Post-harvest data

We analyzed 580 used and 170 available vegetation points post-harvest. Model selection indicated that the only important variable for breeding habitat selection, post-harvest, was midstory vegetation (Table 4). Selection strength increased as % of midstory vegetation increased ($\beta = 1.5$, 95% confidence interval: 1.2, 1.7; Fig. 6). The remaining variables did not influence cerulean breeding habitat selection post-harvest.

4. Discussion

4.1. Overall changes in territory size

Territory size decreased each year between pre-harvest and 2 years post-harvest, but returned to 1 year post-harvest mean territory size 3 years post-harvest. The increase 3 years post-harvest could have been due to a smaller sample size (almost half that of 1 year and 2 years post-harvest). Territory density also decreased 3 years post-harvest (Nareff et al. 2019) and perhaps less competition allowed birds to expand their territory.

The cerulean has a relatively short breeding season in the central Appalachian region. The males have approximately 1 week to select and begin defending a territory prior to the arrival of the females (pers. obs.). Within their brief breeding season, they have to secure enough resources or select habitat features that will provide their basic needs for survival and reproduction. It is intuitive to expect an animal, particularly one that is socially monogamous (Hamel 2000, Boves and Buehler 2012), to select the smallest space in which it can find or predict adequate resource availability and be able to defend that space from inter- and intraspecific competition. The correlation between habitat quality and territory size in wildlife has been well studied (e.g., Krebs 1971, Smith and Shugart 1987) and we posit that one explanation for the decrease in territory size is an improvement in habitat quality or resource availability post-harvest. Opening the forest canopy through natural or artificial means (i.e., timber harvests) allows sunlight to reach the overtopped trees and the forest floor, which supports vegetative regeneration. The resulting structure provides niches for wildlife and their plant and insect food resources. The regenerating forest also provides potential nest sites and understory vegetation for protection of foraging female birds and their fledglings (Boves et al. 2013b). Our harvests appear to have improved habitat quality for breeding ceruleans and allowed for males to defend smaller territories. Territory density also increased 2 years post-harvest (Nareff et al. 2019) and the change in density is evident here in the large increase in territory vegetation points relative to territory mapping plot points post-harvest (173 to 68 pre-harvest and 580 to 170 post-harvest). While density is not necessarily an indicator of habitat quality (Van Horne 1983), it is unlikely that a species declining as quickly as the cerulean (Rosenberg et al. 2016, Sauer et al. 2017) would increase in density in a population sink. Sampling productivity of the population in our regional study area could better elucidate causes or confirm our interpretation that harvests provided higher quality habitat at our study areas (Boves et al. 2015).

Our final year of sampling in 2016 (2 years post-harvest at SJ and WC; CR and DY were not sampled in 2016) coincided with the emergence of 17-year cicadas (*Magicicada* sp.). The noise from the cicadas was nearly deafening at times and certainly made it difficult for songbirds to effectively communicate with mates or conspecifics (Hart et al. 2015). We speculate this could affect territory size in two ways. First, because we assume conspecifics could not communicate well, the birds might have smaller territories for defense purposes. However, this would mean those smaller territories would have to provide adequate resources and would be smaller even

without the cicadas. The second possible explanation is that the cicadas provided such a reliable food source, the birds would not have to move far from the nest patch, resulting in very small territories. Cerulean Warblers are among the smallest North American breeding warblers and would not be able to capture active cicadas, but they could take advantage of the insect's vulnerability as it sheds its exoskeleton and peck or rip the insect into manageable sized pieces to feed itself or its young. We queried the local birding listserv in West Virginia to find out what birds were observed consuming cicadas during the emergence and although no one reported seeing ceruleans eating them, there were reports of other small birds consuming cicadas (e.g., Carolina Wren [*Thryothorus ludovicianus*], Red-eyed Vireo [*Vireo olivaceus*]). This could be an alternative explanation for reduced territory size 2 years post-harvest, which was quite small (0.10 ± 0.1 ha). However, mean territory size from post-only territory data decreased between 1 year and 2 years post-harvest and this time period was 2014–2015 for CR and DY, not during the cicada emergence.

4.2. Territory clustering

Territory clustering has been observed throughout the cerulean breeding range, indicating the species may be exhibiting social or colonial nesting behavior (Oliarnyk and Robertson 1996, Roth and Islam 2007, Buehler et al. 2013). Clustering of territories should be expected when resources are limited or because landscape features may inherently lead to clumped resources (i.e., canopy gaps on upper slopes; Danchin and Wagner 1997). Based on this theory, territory clustering should be directly proportional to availability of high-quality habitat (Roth and Islam 2007). Some clustering was visually evident to us in our territory mapping and delineation (Appendix A), but spacing of territories varied among territory mapping plots and study areas and the cluster analysis indicated statistical lack of clustering. We were mapping territories at a small scale (i.e., ~16-ha plots) and it may be that clustering is occurring at a larger scale than we studied.

4.3. Habitat selection

Habitat selection studies assume that all habitat being sampled is available to the focal species. Determining what is available to ceruleans may be arbitrary as some of the space within each territory mapping plot may not be “available” (Johnson 1980) based on our understanding of cerulean breeding habitat in this region. Because we tracked unmarked birds, and did not follow individuals throughout an individual survey, our methods for territory mapping inherently

included some opportunities for error in estimating locations of birds and individual territories. We assumed that vegetation points we measured in the field adequately sampled used cerulean habitat. Our use points were locations of singing male ceruleans that we estimated while territory mapping using topo maps and the flagged gridlines. We assumed that each of these points accurately represent habitat used by ceruleans within their territories, but it is important to note that singing locations should be on the boundary of a territory in order to protect that resource against other males. The habitat ceruleans select within the core of their territory may differ, although aside from the actual nest site, that is unlikely.

Midstory structure is likely used by male and female ceruleans differently (Boves et al. 2013a), but it appears to play an important role in habitat selection and subsequently reproductive success in some parts of the breeding range (Jones and Robertson 2001, Jones et al. 2001, Wood and Perkins 2012). Females used understory vegetation more than midstory vegetation (Boves et al. 2013a) and tended to place nests at least 5 m above open spaces (Hamel 2000), but males used midstory vegetation for foraging more than expected within core areas of territories than in non-core areas in West Virginia (Wood and Perkins 2012). We modeled resource selection based on habitat used by singing males and our result corroborates the importance of midstory structure to ceruleans. As previously discussed, territories should provide adequate resources for the pair using it, but males and females have different needs, requiring a mixture of patches or levels of structure (Orians and Wittenberger 1991).

5. Conclusions

Only 2 of 9 variables were important to male cerulean breeding habitat selection; 1 pre-harvest and 1 post-harvest. Pre-harvest, increasing Beers aspect was selected for while tree species composition was not important for territory habitat selection. Conversely, post-harvest, Beers aspect was the least important variable to cerulean habitat selection (largest $\Delta AICc$ value). Vegetation structure, specifically the % of basal area that was trees intermediate with or overtopped by the canopy (variable “midstory”) was more important than topography, tree species composition, or tree size classes in selecting habitat post-harvest. Appropriate breeding habitat was available across a wider range of conditions post-harvest than pre-harvest. The harvests provided conditions in which male ceruleans appeared to be less restricted by where their preferred tree species or range of basal area were located on the landscape. Pre-harvest,

ceruleans had to rely on natural canopy gaps on their preferred aspects to find suitable habitat for singing, whereas harvests provided those conditions in otherwise unsuitable stands. Silvicultural prescriptions in mature forests at our 4 study areas in the central Appalachian region improved breeding habitat for Cerulean Warblers, at least for 2 years post-harvest. Territory size decreased indicating that ceruleans found resources in a smaller area compared to pre-harvest, and male habitat selection was less restricted by topographic conditions following harvests. Silvicultural prescriptions intended to manage for Cerulean Warblers can be designed to provide the range of residual basal area recommended by the Guidelines ($\sim 9.2\text{--}20.7\text{ m}^2/\text{ha}$) while mimicking mature forest conditions by providing stands of large canopy trees interspersed with canopy gaps that provide regenerating vegetation and complex midstory structure.

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Table 1. Topographic and vegetation variables used to model breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) in the central Appalachian region at 4 harvested study areas 2013–2016.

Code	Covariate Type	Variable Description	Habitat Component or Use in Models
beers	Study area	Beers aspect (0–2; 0 is xeric and 2 is mesic)	Topography
slope	Study area	Slope position (lower, middle, ridge)	Topography
ba ¹	Vegetation	Mean basal area (m ² /ha) of tree stems ≥ 10 cm dbh	Canopy structure
baavoid	Vegetation	% basal area (m ² /ha) composed of red maple, red oak group ≥ 10 cm dbh	Relationship to avoided tree species
bapref	Vegetation	% of basal area (m ² /ha) composed of sugar maple, hickories, white oak group, and tulip poplar ≥ 10 cm dbh	Relationship to preferred tree species
large	Vegetation	% basal area (m ² /ha) of large diameter trees (≥ 22.9 cm dbh)	Relationship to larger trees
cwlarge	Vegetation	% basal area (m ² /ha) of large diameter trees (≥ 40.6 cm dbh)	Relationship to larger trees preferred by Cerulean Warblers
cwpref	Vegetation	% of basal area (m ² /ha) composed of sugar maple, hickories, white oak group, and tulip poplar ≥ 40.6 cm dbh	Relationship to larger trees and species preferred by Cerulean Warblers
snag	Vegetation	basal area (m ² /ha) of standing dead trees	Relationship to canopy openness
mid	Vegetation	% of basal area (m ² /ha) composed of intermediate or overtopped trees	Relationship to vertical structure

¹Quadratic form also tested

Table 2. Means $\pm$ standard error of vegetation and topographic variables used to calculate resource selection functions for male Cerulean Warbler (*Setophaga cerulea*) habitat selection in 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. Variables are defined in Table 1.

Variable	Pre-harvest		Post-harvest	
	Used	Available	Used	Available
ba (m ² /ha)	28.1 $\pm$ 0.6	28.4 $\pm$ 0.9	20.1 $\pm$ 0.4	19.8 $\pm$ 1.0
bapref	0.25 $\pm$ 0.02	0.42 $\pm$ 0.03	0.71 $\pm$ 0.01	0.63 $\pm$ 0.02
baavoid	0.11 $\pm$ 0.01	0.16 $\pm$ 0.02	0.17 $\pm$ 0.01	0.26 $\pm$ 0.02
snag (m ² /ha)	2.2 $\pm$ 0.2	2.1 $\pm$ 0.4	–	–
cwlarge	0.59 $\pm$ 0.01	0.54 $\pm$ 0.02	0.53 $\pm$ 0.01	0.48 $\pm$ 0.03
midstory	0.22 $\pm$ 0.01	0.23 $\pm$ 0.02	0.27 $\pm$ 0.01	0.19 $\pm$ 0.02
large	0.83 $\pm$ 0.02	0.87 $\pm$ 0.01	0.77 $\pm$ 0.02	0.80 $\pm$ 0.03
cwpref	0.42 $\pm$ 0.2	0.39 $\pm$ 0.3	0.37 $\pm$ 0.01	0.31 $\pm$ 0.2
slope ¹				
lower	28%	24%	21%	23%
middle	13%	15%	22%	24%
ridge	59%	62%	58%	53%
beers	1.34 $\pm$ 0.08	1.05 $\pm$ 0.08	1.09 $\pm$ 0.03	1.00 $\pm$ 0.05

¹% of points within each category

Table 3. Models to calculate resource selection functions (rsf) to assess pre-harvest breeding habitat selection by male Cerulean Warblers (*Setophaga cerulea*) within 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. “rsf” is the resource selection function, “use” is a binomial variable for used or available habitat, B is the number of bootstrap iterations, and m is the argument describing the matching of use-availability data by mapping plot, which required a long string of characters, not shown here. Models are presented in order of AICc value with the top model (i.e., lowest AICc value) first. AICc is the Akaike’s Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model’s AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Variable codes are defined in Table 1.

Selection Strength Models	AICc	$\Delta AICc$	w_i
rsf(use ~ beers, data = terr, B = 99, m=c())	969.10	0.00	1.00
rsf(use ~ large, data = terr, B = 99, m=c())	987.26	18.16	0.00
rsf(use ~ baavoid, data = terr, B = 99, m=c())	991.50	22.40	0.00
rsf(use ~ cwlarge, data = terr, B = 99, m=c())	993.93	24.82	0.00
rsf(use ~ cwpref, data = terr, B = 99, m=c())	999.07	29.96	0.00
rsf(use ~ snag, data = terr, B = 99, m=c()) ¹	1001.92	31.14	0.00
rsf(use ~ bapref, data = terr, B = 99, m=c())	1000.24	32.82	0.00
rsf(use ~ mid, data = terr, B = 99, m=c())	1002.02	32.91	0.00
rsf(use ~ ba, data = terr, B = 99, m=c())	1002.09	32.98	0.00
rsf(use ~ ba^2, data = terr, B = 99, m=c())	1003.31	34.21	0.00

¹Pre-harvest data only

Table 4. Models to calculate resource selection functions (rsf) to assess post-harvest breeding habitat selection by male Cerulean Warblers (*Setophaga cerulea*) within 10 territory mapping plots at 4 study areas in West Virginia 2013–2016. “rsf” is the resource selection function, “use” is a binomial variable describing either used or available habitat data, B is the number of bootstrap iterations, and m is the argument describing the matching of use-availability data by mapping plot, which required a long string of characters, not shown here. AICc is the Akaike’s Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model’s AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Variable codes are defined in Table 1.

Selection Strength Models	AICc	$\Delta AICc$	w_i
rsf(use ~ mid, data = terr, B = 99, m=c())	3266.02	0.00	1.00
rsf(use ~ ba^2, data = terr, B = 99, m=c())	3292.30	26.29	0.00
rsf(use ~ ba, data = terr, B = 99, m=c())	3313.30	47.28	0.00
rsf(use ~ bapref, data = terr, B = 99, m=c())	3329.52	63.50	0.00
rsf(use ~ cwlarge, data = terr, B = 99, m=c())	3334.80	68.78	0.00
rsf(use ~ baavoid, data = terr, B = 99, m=c())	3341.23	75.21	0.00
rsf(use ~ cwpref, data = terr, B = 99, m=c())	3341.56	75.54	0.00
rsf(use ~ large, data = terr, B = 99, m=c())	3348.97	82.95	0.00
rsf(use ~ beers, data = terr, B = 99, m=c())	3350.38	84.36	0.00

Figure 1. Location of the 4 study areas within the Appalachian Mountains Bird Conservation Region for this investigation of Cerulean Warbler (*Setophaga cerulea*) habitat selection. Study areas are Coopers Rock State Forest (CR), Stonewall Jackson Lake WMA (SJ), and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA in West Virginia.

Figure 2. Estimated locations of Cerulean Warblers (*Setophaga cerulea*) recorded over approximately 6 weeks during territory mapping sampling in 2016 at Stonewall Jackson Lake Wildlife Management Area, Lewis County, West Virginia. Observations are used to delineate territories and select vegetation sampling plots to assess habitat selection.

Figure 3. Example of territory vegetation point assignment at Cerulean Warbler (*Setophaga cerulea*) territories delineated at Stonewall Jackson Lake Wildlife Management Area, Lewis County, West Virginia in 2016. Vegetation was sampled at every-other mapping point and at all territory points (Terr_Veg).

Figure 4. Cerulean Warbler (*Setophaga cerulea*) mean territory size $\pm$ standard error pre-harvest, 1 year post-harvest (1 YPH), 2 years post-harvest (2 YPH), and 3 years post-harvest (3 YPH) on 10 territory mapping plots at 4 study areas in West Virginia. The 4 study areas were Stonewall Jackson Lake Wildlife Management Area, Wolf Creek and Dynamite at Elk River Wildlife Management Area, and Coopers Rock State Forest.

Figure 5. Cerulean Warbler (*Setophaga cerulea*) selection of Beers aspect (x-axis), pre-harvest. Beers aspect (0–2) represents forest productivity with the least productive, xeric aspects approaching 0 and the most productive, mesic aspects having values approaching 2. Selection strength (y-axis) with median (gold line) 95% confidence intervals is shown. Selection strength increased as Beers aspect increased. Resource selection functions were calculated from logistic regression on used-available habitat data on 4 plots at 2 study areas with pre- and post-harvest data in West Virginia 2013–2016.

Figure 6. Cerulean Warbler (*Setophaga cerulea*) selection of midstory vegetation (x-axis), post-harvest. Midstory vegetation, stems ≥ 10 cm dbh that were intermediate to or overtopped by the forest canopy, was assessed as a percentage of overall basal area at sampling points, shown here as a decimal rather than percentage (i.e., 1 = 100% of basal area was intermediate or overtopped by the canopy). Selection strength (y-axis) with median (gold line) and 95% confidence intervals is shown. Selection strength increased as % of midstory increased. Resource selection functions were calculated from logistic regression on used-available habitat data on 10 plots at 4 study areas in West Virginia 2013–2016.

Appendix A. Cerulean Warbler territories on 10 territory mapping plots at 4 study areas in West Virginia during 2013–2016.

Coopers Rock State Forest post-harvest, 2013 and 2015.

Dynamite post-harvest, 2013–2015.

Stonewall Jackson pre-harvest, 2013–2014.

Stonewall Jackson post-harvest, 2015–2016.

Wolf Creek pre-harvest, 2013–2014.

Wolf Creek post-harvest, 2014–2016.

Appendix B. Forest Inventory Analysis crown class codes.

Image from Dana Witwicki, National Park Service.

D =dominant, C = codominant, I = intermediate, O = overtopped

CHAPTER 4: Avian community response to forest management in the central Appalachian region: Effects of operational silviculture for the Cerulean Warbler (*Setophaga cerulea*)

Abstract. The Cerulean Warbler (*Setophaga cerulea*) is a species of conservation concern throughout its range. Harvest treatments were implemented with the objective of creating breeding habitat for Cerulean Warblers and here we evaluate the response of other species that breed within central Appalachian hardwood forests (i.e., oak [*Quercus* spp.]-hickory [*Carya* spp.] and mixed-mesophytic forests). We quantified and compared the broad-scale influence of harvest treatments on estimated territory density and abundance of common songbird species representing a range of seral stages. We conducted territory mapping at 4 study areas in West Virginia and point counts at 9 study areas across 4 states within the central Appalachian region (Kentucky [n=1], Pennsylvania [n=2], Virginia [n=2], West Virginia [n=4]) for up to 5 breeding seasons from 2013–2017. Seven of the 9 study areas were sampled pre- and post-harvest with the remaining 2 sampled only during post-harvest. Pre-harvest mean basal area among study areas was 29.3 m²/ha. Harvesting reduced mean basal area among study areas by 38% (mean 18.1 m²/ha) at harvest interior and harvest edge points. Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), and Hooded Warbler (*S. citrina*) territory densities and abundances increased significantly post-harvest and continued to increase with years-post-harvest. Scarlet Tanager (*Piranga olivacea*) abundance initially decreased immediately following harvest, but then increased slightly at harvest edge and reference points 1–3 years post-harvest. Wood Thrush (*Hylocichla mustelina*) territory density initially decreased 45% from pre-harvest to 1 year post-harvest, but remained similar across 1–3 years post-harvest. Wood Thrush abundance initially decreased at all point types immediately following harvest; however, the decline at harvest edge points was slower than the decline at harvest interior points and abundance increased at reference points 1–3 years post-harvest. Our results suggest that 3 of the 5 species considered here responded positively to these silvicultural prescriptions, whereas the 2 forest interior species, Scarlet Tanager and Wood Thrush, remained on the study areas despite declines in abundance and may have benefitted from some aspect of the harvest mosaics, such as increased availability of refuge for fledglings within the regenerating harvests. The overall avian community structure did not differ among point types pre-harvest, but was increasingly different among point types across years-post-harvest.

Keywords: Breeding forest birds, silviculture, songbird habitat management, *N*-mixture modeling, community structure, NMDS, ANOSIM

1. Introduction

Much of the eastern United States was clearcut during the 19th and early 20th centuries (e.g., Kelty and D’Amato 2005, Johnson and Govatski 2013, Thompson et al. 2013).

Subsequent regeneration of forests and wildfire suppression following widespread clearcutting produced predominantly even-aged forests, with little heterogeneity in forest structure (Miller et al. 2004). Forest structure dictates available niches for both forest breeding songbirds and their insect prey, with a greater diversity of habitat types intuitively leading to a more diverse songbird community.

Forest habitat management often targets one individual species of conservation concern or game species of interest. The Cerulean Warbler (*Setophaga cerulea*; hereafter “cerulean”) is a species of greatest conservation need (SGCN), with declines linked in part to loss of forest habitat and structural diversity on its breeding grounds (Rosenberg et al. 2016). Active management of forests can benefit the cerulean by creating the complex structural conditions preferred by the species (Sheehan et al. 2013, Wood et al. 2013, Nareff et al. 2019). Harvest treatments that benefit the cerulean will inherently affect abundance and territory density of other songbird species using the same forest stands, either positively or negatively, depending on the species and its breeding habitat requirements. The cohort of songbirds that uses the same breeding habitat as ceruleans is diverse and includes other species considered SGCN in multiple states (Sheehan et al. 2013, Wood et al. 2013). Responses to harvests are species-specific and while it is important to consider each focal species independently for management (Haché et al. 2013), multiple species may be managed under one or diverse silvicultural prescriptions (e.g., those that provide mosaics of habitats).

We recently completed a study to examine the response of ceruleans to timber harvest treatments implemented through operational silviculture as recommended by the Cerulean Warbler Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests (Wood et al. 2013; hereafter “Guidelines”). The objective of the study was to update the Guidelines and further recommend ways to improve breeding habitat for this severely

declining songbird species (Nareff et al. 2019). Here, we use the same harvests to evaluate the response of a group of associated songbird species that represent diverse seral stages. We assessed changes in abundance ($n=5$) and territory density ($n=4$) of focal species to examine the response to harvests placed within a matrix of relatively intact, mature deciduous forests in the central Appalachian region. The focal species were selected as representative species of different seral stages or species of conservation concern that are commonly found in deciduous forests in the central Appalachian region. The 5 focal species are Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), Hooded Warbler (*S. citrina*), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*).

Data presented here were collected at 7 study areas 1–4 years prior to harvest and 1–3 years-post-harvest and at 2 study areas with post-harvest data for up to 3 years post-harvest (Table 1). Study areas were in Kentucky ($n=1$), Pennsylvania ($n=2$), Virginia ($n=2$), and West Virginia ($n=4$). We used point counts in Kentucky, Pennsylvania, Virginia, and West Virginia to evaluate changes in songbird abundance post-harvest and among years-post-harvest. We considered the influence of topographic and vegetation variables on abundance of each species (Table 2). We used territory mapping in West Virginia to evaluate changes in songbird territory density post-harvest and among years-post-harvest.

1.1. Natural History of Focal Species

We selected focal species that use the range of seral stages available in the central Appalachian region or that can be created and maintained through operational silviculture (i.e., early successional to mature forest). Eastern Towhee, Indigo Bunting, and Hooded Warbler are disturbance-dependent species that rely on shrubby habitat for breeding (Payne 2006, Sheehan et al. 2013, Greenlaw 2015, Kellner et al. 2016). In addition to using regenerating timber harvests or abandoned fields, all three of these species may be found in the developing understory below canopy gaps in mature forest (Bell and Whitmore 1997, Rush et al. 2012, Sheehan et al. 2013). Abundance of Eastern Towhee and Indigo Bunting were negatively related to residual basal area in a previous regional study in the central Appalachian region (Sheehan et al. 2013). The other 2 species, Wood Thrush and Scarlet Tanager, are interior forest species that rely on the complexity of mature forests for breeding (Kellner et al. 2016, Lambert et al. 2017); however, Scarlet Tanagers tolerate lower basal areas than Wood Thrush (Sheehan et al. 2013). We added Scarlet Tanager as a focal species

after completion of field work and thus did not assess changes in territory density. We initially intended to include Worm-eating Warbler (*Helminthos vermivorum*) as the fifth focal species and second forest interior species, but they were uncommon or absent from multiple study areas and did not provide enough data for analyses. We selected Scarlet Tanager as the replacement because it was a common species at all study areas, it shows attraction and aversion to the same tree species as ceruleans, and guidelines for concurrently managing habitat for Wood Thrush and Scarlet Tanagers were published in 2017 (Lambert et al. 2017).

Eastern Towhee is an edge associated specialist that spends most of its time foraging on the ground, in leaf litter, for berries, seeds, and various insects (Greenlaw 2015). It will take advantage of food sources in the shrub or midstory layers when caterpillars are abundant or in the late spring when new leaves are emerging. It occupies mid- to late-seral stages of secondary succession in thickets, edges of woodlots, and ditches or trails (Greenlaw 2015). Partners in Flight (PIF) does not consider the Eastern Towhee to be a threatened species globally, but reported a 43% decline in abundance between 1970 and 2014 (Rosenberg et al. 2016).

Indigo Bunting nests and forages in shrubby, weedy habitats, commonly in abandoned upland field areas beginning ca. 3 years after clearing or abandonment and in young harvests (Yahner et al. 2002, Kabrick et al. 2004, Payne 2006, McDermott and Wood 2010). Range wide in North America, Indigo Bunting populations have declined by 25% since 1970 (Rosenberg et al. 2016).

Hooded Warbler is a gap specialist (Chiver et al. 2011) and is strongly associated with edge habitat, typically in large tracts of continuous mature forest where trees are large enough to create significant treefall gaps (Robbins 1979). Its territories usually include small clearings with an available shrubby understory (Bisson and Stutchbury 2000, Whittam et al. 2002). Partners in Flight does not consider the Hooded Warbler to be a threatened species as it has increased in abundance by 103% between 1970 and 2014, one of the few mature forest species with an increasing trend (Rosenberg et al. 2016)

Eastern Towhee, Indigo Bunting, and Hooded Warbler use understory species including blackberry (*Rubus* spp.), black cohosh (*Actaea racemosa*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), wild rose (*Rosa*

acicularis), and hawthorn (*Crataegus* sp.). These species were common understory shrubs and saplings in natural and created canopy gaps and heavy harvests within our study areas. Distribution constraints and regional declines of Eastern Towhee and Indigo Bunting are likely related to the absence of early successional habitat, including young forests, and poor understory development (Payne 2006, Greenlaw 2015). Their breeding requirements are often met in stands that support breeding ceruleans in which an uneven canopy structure and canopy gaps provide a developed understory. Timber harvesting facilitates mid-seral-stage growth and understory development during the setback of succession (e.g., Dugay et al. 2001, Greenberg et al. 2014, Perkins and Wood 2014, Murray et al. 2017).

Wood Thrush and Scarlet Tanager are both forest interior species that some consider sensitive to fragmentation of breeding habitat (Mowbray 1999, Dugay et al. 2001, Evans et al. 2011); however, Sheehan et al. (2013) observed that Scarlet Tanager was tolerant to moderate timber harvesting. The central Appalachian region hosts the highest densities of both species relative to their breeding ranges (Rosenberg et al. 2016, Lambert et al. 2017). They prefer mature deciduous or mixed forests where oaks are common, deciduous tree diversity is high, and there is a mix of tree sizes (Mowbray 1999, Evans et al. 2011, Lambert et al. 2017). Their breeding requirements are similar to the cerulean in that they breed in habitats with large trees, hilly terrain, an uneven canopy structure, and a developed understory; characteristics found in mature forests. Further, Scarlet Tanager in the Northeast and Mid-Atlantic populations, shows the same affinity for white oaks and aversion to red oaks and red maples for nesting as the cerulean (Lambert et al. 2017). Wood Thrush commonly forage on the ground in leaf litter and nest in understory shrubs or bent trees, whereas Scarlet Tanager typically remains in the canopy or midstory, above 7.6 m (Lambert et al. 2017).

Scarlet Tanager populations in the Appalachian Mountains Bird Conservation Region (BCR) appear to be relatively stable based on Breeding Bird Survey (BBS) data (Sauer et al. 2017). Range wide in North America, Scarlet Tanager populations have declined by 7% since 1970 (Rosenberg et al. 2016). According to BBS data, Wood Thrush declined significantly in the Appalachian Mountains BCR between 1966 and 2015 (Sauer et al. 2017). It is considered a “watch list” species and a species of continental importance (Rosenberg et al. 2016).

2. Methods

2.1. Regional Study Area

We conducted fieldwork during 2013–2016 (Kentucky, Pennsylvania, West Virginia) and 2013–2017 (Virginia) in contiguous, mature forest landscapes at 9 study areas within the central Appalachian region of the Appalachian Mountains BCR (NABCI 2000; Fig. 1). The region is characterized by a series of parallel, southwest- to northeast-trending narrow valleys and high ridges, or plateaus dissected by headwater streams from the Appalachian Mountains; dry-mesic and mixed-mesophytic forest types dominated the study areas (USDA Forest Service 1994). Because all study areas were on Wildlife Management Areas (WMA) or State Forests (SF), they had been managed for a variety of objectives including experimental and teaching harvests, creation of wildlife food plots, or clearings for recreation and skid roads. The study areas (Fig. 1) were Grayson Lake WMA, Kentucky (GL); Clear Creek State Forest (CCSF), Pennsylvania; Rabbit Hole (RH; State Game Land 86), Pennsylvania; T.M. Gathright WMA, Virginia (GA); Highland WMA, Virginia (HI); Wolf Creek (WC) and Dynamite (DY) within the Elk River WMA, West Virginia; Stonewall Jackson Lake WMA, West Virginia (SJ); and Coopers Rock SF, West Virginia (CR). They fell within 3 physiographic provinces: GL in the Cumberland Plateau, GA and HI in Ridge and Valley, and all Pennsylvania and West Virginia study areas in the Allegheny Plateau. Elevation at the sampled sites ranged from 214 to 1123 m (mean 587 m).

State partners identified areas for management that represented a range of available slope positions, aspects, and elevations. Tree species composition differed somewhat among study areas, but common overstory tree species included oaks (northern red oak [*Quercus rubra*], scarlet oak [*Q. coccinea*], black oak [*Q. velutina*], white oak [*Q. alba*], chestnut oak [*Q. montanus*]), hickories (*Carya* spp.), red maple (*Acer rubrum*), sugar maple, black cherry, and tulip poplar (*Liriodendron tulipifera*).

2.2. Harvests

The total area harvested at each study area for this project comprised a small proportion of each WMA, state forest, or State Game Land (0.01–1.5%). The total area harvested at each study area (Table 1) was 16.4–77.2 ha (mean 36.3 ± 6.6 ha) and comprised small harvest blocks (0.4–6.9 ha), linear harvests (8.8–18.5 ha), or harvest mosaics (Fig. 2) encompassing a diversity of harvest types (i.e., shelterwood, group selection, clearcut with

residuals) that resulted in a range of canopy openness. Many of the harvests were described by the local land managers as shelterwood systems, whereby the mature community is removed in two or more successive cuttings separated in time by 5–10 years, temporarily leaving mature seed trees and resulting in a new even-aged system (Nyland 2007). However, our study ended before any overstory removal harvests were implemented. The other silvicultural systems used on the study areas included clearcuts with residuals and single-tree to group selection harvests. The ultimate goal of the harvests, outside of the intended use for our study, was to provide conditions where oaks and hickories would make up the bulk of the regenerating class, providing conditions that would allow desired, valuable saplings to outcompete less desirable species (e.g., red maple; WVDOP 2006). We did not evaluate songbird response to specific harvest types, but to the resulting conditions in basal area and tree species composition. We designated three point types to make our assessments: harvest interior, harvest edge, and reference (detailed description in Section 2.4.2). We used unharvested areas around, and interspersed with harvests in order to compare abundances between harvested and reference points (Fig. 2). The harvests and surrounding unharvested areas that contained sample points was considered a study area and they ranged 32–224 ha in size (Table 1).

Harvest treatments were applied based on the Guidelines (Wood et al. 2013), and were placed on all available slope positions and aspects by state managers of each study area. Harvests were limited to the dormant season because the entire study region was within the range of the endangered Indiana bat (*Myotis sodalis*) that relies on trees and snags for day-roosts in the maternity season and therefore summer harvests were precluded (Silvis et al. 2016, Johnson and King 2018). Our original study design planned for 1 year of pre-harvest data collection followed by 3 years of post-harvest data collection at all study areas. However, poor winter weather and logistics related to harvest contracts delayed harvests at all but one of the study areas such that number of years sampled pre-harvest varied from 1 to 4 and post-harvest varied from 1 to 3 years per study area (Table 1). Consequently, we sampled 2 additional study areas (DY and CR) that were harvested the winter before initiation of our study to increase post-harvest sample size to allow us to examine the influence of years-post-harvest on songbird abundance. Harvests were applied at DY and CR

over the winter of 2012–2013 and were initially sampled during the 2013 breeding season (i.e., first year post-harvest).

2.3. *Vegetation Sampling*

We used standardized protocols across the study areas to quantify tree basal area and tree species composition pre-harvest and the first year post-harvest. We placed 4 plots at each systematically placed point count location; one at the point center, one 35 m away from the center at magnetic north, and the remaining two at 120° intervals 35 m away from the center point (hereafter, “subplots”). We measured post-harvest basal area for 7 points at HI on only three subplots. We completed variable radius prism plots using a wedge prism (10-factor English or 2.5-factor metric) to tally live trees and snags at every subplot. Tree tallies from variable radius prism plots rely on the relationship between the diameter at breast height (dbh) of each tree and the distance between those trees and the observer. By holding the prism at a fixed distance from the eye over the plot center and rotating 360° around the prism, the observer can tally trees that are in the plot. For each live tree and snag in a prism plot, we measured dbh to the nearest centimeter (cm) using a Biltmore stick or dbh tape. For each live tree, we also recorded tree species or group (e.g., hickory group, red oak group). Borderline live trees and snags were counted and included for tree composition values, but every other borderline live tree was removed to calculate total basal area. We sampled harvested subplots once pre-harvest and once post-harvest; we sampled unharvested subplots only once because vegetation did not change.

We calculated mean basal area of stems ≥ 10 cm dbh per point from the measured subplots at every point within the three point types (Boves et al. 2013b, Sheehan et al. 2013). We also calculated mean basal area of tree species ≥ 10 cm dbh that are preferred and avoided by Scarlet Tanagers and ceruleans. To assess each focal species’ response to vegetation structure, we summarized data into four size classes of dbh (< 7.6 cm, ≥ 7.6 – 22.9 cm, ≥ 22.9 cm, and ≥ 40.6 cm dbh), midstory trees ≥ 10 cm dbh, upper canopy trees ≥ 10 cm dbh, and snags ≥ 10 cm dbh (Table 2). Although the two largest size classes of dbh overlap and thus are highly correlated, we wanted to assess the relationship between Hooded Warbler, Scarlet Tanager, and Wood Thrush abundances and large trees (> 22.9 cm), as well as the relationships between each species’ abundance and trees the size preferred by ceruleans for nesting (≥ 40.6 cm dbh, cwlarge; Boves et al. 2013a). Preferred tree species included sugar

maple, white oaks, and hickories whereas avoided tree species included red maple and red oaks (Wood and Perkins 2012, Wood et al. 2013, Lambert et al. 2017). Midstory trees were those placed into crown classes of intermediate or overtopped, whereas upper canopy trees were those classified as codominant, dominant, or open growth (USDA Forest Service Forest Inventory and Analysis classification system). We then summed the basal areas within each vegetation category at the point level and calculated the percentage of basal area for each.

2.4. Avian Surveys

2.4.1. Territory mapping

At all 4 West Virginia study areas, we quantified Eastern Towhee, Indigo Bunting, Hooded Warbler, and Wood Thrush territory densities annually using territory-mapping (Bibby et al. 2000). We did not map Scarlet Tanager territories because it was added as a focal species after completion of field work. We centered 2 or 3 16–17-ha plots over the harvest mosaics at each study area, depending on the size of the area for a total of 10 territory mapping plots. We situated plot boundaries so that each plot would encompass mostly harvested area, although each included a small amount of unharvested area (Fig. 2). We placed plot boundaries at least 100 m apart to avoid counting the same territory on more than one plot. We marked plot boundaries and an internal grid of 50-m intervals with plastic flagging before each field season. Unless a flagged tree was harvested, the flagging remained on the same trees for the duration of the study.

We initiated territory-mapping surveys in mid-April and mapped focal species' territories during 7–8 visits per plot through early June 2013–2016. Surveys continued for 6 weeks with a minimum of 4 days between surveys (Bibby et al. 2000). One person surveyed an entire plot within a single morning from dawn to approximately 1100 hours. The same person sampled each plot within a season when logistically possible to maximize detections over repeated visits. We varied the starting points and routes taken through the plots between surveys to reduce time-of-day bias. We recorded singing, calling, and behavioral observations on topographic maps overlaid with the plot grids to accurately note slope position and aspect. We directed special attention to accurately noting multiple individuals that could be heard or seen concurrently (i.e., counter-singing, aggressive interactions) due to the importance in territory delineation.

We identified territories using detections and instances of counter-singing during the 7–8 visits annually. We estimated approximate territory locations in a geographic information system (GIS; ArcMap 10.3, ESRI 2014) by using recurring locations of singing individuals. A territory can be delineated from a minimum of 2 territory mapping detections separated by 10 days over 8 territory mapping visits (Bibby et al. 2000, Haché et al. 2013). However, most of the individuals we mapped were reliable in their territorial behavior and once established, they were encountered during ≥ 3 territory-mapping events. We calculated annual territory density (# territory/ha) of individual territory mapping plots by summing the number of territories within a plot and dividing by the total area of the territory mapping plot.

2.4.2. *Point Counts*

We systematically placed point count locations (points) throughout the harvest and reference stands, spacing points ≥ 200 m from each other to avoid double counting birds. We placed harvest interior points within harvest units ≥ 50 m from the closest edge of a harvest (mean distance 65.9 ± 3.4 m); harvest edge points could be inside or outside the harvest boundaries but all were < 50 m from the closest edge of a harvest (mean distance 8.2 ± 2.0 m); and reference points ≥ 50 m, but generally ≥ 100 m from harvests (mean 307.7 ± 26.2 m; 83% of points ≥ 100 m). Edge effects for avian species are generally considered to occur within 50 m of forest edge (Paton 1994). We placed reference points in areas that were similar to pre-harvest conditions at the treatment points and where no harvests would take place for the duration of the project. Thus, reference points represented mature forest conditions generally available in our study landscape, and did not occur in pristine mature forest conditions without internal edges (e.g., hiking trails, campgrounds, skid roads, water features).

We surveyed for songbird abundance at a total of 207 points including 134 pre-post points (36 harvest interior, 27 harvest edge, and 71 reference) and 73 post-only points (27 harvest interior, 11 harvest edge, and 35 reference; Table 1). All points were sampled 2013–2016 except the post-only sites (CR and DY), which we dropped in 2016 because we had acquired data for 1–3 years post-harvest. In 2017, we sampled only the VA study areas (GA and HI; Table 1) to acquire the 1 year post-harvest data for these study areas. We surveyed from 15 May to 29 June each year, which coincides with the peak breeding season for songbirds in the central Appalachian region (e.g., Newell and Rodewald 2012, Wood and

Perkins 2012, Boves et al. 2013a, Sauer et al. 2017). Surveys were conducted on days without steady rain or sustained winds >19 kilometers per hour (i.e., >3 on the Beaufort scale), between sunrise and 1100 hours. We recorded noise level, start time, date, and observer for each survey to incorporate into detection models (Table 2).

At each study area, a field crew of point count surveyors conducted the avian sampling. Most surveyors were experienced prior to the initiation of the study, but all were trained in bird identification, distance estimation, and sampling protocols before surveys began. We surveyed each point 3 times each year, with approximately 1 week between visits when possible. We attempted to survey points in a different order each visit to reduce time-of-day bias and by a different observer to reduce observer bias. We recorded detections within 5 distance bands indicating the distance of the bird from the observer (0–25 m, >25–50 m, >50–75 m, >75–100 m, and >100 m) but used only the first 2 distance bands in analyses (section 2.5.2). We recorded detections by sex and detection type (i.e., sing, call, visual, flyover). All flyovers and detections >50 m were excluded from analyses.

2.4.3. Topographic Metrics

We used a 1:24,000 digital elevation model (DEM; USGS 2017) to calculate 3 topographic metrics (elevation, slope position, and Beers aspect) within the 50-m radius for each point using the “Topography Tools for ArcGIS 10.3 and earlier” toolbox (version 10.3, Dilts 2015). We classified each point with 1 of 6 categories of slope position by obtaining the majority from the raster layer in GIS, using the “zonal statistic as table” tool, within the 50-m point count radius. Three categories were represented as the majority at our sample points: lower, middle, and ridge (Table 2). Beers aspect (0–2; Beers et al. 1966) represents forest productivity with the least productive, xeric aspects approaching 0 and the most productive, mesic aspects having values approaching 2. We assigned the mean Beers aspect within the 50-m point count radius for each point from the raster layer in GIS using the “zonal statistic as table” tool.

2.5. Statistical Analyses

2.5.1. Territory density

We assigned the calculated territory densities described in section 2.4.1 to pre-harvest years (all coded as 0) and individual years post-harvest (coded as 1, 2, or 3) for all 4 West Virginia study areas. We used mixed effects models for each species with territory density as

the dependent variable, years-post-harvest as a fixed effect, and territory mapping plot as a random effect. This method is appropriate when there are violations of homogeneity, when you need to account for variance from random effects (here, territory mapping plots), or because of unbalanced sampling design (Zuur et al. 2009). Coopers Rock, DY, and 1 plot at WC provided data from 3 years post-harvest whereas SJ was sampled for 2 years post-harvest. Additionally, we sampled territories at CR the first and third years post-harvest, but not the second. We tested mixed effects models fit with restricted maximum likelihood (REML), using package nlme (version 3.1-140, Pinheiro et al. 2019) in program R (version 3.5.0, R Core Team 2018). We used visual exploratory methods to identify violations of assumptions on linearity, normal distribution of residuals, and homogeneity of variance by plotting residuals vs observed values and residuals vs fitted values (Zuur et al. 2009). We used a Bartlett test to test for homoscedasticity and considered test results significant at $\alpha = 0.05$.

2.5.2. *Point counts*

We included detections of singing male Hooded Warbler, Scarlet Tanager, and Wood Thrush, and singing and calling male Eastern Towhee and Indigo Bunting within 50 m of the point count (point) center in our analyses to more closely relate abundance to vegetation and topographic characteristics measured within the 50-m radius of each point. Any bird detected beyond 50 m of the point center will likely have little to no relationship with the vegetation and topographic characteristics at that point (Hutto 2016).

We used an *N*-mixture modeling approach to estimate abundance using all pre- and post-harvest count data across the 5 years of surveys at the 9 study areas. This resulted in up to 4 years of pre-harvest data and up to 3 years of post-harvest data within a study area. *N*-mixture models use spatially and temporally repeated counts to estimate abundance as a product of ecological processes and imperfect detection by linking two sub-models (Royle 2004, Dail and Madsen 2011, Kéry 2018). This is important because birds are likely not distributed randomly in space, as the landscape is heterogeneous, providing some patches of habitat suitable for breeding within an unsuitable matrix. Habitat and topographic covariates can be used to explain this distribution explicitly in the abundance estimation sub-model (Royle 2004), whereas survey-specific covariates (e.g., observer, weather) can be used to explain detection probability (Table 2). Using this approach, average abundance across

points that share a spatial attribute (e.g., all harvest interior points, all points on ridges) can be estimated, as can temporal changes in abundance using covariates for time, as we do here (Dail and Madsen 2011, Bellier et al. 2016).

N -mixture models are valuable to ecology, conservation, and monitoring wildlife populations because they provide an analysis method that is more efficient, less expensive, and can be applied to more easily attainable data, over a larger spatiotemporal extent than true mark-recapture studies (Kéry 2018). Use of N -mixture models to analyze count data (e.g., Barker et al. 2018) has been criticized because detection probability is assumed constant for all visits, after adjusting for covariate effects, and auxiliary data are not used to estimate detection probability. However, N -mixture modeling is also considered a significant advancement in abundance modeling and some of the doubts projected on this method have been tested and determined unfounded (Joseph et al. 2009, Kéry 2018).

2.5.3. Hierarchical model configuration

We modeled the 5-year abundance dataset in a single-season format because some points were monitored only during 3 years of post-harvest conditions (CR and DY) whereas others were monitored for differing numbers of years pre-harvest and post-harvest (described in section 2.2). This approach achieves a larger effective sample size and is useful in cases with limited data or unequal sample sizes (Burnett and Roberts 2015, Fuller et al. 2016). This approach required us to use a static population N -mixture model (Royle 2004), which assumes closure among the 3 within-season visits, but the population is open across years. While this modeling structure ignores some of the variability by assuming that abundance from each point count is independent across years, it is still reasonable for estimating temporal trends conditional on the explicit covariates (Linden and Roloff 2013, Kéry and Royle 2015, Ahlering and Merckford 2016, Fuller et al. 2016). Static population N -mixture models estimate 2 parameters: abundance and detection probability. Model convergence was verified through sensitivity analysis by increasing K (the upper summation limit for the summation over the random effects in the integrated likelihood) and confirming no change in beta estimates (Kéry and Royle 2016). We used package unmarked (version 0.11-0, Fiske and Chandler 2011) in program R (version 3.5.0, R Core Team 2018) for all hierarchical modeling. We specified the closed population model for the dataset using the function

“pcount”. We used Akaike’s Information Criterion corrected for small sample size bias (AICc, Burnham and Anderson 2002) for all model selection.

2.5.4. *Detection probability covariates*

We used model selection to determine important detection probability covariates for inclusion in final analyses (Fuller et al. 2016). All candidate models included a covariate for observer proficiency, which was based on an observer’s previous experience as evaluated by team leaders in each state. The 39 observers were ranked as either low, moderate, or high proficiency, relative to all other observers that sampled birds during the study. We tested all combinations of observer with time-since-sunrise, ordinal date, and noise. Using AICc (Burnham and Anderson 2002), we selected the top detection probability model for each species and used them for all subsequent analyses.

2.5.5. *Point-count analyses*

For each species, we first used AICc model selection to determine if a Poisson or Zero-inflated Poisson (ZIP) distribution fit the data for each species (Poisson used for Eastern Towhee, Hooded Warbler, and Scarlet Tanager and ZIP used for Indigo Bunting and Wood Thrush). We then used the abundance dataset to test 3 sets of models (Table 3). We had data from 207 points across the 9 study areas resulting in 795 independent samples (pre-harvest points n=134, 1 year post-harvest points n=207, 2 years post-harvest n=184, 3 years post-harvest n=123). We included calendar year in the abundance parameter for all models to account for inherent differences in each species’ abundance among calendar years because harvests occurred in different years among study areas. We included study area in the abundance parameter for all models to account for inherent differences in each species’ abundances among study areas (Table 4). We removed the two Pennsylvania study areas for Wood Thrush analyses because there were no detections of this species <50 m from a point and this caused problems with model convergence (inflated standard errors).

In the first model set (Table 3), we examined the influence on focal species abundance of point type (pttype), basal area of tree species preferred by ceruleans for nesting and foraging (stems ≥ 10 cm dbh; bapref), and percentage of basal area that was large diameter trees selected by ceruleans for nesting (≥ 40.6 cm dbh; cwlarge). Those 3 variables had the most influence on abundance and population growth of ceruleans at some of the same

study areas (Nareff et al. 2019) and we wanted to evaluate their influence on each focal species.

In a second model set, we developed 4 models using the point type and years-post-harvest (yph) variables to estimate the influence of years-post-harvest on our focal species' abundances (Table 3). We added a years-post-harvest covariate (years 0–3 where 0 = pre-harvest) for each point to compare pre- to post-harvest abundances and abundances among years-post-harvest.

In a third model set, we examined the influence of additional topographic and vegetation metrics that might influence our 5 focal species' abundances based on their habitat requirements, including the variable from the top model from model set 1 (Cerulean Warbler variables; Table 3). Topographic variables (i.e., slope position and Beers aspect) were tested for every species alone and in additive models with the point type variable to examine if placement of harvests on the landscape with regard to slope position or aspect was important to any of the focal species. Vegetation covariates included in models differed for each focal species based on their preferred seral stage or habitat requirements (e.g., basal area of small stems for shrub-dependent species and percentage of basal area that was canopy trees for mature forest species). We evaluated response of Scarlet Tanager and Wood Thrush to tree species richness (all live stems; Lambert et al. 2017). We tested the relationship between disturbance-dependent species' abundance and point type + basal area of snags. Depending on the overall canopy conditions (i.e., closure) at a point, the presence of snags may result in canopy gaps and subsequent regeneration, providing habitat for these three species.

For each model set and species, we again used AICc to determine the most parsimonious model. We used the selected model from the years-post-harvest model set (second set) to predict focal species' abundance by point type across years-post-harvest. For the third model set with species-specific variables, we evaluated the relationships between abundance and influential variables by assessing the sign and 95% confidence intervals (CI) of the slope (β coefficient).

2.5.6. *Community structure*

We calculated the maximum number of detections per years-post-harvest for 80 species detected well by point counts within 50 m of each point (Appendix A) using all 795 samples described in section 2.5.5. We excluded species that were late migrants that did not

typically breed in the study area (e.g., Bay-breasted Warbler [*S. castanea*]). We included all detection types except flyovers (i.e., singing, visual, call) as any individual of a breeding species detected within 50 m of the point can be considered part of the community.

We performed a one-way analysis of similarity (ANOSIM) on the avian community data to test for differences in the avian community structure by point type among years-post-harvest and among point types within pre-harvest or each year-post-harvest. Analysis of similarity uses a matrix of dissimilarity values to compare within-group and between-group variation in community composition. The ANOSIM uses a permutation test to assess the level of beta diversity and results in an R -statistic based on the difference of mean ranks between groups where $R = 1$ means the groups are completely different and $R = 0$ means the groups are identical. The dissimilarity matrix comprises point-level ranks based on differences in point-level species richness. A significant P -value (<0.05) indicates the communities differ in their species composition. Boxplots are used to show variation between groups vs within groups. When communities are dissimilar, the variation between groups (i.e., years-post-harvest or point type) will be greater than within groups. We used function “vegdist” (version 2.5-3, Oksanen et al. 2018) in program R (version 3.5.0, R Core Team 2018) to calculate the dissimilarity matrix from the species compositions at each point.

Nonmetric multidimensional scaling (NMDS) was used to visualize the community structure data used in the ANOSIM test for years-post-harvest and point type (i.e., 7 ordinations). This ordination technique represents communities in multidimensional space using a reduced number of dimensions and shows clustering of data points (here, avian species) with similar relationships to chosen variables. We used the “metaMDS” function in package vegan (version 2.5-3, Oksanen et al. 2018) in program R (version 3.5.0, R Core Team 2018). We then used the “ordisurf” and “envifit” functions in vegan to assess the relationships between the avian community and vegetation variables. These functions correlate environmental variables with the ordination scores. Ordisurf fits a smooth surface using generalized additive modeling with thin plate splines (Oksanen et al. 2018) and envifit finds the direction of maximum correlation for vectors. The latter function uses a permutation test to assess the significance of the vectors. For post-harvest ordinations, we fit all vegetation variables from Table 2 except % basal area of small trees. We evaluated the correlation (R^2) between the environmental variables and the ordination patterns, and tested

for statistical significance. We used $n=999$ permutations for the envifit permutation testing procedure.

3. Results

3.1. *Vegetation*

Within each harvest stand on each study area except GL, basal area was decreased substantially in relation to the unharvested reference stands. Basal area at harvested points was reduced by 13% at GL and by 35–60% (mean 41%) at the remaining study areas. Basal area at reference points was 24.4–37.8 m²/ha. At harvested points, post-harvest basal area was 7.0–25.3 m²/ha at harvest interior points and 18.1–27.0 m²/ha at harvest edge points. We recorded 33 tree species pre-harvest and 37 species post-harvest (Appendix B). Pre-harvest, the dominant tree species (i.e., those with highest basal area), in order, were chestnut oak, red maple, northern red oak, tulip poplar, and white oak. Post-harvest, the same 5 species were dominant, but there were fewer northern red oak than tulip poplar.

3.2. *Territory density*

Years-post-harvest had a positive effect on Eastern Towhee, Indigo Bunting, and Hooded Warbler mean territory density (Table 5). From pre-harvest to 3 years post-harvest, Eastern Towhee increased from 0.06 ± 0.03 to 0.67 ± 0.09 territories/ha and Hooded Warbler increased from 0.10 ± 0.04 to 0.93 ± 0.29 territories/ha (Fig. 3). Indigo Bunting territory density increased from 0.0 pre-harvest to 0.64 ± 0.14 territories/ha 3 years post-harvest. Wood Thrush mean territory density declined 45% between pre- and 1 year post-harvest, and then remained the same across years-post-harvest (Fig. 3).

3.3. *Detection probability*

The top detection model for Eastern Towhee and Indigo Bunting abundance included observer and ordinal date. The top detection model for Hooded Warbler included observer and noise. The top detection models for Scarlet Tanager included all detection covariates and for Wood Thrush included observer, ordinal date, and time-since-sunrise (Table 4). The top detection model for each species was included in all subsequent model sets tested.

3.4. Point count analysis

3.4.1. Model set 1: Cerulean Warbler variables

Model selection results for the first model set indicated that point type was the most important variable influencing abundance of Eastern Towhee, Indigo Bunting, Hooded Warbler, and Wood Thrush (Table 4). Hooded Warbler increased in abundance at all three point types. Eastern Towhee and Indigo Bunting increased in abundance at harvest interior points and decreased at reference points; Indigo Bunting also increased at harvest edge points whereas Eastern Towhee abundance remained the same (Table 6; Fig. 4). Wood Thrush abundance decreased at harvest interior points and increased at reference points (Fig. 4). Eastern Towhee ($\Delta AICc = 0.78$) abundance also was negatively influenced by *bapref* (Table 6). Hooded Warbler ($\Delta AICc = 0.06$; negative slope) and Scarlet Tanager (positive slope) abundance was influenced by *cwlarge*. All relationships were significant based on 95% confidence intervals that did not include zero, except for Scarlet Tanager's relationship with *cwlarge* and Wood Thrush's relationship to harvest edge points (Table 6). Variables from the top models were incorporated into model set 3 analyses for each species.

3.4.2. Model set 2: years-post-harvest models

The interactive relationship between point type and years-post-harvest was included in the top model for 4 of the 5 species, indicating that response to point type was dependent on years-post-harvest (Table 4, Table 7). The top model for Scarlet Tanager included years-post-harvest alone, and the additive relationship had nearly equal support. Eastern Towhee, Indigo Bunting, and Hooded Warbler increased at harvest interior and harvest edge points as years-post-harvest progressed, but Eastern Towhee and Indigo Bunting decreased at reference points (Table 7; Fig. 4). Hooded Warbler initially decreased at reference points, but rebounded and increased some with years-post-harvest. Conversely, Wood Thrush decreased at harvest interior and harvest edge points with years-post-harvest and increased at reference points. Scarlet Tanager had a significant negative relationship with years-post-harvest, a negative relationship at harvest interior, and a positive relationship at harvest edge and reference points; however, none of the relationships with point type were significant (Table 7; Fig. 4).

3.4.3. Model set 3: species-specific variables

Basal area or the quadratic form of basal area was included in the top models for Eastern Towhee, Indigo Bunting, Hooded Warbler, and Wood Thrush (Table 4). Each species had a negative relationship to basal area (ba) or ba^2 , except Wood Thrush which showed a positive relationship; 95% CI for Indigo Bunting, Hooded Warbler, and Wood Thrush did not include zero, indicating their significance (Table 8). At harvested points post-harvest, Eastern Towhee abundance peaked at 15.5 m²/ha basal area and Indigo Bunting and Hooded Warbler abundance was highest where basal area was <15 m²/ha (Fig. 5). Wood Thrush abundance was highest where basal area at harvested points was 20.1–25.3 m²/ha. Tree species richness was the most important variable for Scarlet Tanager (Table 4) and was significantly positive (Table 8). None of the other 10 variables were influential on our focal species' abundance.

3.5. Community structure

We detected 80 species of breeding birds within 50 m of point count stations 2013–2017 that were well-sampled by point counts and available for community structure analysis (Appendix A). Pre-harvest, the most abundant species were Ovenbird (*Seiurus aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), and American Redstart (*Setophaga ruticilla*). Post-harvest, the most abundant species were Red-eyed Vireo, Ovenbird, and Scarlet Tanager; Red-eyed Vireos were detected in 93% of the 795 samples. The songbird community structure did not differ among point types pre-harvest ($R = 0.006$, $P = 0.372$). However, the songbird community structure was progressively different among point types 1 year post-harvest ($R = 0.074$, $P = 0.002$), 2 years post-harvest ($R = 0.188$, $P = 0.001$), and 3 years post-harvest ($R = 0.309$, $P = 0.001$), based on increasing R -values (Fig. 6). Within point types (Fig. 7), the songbird community structure was different among the 0–3 post-harvest years at harvest interior ($R = 0.181$, $P = 0.001$) and harvest edge points ($R = 0.04$, $P = 0.025$), but similar at reference points ($R = 0.004$, $P = 0.34$). Although R -values were small, indicating small differences, the songbird community at harvest interior points was the most dissimilar among years of sampling (Fig. 7).

Two- to 8-dimensional solutions were required for 6 of the 7 ordinations for the avian community; NMDS for 2 years post-harvest did not converge. These dimensions sufficiently characterized the avian community structure based on scree plots (all stress levels were

<0.20). Of the 10 variables tested on pre- and post-harvest avian communities, 4 showed the strongest fit for the avian community data: % basal area of tree species avoided by ceruleans, % basal area of medium-sized trees (7.6–22.9 cm dbh), tree species richness, and overall mean basal area (Table 9). For point type, mean basal area of medium-sized trees (7.6–22.9 cm dbh; harvest interior points) and % basal area of tree species avoided by ceruleans (harvest edge and reference points) had the strongest influence on the avian community structure. The effect of mean basal area was also strong at harvest interior points ($R^2 = 0.3254$, $P = 0.001$) compared to harvest edge ($R^2 = 0.1339$, $P = 0.001$) and reference points ($R^2 = 0.0560$, $P = 0.001$). Pre-harvest, the strongest influence on the avian community structure was % basal area of tree species avoided by ceruleans, whereas tree species richness and overall mean basal area influenced the community structure 1 year and 3 years post-harvest, respectively (Table 9).

Based on the results of the community structure analysis, we show the ordination for 3 years post-harvest and overlaid the surface fit of basal area with the point type groupings (Fig. 8). Early successional, gap-dependent, and shrubland species such as Eastern Towhee (EATO), Indigo Bunting (INBU), American Goldfinch (AMGO; *Spinus tristis*), Chestnut-sided Warbler (CWSA; *Setophaga pensylvanica*), Common Yellowthroat (COYE; *Geothlypis trichas*), and Chipping Sparrow (CHSP; *Spizella passerina*), were located at the low end of basal area (Fig. 8). The remaining species were associated with intermediate to higher basal area available at our study areas. Species clustered at the center of the ordination graphs can be found in intermediate levels of basal area such as Cerulean Warbler (CERW), Blue-gray Gnatcatcher (BGGN; *Polioptila caerulea*), and American Redstart (AMRE). Species associated with closed canopy forests (e.g., Wood Thrush [WOTH], Ovenbird [OVEN], Yellow-billed Cuckoo [YBCU; *Coccyzus americanus*], Acadian Flycatcher [ACFL; *Empidonax virescens*], Worm-eating Warbler [WEWA]) were located at the high end of basal area. (Fig. 8).

4. Discussion

Disturbed forests typically have higher species diversity because of the heterogeneity and diversity of available habitat (Greenberg et al. 2014, Annand and Thompson 1997, McDermott and Wood 2009, Duguay et al. 2001, Newell and Rodewald 2012). The harvests

implemented for our research created mosaics of varying residual basal area, canopy openness, and vertical structure, ranging from sparsely vegetated clearcuts immediately following harvests, to a dense understory of regenerating pawpaw (*Asimina triloba*) beneath a group selection harvest, to mature closed canopy stands that were left unharvested. Similarity in the avian community among point types pre-harvest confirms that any post-harvest differences were not biased by placement of point types in inherently different pre-harvest conditions. However, post-harvest, the avian community composition at our study areas significantly differed by point type. Thus, the harvest mosaics provided breeding habitat for a diversity of songbird species that require very different conditions for their needs. Additionally, the avian community structure among point types was the most dissimilar 3 years post-harvest, indicating that our harvests attracted new species over time as components of the habitat changed (e.g., regeneration of the understory or clearcuts). We detected 16 species post-harvest that were not detected pre-harvest indicating that the mosaics provided habitat for species that were not previously supported by the mature, closed canopy stands. Although it should be noted that 5 of those species were detected only at CR and DY which were only sampled post-harvest and we do not have data for the pre-harvest avian communities. Additionally, 2 of our study areas were in Northern Pennsylvania where the bird community can differ from the general area of the other study areas. Two species of warbler were found only at the Pennsylvania study areas, post-harvest.

Canopy gaps allow sunlight to penetrate the overstory, increasing the vigor of desired seed trees, and to reach the forest floor where the sunlight aids in regeneration of multiple strata in the mid- and understories. The regeneration of this vegetation supports invertebrate prey species and early successional fruiting vines and shrubs and thus spatially diverse foraging opportunities for insectivorous and frugivorous birds (Hoppes 1987, Duguay et al. 2001, McDermott and Wood 2010, Newell and Rodewald 2012, Nadeau et al. 2015). Regeneration also provides nest structure for ground- and understory-nesting species (Bell and Whitmore 1997, Chiver et al. 2011, Morris et al. 2013, Greenberg et al. 2014, pers. obs.) and partial harvests create habitat for breeding birds associated with shrubby, early successional habitat and young forests (Becker et al. 2011, Newell and Rodewald 2012, Morris et al. 2013, Sheehan et al. 2013, Greenberg et al. 2014). Avian community structure was most dissimilar among years-post-harvest at harvest interior points and among point

types 3 years post-harvest, based on our ANOSIM tests, which we posit is related to differences in basal area or canopy structure and regeneration. Greater changes in the community structure may be more evident at individual study areas and in the future as succession progresses further.

Three of our focal species rely on a developed understory for breeding, so a lag in response was expected for Eastern Towhee, Indigo Bunting, and Hooded Warbler. Indigo Bunting was uncommon at our study areas pre-harvest and we did not detect any territories until post-harvest. Eastern Towhee and Hooded Warbler were also absent from or in very low densities pre-harvest. Regeneration at DY, for example, resulted in nearly impenetrable swaths of *Rubus* sp., often ≥ 4 feet high, which likely aided in nest protection and provided abundant refuge and food resources for fledglings and post-breeding adults (McDermott and Wood 2010, Greenlaw 2015). As expected, these three species that rely on a developed understory showed significant positive increases at harvest interior and harvest edge points as time progressed.

Eastern Towhee, Indigo Bunting, and Hooded Warbler abundances were influenced more by the overall canopy disturbance than specific vegetation characteristics as indicated by the importance of point type and basal area to their abundances, relative to the other variables tested. Access to openings may be more important than specific vegetation structure. However, openings in mature forests inherently provide heterogeneous structure post-harvest (i.e., the variables tested in model set 3, species-specific models). As such, we expected at least some of the multiple variables describing that structure (Table 2) to influence abundances of these three species. However, none were deemed important in model selection and it is possible that because this study was designed specifically for Cerulean Warbler habitat management, we needed to measure different characteristics for the focal species, or that conditions within harvested stands provided appropriate habitat irrespective of measurable differences in characteristics. It may require more time after harvesting for vegetation to grow enough to detect differences in variables. For instance, the amount of basal area of small (< 7.6 cm dbh) or medium (7.6–22.9 cm dbh) stems may not increase significantly between 2 and 3 years post-harvest. The substantial regeneration of *Rubus* spp. and pawpaw post-harvest would not have been captured by measuring vegetation with a 10 factor prism. Based on our results, targeting the range of basal areas preferred by these

species should inherently provide conditions these species require for breeding. Specifically, providing basal area up to 15 m²/ha provided the best conditions for Eastern Towhee, Indigo Bunting, and Hooded Warbler at our study areas. This closely aligns with the Guidelines study in which the highest abundance or territory density of Eastern Towhee was where basal area was <13 m²/ha and <18 m²/ha for Indigo Bunting and Hooded Warbler (Wood et al. 2013).

Scarlet Tanager and more so Wood Thrush were at least in part negatively impacted by the harvests. However, it appeared that Wood Thrush and Scarlet Tanager were able to find suitable habitat interspersed with the harvests by moving from harvested points to reference points in the first year post-harvest. While Wood Thrush and Scarlet Tanager decreased in abundance at harvest interior points, their declines at harvest edge points were not as steep and Scarlet Tanager subsequently increased in abundance at harvest edge points between 2 years and 3 years post-harvest. Wood Thrush experienced a fairly steep increase at reference points among 1 and 3 years post-harvest (Table 7; Figs. 3–4). Similarly, the harvest mosaics retained species such as Worm-eating Warbler, Ovenbird, and Acadian Flycatcher, which are mature forest species. Although we did not assess nesting success or track fledglings, the regeneration conditions described above should provide abundant post-fledging refuge for forest interior species, such as Ovenbird and Wood Thrush, whose fledglings inhabit young forests or regenerating openings prior to southern migration (Pagen et al. 2000, Vitz and Rodewald 2006, Evans et al. 2011, Streby and Andersen 2012, Porneluzi et al. 2014, Raybuck 2016, Ruhl et al. 2018). Additionally, post-breeding adults may use regenerating harvests where prey abundance can be greater than in mature forest conditions. Capture rates of adults of mature forest species was positively related to increasing vertical complexity and negatively related to increasing basal area at one study in West Virginia (McDermott and Wood 2010).

5. Conclusions

This study has important implications for Wood Thrush habitat management. Given that Wood Thrush is a species of conservation concern and its densities are highest in the central Appalachian region (Lambert et al. 2017), they may require extra consideration when designing silvicultural prescriptions. Within the Appalachian Mountains BCR, it has declined

by 34% since 1970 (Rosenberg et al. 2016). Wood Thrush have an estimated half-life of 43 years by PIF meaning that under status quo management, Wood Thrush populations would decline by an additional 50% in 43 years (Rosenberg et al. 2016). Although Wood Thrush territory density initially decreased by 45% and territory densities did not rebound by the end of the study, they remained on the study areas and increased at reference points.

Additionally, our regenerating harvests may have provided abundant post-fledging, post-breeding habitat for birds preparing for southward migration, supported by the lack of extirpation from the study areas. We emphasize the importance of providing spatially and temporally diverse harvest mosaics to provide breeding or post-breeding habitat for species of greatest conservation need whose ranges overlap but require different habitat characteristics during the breeding season. Providing breeding habitat for Cerulean Warblers at the higher end of their preferred basal area would be less detrimental to Wood Thrush.

Integration of conservation and management of avian species that use different forest age classes is possible by providing a variety of habitat types through a shifting mosaic (Anders et al. 1998, Askins 2001, Greenberg et al. 2016, Rosenberg et al. 2016, Ruhl et al. 2018), attainable with operational silviculture techniques. Implementing harvests based on the Cerulean Warbler Management Guidelines for Enhancing Breeding Habitat in Appalachian Hardwood Forests (Wood et al. 2013), but without restrictions for specific topographic conditions, led to increases in abundance and territory density of songbird species that span a range of seral stages. Further, the results of our study also show that Wildlife Management Areas and State Forests, which are managed for multiple types of public use, may simultaneously be managed for declining avian species of conservation need.

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Table 1. Summary of study areas sampled to evaluate avian response to harvests at 9 study areas in the central Appalachian region during 2013–2017. Point count surveys and territory mapping were conducted pre- and post-harvest at 7 study areas and point count surveys for 3 years post-harvest at 2 additional study areas harvested prior to the initiation of our study. Point counts were surveyed up to 3 years post-harvest.

Point type with # sampled								
State	Study Area ¹	Harvest interior	Harvest edge	Reference	Study Area Size (ha)	Harvested Area (ha)	Harvest year ²	Years-post-harvest ³
Pre-post study areas								
KY	Grayson Lake WMA (GL)	7	7	7	92	16.4	2013	1–3 (n=14)
PA	Clear Creek SF (CC)	3	2	9	79	22.0	2014	1–2 (n=5)
PA	Rabbit Hole SGL 86 (RH)	-	4	1	32	19.7	2014	1–2 (n=4)
VA	Gathright WMA (GA)	4	1	6	47	35.5	2015	2 (n=5)
VA	Highland WMA (HI)	9	6	22	224	57.1	2014/ 2015/ 2016	1 (n=15) 2 (n=8) 3 (n=3)
WV	Stonewall Jackson Lake WMA (SJ) ⁴	5	5	9	92	32.0	2014/ 2015	1 (n=9) 2 (n=7)
WV	Wolf Creek (WC) ⁴	4	7	16	111	26.6	2013/ 2014	1–2 (n=11) 3 (n=5)
Post-only study areas								
WV	Coopers Rock SF (CR) ⁴	16	5	18	186	77.2	2012	1–3 (n=21)
WV	Dynamite (DY) ⁴	7	10	17	163	39.8	2012	1–3 (n=17)

¹WMA=Wildlife Management Area; SF=State Forest; SGL = State Game Land

²Harvests occurred during the winter following the breeding season indicated (i.e., a 2013 harvest occurred during winter 2013–2014). At some study areas, harvests were completed over 2 winters.

³n = number of harvested points sampled within each year-post-harvest; all reference points were sampled every year post-harvest.

⁴Study areas with territory mapping plots.

Table 2. Survey and study area variables used to model detection probability and abundance, respectively, of 5 songbird species in the central Appalachian region at 9 harvested study areas 2013–2017.

Code	Covariate Type	Variable Description	Habitat Component or Use in Models
noise	Survey	Noise during visits (levels 0-4)	Detection probability
obsv	Survey	3 observer groups based on experience with bird ID and sampling methods	Detection probability
ord	Survey	Ordinal date	Detection probability
tssr	Survey	Time-since-sunrise	Detection probability
asp	Study area	Beers aspect (0-2; 0 is xeric and 2 is mesic)	Topography
slope	Study area	Slope position (cove, middle, ridge)	Topography
SA	Study area	Study area; 7 pre-post, 2 post-only	Inherent regional differences
pttype	Study area	Harvest interior, harvest edge, reference	Treatment
year	Study area	Calendar year (2013–2017)	Inherent annual differences
yph	Study area	Years-post-harvest (1–3 years)	Relationship to regeneration
rich	Vegetation	Tree species richness of stems ≥ 10 cm dbh	Relationship to tree species richness
mid	Vegetation	% basal area (m^2/ha) of tree stems ≥ 10 cm dbh with canopy position intermediate or overtopped	Midstory structure
upper	Vegetation	% basal area (m^2/ha) of tree stems ≥ 10 cm dbh with canopy position co-dominant, dominant, or open growth	Upper canopy structure
small	Vegetation	Mean basal area (m^2/ha) of tree stems 1–7.6 cm dbh	Relationship to smallest stems within prism plots
medium	Vegetation	Mean basal area (m^2/ha) of tree stems 7.6–22.9 cm dbh	Relationship to sapling- and pole-sized trees
large	Vegetation	% basal area (m^2/ha) of large diameter trees ≥ 22.9 cm dbh	Relationship to sawtimber
cwlarge	Vegetation	% basal area (m^2/ha) of large diameter trees ≥ 40.6 cm dbh	Relationship to Cerulean Warbler (<i>Setophaga cerulea</i>) nest trees
ba ¹	Vegetation	Mean basal area (m^2/ha) of all tree stems ≥ 10 cm dbh	Canopy structure
bapref	Vegetation	% of basal area (m^2/ha) composed of sugar maple, hickories, white oak group stems ≥ 10 cm dbh	Relationship to tree species preferred by Cerulean Warbler
baavoid	Vegetation	% basal area (m^2/ha) composed of red maple, red oak group stems ≥ 10 cm dbh	Relationship to tree species avoided by Cerulean Warbler
snag	Vegetation	Basal area of snags ≥ 10 cm dbh	Proxy for canopy openness for gap species

¹Linear and quadratic terms were tested

Table 3. Variables used to model response in abundance of 5 songbird species to timber harvests in the central Appalachian region at 9 harvested study areas 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH). Variables were tested individually or in simple additive models. Model set 1 includes variables that were important to Cerulean Warbler abundance post-harvest at the same study areas (Nareff et al. 2019). Model set 2 includes variables to assess the response to timber harvests over years-post-harvest. Model set 3 includes variables that may be important to the individual focal species based on their breeding habitat preferences. Codes for variables are defined in Table 2. Modeling results are reported in Table 4.

EATO	INBU	HOWA	SCTA	WOTH
Model set 1: top Cerulean Warbler variables				
pptype	pptype	pptype	pptype	pptype
bapref	bapref	bapref	bapref	bapref
cwlarge	cwlarge	cwlarge	cwlarge	cwlarge
Model set 2: years-post-harvest models				
pptype+yph	pptype+yph	pptype+yph	pptype+yph	pptype+yph
pptype	pptype	pptype	pptype	pptype
yph	yph	yph	yph	yph
pptype*yph	pptype*yph	pptype*yph	pptype*yph	pptype*yph
Model set 3: species-specific models				
pptype+asp	pptype+asp	pptype+asp	pptype+asp	pptype+asp
pptype+slope	pptype+slope	pptype+slope	pptype+slope	pptype+slope
pptype	pptype	pptype	pptype	pptype
asp	asp	asp	asp	asp
slope	slope	slope	slope	slope
ba	ba	ba	ba	ba
ba ²	ba ²	ba ²	ba ²	ba ²
mid	mid	mid	mid	mid
upper	upper	upper	upper	upper
small	small	small	small	small
med	med	med	med	med
large	large	large	large	large
—	—	cwlarge	cwlarge	cwlarge
pptype+snag	pptype+snag	pptype+snag	—	—
—	—	—	rich	rich
—	—	—	bapref	—
—	—	—	baavoid	—

Table 4. Model selection process to determine the most parsimonious *N*-mixture models that explain change in 5 focal species' abundances from pre- to post-harvest and among years-post-harvest at 9 study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Modeling was based on 795 samples from 207 sample points (pre-harvest n=134, 1 year post-harvest n=207, 2 years post-harvest n=184, 3 years post-harvest n=123). K is the number of parameters in a model, AICc is the Akaike's Information Criterion value for small sample sizes, which measures the fit of a model relative to other models, $\Delta AICc$ is the difference between each model's AICc value and the lowest AICc value in the candidate set, and w_i is the Akaike weight of each model in relation to the entire candidate set. Codes for variables are defined in Table 2.

Eastern Towhee				
Model set 1: top Cerulean Warbler variables	K	AIC _c	$\Delta AICc$	w_i
p (obsv+ord) λ (SA+year+yph+pttype)	20	3016.38	0.00	0.60
p (obsv+ord) λ (SA+year+yph+bapref)	20	3017.16	0.78	0.40
p (obsv+ord) λ (SA+year+yph+cwsaw)	20	3036.90	20.52	0.00
Model set 2: years-post-harvest models				
p (obsv+ord) λ (SA+year+pttype*yph)	23	2953.81	0.00	1.00
p (obsv+ord) λ (SA+year+pttype+yph)	21	3003.63	49.82	0.00
p (obsv+ord) λ (SA+year+pttype)	20	3016.38	62.57	0.00
p (obsv+ord) λ (SA+year+yph)	19	3035.16	81.35	0.00
Model set 3: species-specific models				
p (obsv+ord) λ (SA+year+yph+ba ²)	21	2908.60	0.00	0.74
p (obsv+ord) λ (SA+year+yph+ba)	20	2910.73	2.13	0.26
p (obsv+ord) λ (SA+year+yph+pttype+snag)	22	3005.59	96.57	0.00
p (obsv+ord) λ (SA+year+yph+pttype+asp)	22	3005.72	97.82	0.00
p (obsv+ord) λ (SA+year+yph+pttype+slope)	23	3007.07	98.82	0.00
p (obsv+ord) λ (SA+year+yph+pttype)	20	3016.38	107.57	0.00
p (obsv+ord) λ (SA+year+yph+med)	20	3021.67	113.82	0.00
p (obsv+ord) λ (SA+year+yph+mid)	20	3032.37	123.82	0.00
p (obsv+ord) λ (SA+year+yph+small)	20	3032.70	124.82	0.00
p (obsv+ord) λ (SA+year+yph+upper)	20	3033.29	124.82	0.00
p (obsv+ord) λ (SA+year+yph+asp)	20	3037.10	128.57	0.00
p (obsv+ord) λ (SA+year+yph+large)	20	3037.18	128.57	0.00
p (obsv+ord) λ (SA+year+yph+slope)	21	3037.58	128.35	0.00

¹ p = detection probability, λ = initial abundance

Table 4. continued

Indigo Bunting				
Model set 1: top Cerulean Warbler variables	K	AIC _c	ΔAIC _c	w _i
p (obsv+ord) λ (SA+year+yph+pttype)	20	1750.70	0.00	1.00
p (obsv+ord) λ (SA+year+yph+bapref)	20	1825.63	74.92	0.00
p (obsv+ord) λ (SA+year+yph+cwsaw)	20	1843.90	93.20	0.00
Model set 2: years-post-harvest models				
p (obsv+ord) λ (SA+year+pttype*yph)	23	1679.21	0.00	1.00
p (obsv+ord) λ (SA+year+pttype+yph)	21	1741.82	62.61	0.00
p (obsv+ord) λ (SA+year+pttype)	20	1750.70	71.49	0.00
p (obsv+ord) λ (SA+year+yph)	19	1842.36	163.15	0.00
Model set 3: species-specific models				
p (obsv+ord) λ (SA+year+yph+ba)	20	1680.63	0.00	0.74
p (obsv+ord) λ (SA+year+yph+ba ²)	21	1682.94	2.31	0.26
p (obsv+ord) λ (SA+year+yph+pttype+slope)	23	1736.53	55.90	0.00
p (obsv+ord) λ (SA+year+yph+pttype+asp)	22	1736.82	56.19	0.00
p (obsv+ord) λ (SA+year+yph+pttype+snag)	22	1739.14	58.51	0.00
p (obsv+ord) λ (SA+year+yph+pttype)	20	1750.70	70.07	0.00
p (obsv+ord) λ (SA+year+yph+med)	20	1811.61	130.98	0.00
p (obsv+ord) λ (SA+year+yph+small)	20	1831.88	151.25	0.00
p (obsv+ord) λ (SA+year+yph+slope)	21	1840.67	160.04	0.00
p (obsv+ord) λ (SA+year+yph+asp)	20	1841.97	161.34	0.00
p (obsv+ord) λ (SA+year+yph+mid)	20	1843.02	162.39	0.00
p (obsv+ord) λ (SA+year+yph+upper)	20	1844.31	163.68	0.00
p (obsv+ord) λ (SA+year+yph+large)	20	1844.34	163.71	0.00

¹ p = detection probability, λ = initial abundance

Table 4. continued

Hooded Warbler				
Model set 1: top Cerulean Warbler variables	K	AIC _c	Δ AIC _c	w _i
p (obsv+noise) λ (SA+year+yph+pttype)	19	2890.74	0.00	0.48
p (obsv+noise) λ (SA+year+yph+cwsaw)	19	2890.80	0.06	0.47
p (obsv+noise) λ (SA+year+yph+bapref)	19	2895.30	4.56	0.05
Model set 2: years-post-harvest models				
p (obsv+noise) λ (SA+year+pttype*yph)	22	2884.27	0.00	0.88
p (obsv+noise) λ (SA+year+pttype+yph)	20	2889.03	4.75	0.08
p (obsv+noise) λ (SA+year+pttype)	19	2890.74	6.47	0.03
p (obsv+noise) λ (SA+year+yph)	18	2894.27	10.00	0.01
Model set 3: species-specific models				
p (obsv+noise) λ (SA+year+yph+ba)	19	1680.63	0.00	0.65
p (obsv+noise) λ (SA+year+yph+ba ²)	20	1682.94	1.63	0.29
p (obsv+noise) λ (SA+year+yph+large)	19	1736.82	4.87	0.06
p (obsv+noise) λ (SA+year+yph+pttype+snag)	21	1739.14	13.23	0.00
p (obsv+noise) λ (SA+year+yph+pttype)	19	1750.70	13.82	0.00
p (obsv+noise) λ (SA+year+yph+cwlarge)	19	1811.61	13.88	0.00
p (obsv+noise) λ (SA+year+yph+pttype+asp)	21	1831.88	14.10	0.00
p (obsv+noise) λ (SA+year+yph+pttype+slope)	22	1840.67	14.40	0.00
p (obsv+noise) λ (SA+year+yph+med)	19	1841.97	15.00	0.00
p (obsv+noise) λ (SA+year+yph+mid)	19	1843.02	16.48	0.00
p (obsv+noise) λ (SA+year+yph+small)	19	1844.31	17.62	0.00
p (obsv+noise) λ (SA+year+yph+upper)	19	1844.31	18.41	0.00
p (obsv+noise) λ (SA+year+yph+asp)	19	1844.31	19.40	0.00
p (obsv+noise) λ (SA+year+yph+slope)	20	1844.34	19.52	0.00

¹ p = detection probability, λ = initial abundance

Table 4. continued

Scarlet Tanager				
Model set 1: top Cerulean Warbler variables	K	AIC _c	ΔAIC _c	w _i
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+bapref)	22	3483.19	0.00	0.66
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+cwsaw)	22	3484.76	1.57	0.30
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+pttype)	22	3488.56	5.36	0.04
Model set 2: years-post-harvest models				
p (obsv+noise+ordinal+tssr) λ (SA+year+yph)	21	3486.24	0.00	0.44
p (obsv+noise+ordinal+tssr) λ (SA+year+pttype+yph)	25	3486.34	0.13	0.42
p (obsv+noise+ordinal+tssr) λ (SA+year+pttype)	23	3486.38	2.31	0.14
p (obsv+noise+ordinal+tssr) λ (SA+year+pttype*yph)	22	3488.56	18.21	0.00
Model set 3: species-specific models				
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+rich)	21	3467.64	0.00	1.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+ba ²)	22	3479.04	11.40	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+ba)	21	3480.53	12.89	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+bapref)	21	3481.08	13.44	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+cwlarge)	21	3482.64	15.00	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+large)	21	3484.22	16.58	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+small)	21	3484.52	16.88	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+baavoid)	21	3484.99	17.45	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+mid)	21	3485.38	17.74	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+med)	21	3485.56	17.92	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+pttype+asp)	23	3485.63	17.99	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+asp)	21	3485.88	18.24	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+upper)	21	3485.92	18.27	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+slope)	22	3486.02	18.38	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+pttype+slope)	24	3486.20	18.56	0.00
p (obsv+noise+ordinal+tssr) λ (SA+year+yph+pttype)	21	3486.44	18.80	0.00

¹ p = detection probability, λ = initial abundance

Table 4. continued

Wood Thrush				
Model set 1: top Cerulean Warbler variables	K	AIC _c	ΔAIC _c	w _i
p (obsv+ordinal+tssr) λ (year+yph+pttype)	19	2217.85	0.00	0.98
p (obsv+ordinal+tssr) λ (year+yph+bapref)	19	2227.12	9.27	0.01
p (obsv+ordinal+tssr) λ (year+yph+cwsaw)	19	2228.23	10.38	0.01
Model set 2: years-post-harvest models				
p (obsv+ordinal+tssr) λ (year+pttype*yph)	21	2186.42	0.00	1.00
p (obsv+ordinal+tssr) λ (year+pttype+yph)	20	2217.10	30.63	0.00
p (obsv+ordinal+tssr) λ (year+pttype)	19	2217.85	31.43	0.00
p (obsv+ordinal+tssr) λ (year+yph)	18	2226.60	40.18	0.00
Model set 3: species-specific models				
p (obsv+ordinal+tssr) λ (year+yph+ba)	19	2193.86	0.00	0.96
p (obsv+ordinal+tssr) λ (year+yph+ba ²)	19	2200.14	9.28	0.04
p (obsv+ordinal+tssr) λ (year+yph+pttype+slope)	22	2212.65	18.79	0.00
p (obsv+ordinal+tssr) λ (year+yph+pttype)	19	2217.85	23.99	0.00
p (obsv+ordinal+tssr) λ (year+yph+rich)	19	2217.95	24.09	0.00
p (obsv+ordinal+tssr) λ (year+yph+pttype+asp)	21	2218.67	24.81	0.00
p (obsv+ordinal+tssr) λ (year+yph+slope)	20	2223.31	19.45	0.00
p (obsv+ordinal+tssr) λ (year+yph+med)	19	2223.46	29.60	0.00
p (obsv+ordinal+tssr) λ (year+yph+mid)	19	2225.70	31.84	0.00
p (obsv+ordinal+tssr) λ (year+yph+small)	19	2227.07	33.21	0.00
p (obsv+ordinal+tssr) λ (year+yph+upper)	19	2227.48	33.61	0.00
p (obsv+ordinal+tssr) λ (year+yph+cwlarge)	19	2228.23	34.37	0.00
p (obsv+ordinal+tssr) λ (year+yph+asp)	19	2228.59	34.73	0.00
p (obsv+ordinal+tssr) λ (year+yph+large)	19	2228.69	34.83	0.00

¹ p = detection probability, λ = initial abundance

Table 5. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from mixed effects models examining change in territory density from pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 4 harvested study areas in West Virginia 2013–2016.

Species	β estimate	SE	Lower 95% CI	Upper 95% CI
EATO	0.19	0.03	0.13	0.25
INBU	0.16	0.04	0.09	0.24
HOWA	0.26	0.07	0.11	0.41
WOTH	-0.04	0.02	-0.08	0.01

Table 6. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked (i.e., $\Delta\text{AICc} < 2$) *N*-mixture models estimating abundance pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Variables tested were from the top ranked models explaining Cerulean Warbler (*Setophaga cerulea*) abundance in 2013–2017 (Nareff et al. 2019). Codes for variables in models are defined in Table 2.

Species	Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI
Model set 1: top Cerulean Warbler variables					
EATO	pttype				
	Harvest interior*	0.6	0.1	0.4	0.8
	Harvest edge*	0.3	0.1	0.03	0.6
	Reference*	-0.6	0.1	-0.8	-0.4
	bapref*	-1.4	0.3	-2.1	-0.8
INBU	pttype				
	Harvest interior*	1.7	0.2	1.4	2.0
	Harvest edge*	1.0	0.2	0.6	1.4
	Reference*	-1.7	0.2	-2.0	-1.4
HOWA	pttype				
	Harvest interior*	0.3	0.1	0.1	0.4
	Harvest edge*	0.3	0.1	0.01	0.5
	Reference*	-0.3	0.1	-0.5	-0.1
	cwlarge*	-0.6	0.3	-1.1	-0.1
SCTA	bapref*	0.6	0.3	0.1	1.1
	cwlarge	0.4	0.2	-0.01	0.8
WOTH	pttype				
	Harvest interior*	-0.5	0.1	-0.7	-0.2
	Harvest edge	0.03	0.1	-0.2	0.3
	Reference*	0.5	0.1	0.2	0.7

*Confidence intervals do not include zero, indicating significance

Table 7. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked *N*-mixture models estimating abundance by years-post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2.

Species	Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI
Model set 2: years-post-harvest models					
EATO	pttype x yph				
	Harvest interior x yph*	0.7	0.1	0.5	0.9
	Harvest edge x yph*	0.5	0.1	0.3	0.7
	Reference x yph*	-0.7	0.1	-0.9	-0.5
	yph*	0.7	0.1	0.5	0.9
INBU	pttype x yph				
	Harvest interior x yph*	1.3	0.2	0.9	1.6
	Harvest edge x yph*	1.2	0.2	0.8	1.7
	Reference x yph*	-1.3	0.2	-1.6	-0.9
	yph*	0.7	0.2	0.5	1.1
HOWA	pttype x yph				
	Harvest interior x yph*	0.3	0.1	0.1	0.5
	Harvest edge x yph	0.2	0.1	-0.03	0.4
	Reference x yph*	-0.3	0.1	-0.5	-0.1
	yph*	0.4	0.1	0.1	0.6
SCTA	yph*	-0.2	0.1	-0.3	-0.002
	pttype + yph				
	Harvest interior	-0.2	0.1	-0.3	0.0
	Harvest edge	0.1	0.1	-0.2	0.3
	Reference	0.2	0.1	0.0	0.3
	yph*	-0.1	0.1	-0.5	-0.1
WOTH	pttype x yph				
	Harvest interior x yph*	-0.8	0.1	-1.1	-0.6
	Harvest edge x yph*	-0.4	0.1	-0.6	-0.1
	Reference x yph*	0.8	0.1	0.6	1.1
	yph*	-0.9	0.1	-1.2	-0.5

*Confidence intervals do not include zero, indicating significance

Table 8. Parameter estimates, standard errors (SE), and 95% lower and upper confidence intervals (CI) from top ranked N-mixture models estimating abundance pre- to 3 years post-harvest of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*; SCTA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2.

Species	Parameter	β estimate	SE	Lower 95% CI	Upper 95% CI
Model set 3: species-specific models					
EATO	ba ²	-0.001	0.0	-0.002	0.0
INBU	ba*	-0.1	0.01	-0.1	-0.08
HOWA	ba*	-0.02	0.004	-0.03	-0.01
	ba ²	-0.001	0.0	-0.001	0.0
SCTA	rich*	0.1	0.02	0.04	0.1
WOTH	ba*	0.04	0.01	0.03	0.05

*Confidence intervals do not include zero, indicating significance

Table 9. Fits of variables tested on avian community data by point type (top) and years-post-harvest (bottom; YPH) using non-metric multidimensional scaling (NMDS) ordinations. Models using data from 2 years post-harvest did not converge. Ordinations incorporate the songbird community represented by detections of birds sampled well by point counts (Appendix A) within 50 m of 207 points at 9 harvested study areas in Kentucky, Pennsylvania, Virginia, and West Virginia 2013–2017. Codes for variables in models are defined in Table 2. Bolded values indicated the strongest fits (highest R^2 values).

Variable	Harvest interior		Harvest edge		Reference	
	R^2	P	R^2	P	R^2	P
yph	0.3212	0.001	0.1469	0.001	0.0200	0.020
ba	0.3254	0.001	0.1339	0.001	0.0560	0.001
pref	0.0184	0.122	0.0778	0.005	0.2324	0.001
avoid	0.0940	0.001	0.2513	0.001	0.3421	0.001
large	0.1153	0.001	0.1150	0.001	0.1295	0.001
cwlarge	0.1517	0.001	0.0775	0.006	0.1111	0.001
medium	0.4235	0.001	0.1228	0.001	0.0354	0.001
rich	0.2692	0.001	0.2217	0.001	0.1254	0.001
snag	0.1077	0.001	0.0359	0.081	0.1554	0.001
mid	0.2450	0.001	0.0184	0.273	0.0916	0.001
upper	0.1214	0.001	0.0258	0.152	0.0697	0.001

Variable	Pre-harvest		1YPH		3YPH	
	R^2	P	R^2	P	R^2	P
pttype	0.0415	0.087	0.0464	0.003	0.2666	0.001
ba	0.0225	0.043	0.0603	0.003	0.4221	0.001
pref	0.2245	0.001	0.0361	0.025	0.1376	0.001
avoid	0.3625	0.001	0.0472	0.009	0.1831	0.001
large	0.0930	0.001	0.0756	0.001	0.1176	0.002
cwlarge	0.0360	0.010	0.0620	0.005	0.0672	0.016
medium	0.0990	0.001	0.1132	0.001	0.2880	0.001
rich	0.1358	0.001	0.2062	0.001	0.3531	0.001
snag	0.0448	0.002	0.0241	0.096	0.1525	0.001
mid	0.2323	0.001	0.0491	0.008	0.0653	0.013
upper	0.1381	0.001	0.0387	0.024	0.0823	0.007

Figure 1. Location of the 9 study areas within the Appalachian Mountains Bird Conservation Region (BCR) for this investigation of avian response to harvest treatments. Study areas are Grayson Lake (GL) Wildlife Management Area (WMA) in Kentucky; Rabbit Hole (RH) and Clear Creek State Forest (CCSF) in Pennsylvania; Gathright WMA (GA) and Highland WMA (HI) in Virginia; and Wolf Creek (WC) and Dynamite (DY) at the Elk River WMA, Stonewall Jackson Lake WMA (SJ), and Coopers Rock State Forest (CR) in West Virginia.

Figure 2. Wolf Creek harvest within the Elk River Wildlife Management Area in West Virginia shown as an example of our experimental design and a harvest mosaic. Here, harvest interior, harvest edge, and reference point count locations and territory mapping plots were monitored during 2013–2016 for songbird abundance and territory density across a timber harvest mosaic. Harvests (clear cut [CC], variable retention, single-tree selection, and group selection) are labeled as described by land managers and were not uniform across each harvest block.

Figure 3. Mean territory density (territory/ha) and standard error of Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH) at 4 study areas (n=10 plots) in West Virginia, pre-harvest and 1, 2, and 3 years-post-harvest (YPH).

Figure 4. Abundance (birds/point) of 5 focal songbird species pre-, 1 year (1YPH), 2 years (2YPH), and 3 years (3YPH) post-harvest at 9 study areas in Kentucky (n=1), Pennsylvania (n=2), Virginia (n=2), and West Virginia (n=4) 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*; WOTH). Modeled abundance is based on the top model examining response to years-post-harvest for each species (Table 4).

Figure 5. Abundance (birds/point) of 4 focal songbird species at harvested point counts at 9 study areas in Kentucky (n=1), Pennsylvania (n=2), Virginia (n=2), and West Virginia (n=4) 2013–2017. Species are Eastern Towhee (*Pipilo erythrophthalmus*; EATO), Indigo Bunting (*Passerina cyanea*; INBU), Hooded Warbler (*Setophaga citrina*; HOWA), and Wood Thrush (*Hylocichla mustelina*; WOTH). Modeled abundance is based on the top model examining response to species-specific variables for each species (Table 4).

Figure 6. Analysis of similarity (ANOSIM) was used to test for differences in songbird community structure among point types (harvest interior [H], harvest edge [E], and reference [R]) among pre-harvest (PRE) and 1 year (1YPH), 2 years (2YPH), and 3 years (3YPH) post-harvest at 9 study areas in the central Appalachian region. The songbird community differed among point types all years post-harvest, but was similar pre-harvest. The y-axis shows the dissimilarity rank, calculated based on the species richness at each sample point.

Figure 7. Analysis of similarity (ANOSIM) was used to test for differences in songbird community structure among pre-harvest (0) and years-post-harvest (1–3) at harvest interior (HI), harvest edge (HE), and reference (Ref) point types at 9 study areas in the central Appalachian region. The songbird community differed among pre-harvest and the three years post-harvest at harvest interior and harvest edge points, but was similar at reference points. The y-axis shows the dissimilarity rank, calculated based on the species richness at each sample point.

Figure 8. Non-metric multidimensional scaling (NMDS) was used to ordinate the songbird community 3 years post-harvest at 9 study areas in the central Appalachian region. The ordination shows alpha codes for avian species (Appendix A) and the significant fit of the mean basal area ($\geq 10 \text{ m}^2/\text{ha}$) surface gradient. The avian community is grouped by point type: harvest interior (red), harvest edge (blue), and reference (black).

Appendix A. All avian species detected on unlimited radius point counts pre- and post-harvest, including their common and scientific names and American Ornithological Society (AOS) banding codes. Species in bold were included in one-way analysis of similarity on the avian community data to test for differences in the avian community structure among point types. Forest type describes where the species most commonly breeds: mature forest (mature), early successional (early), mid-successional (mid), gap specialist (gap).

AOS code	Common Name	Scientific Name	Forest type
ACFL	Acadian Flycatcher	<i>Empidonax virescens</i>	Mature
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	
AMGO	American Goldfinch	<i>Spinus tristis</i>	Early
AMRE	American Redstart	<i>Setophaga ruticilla</i>	Mid
AMRO	American Robin	<i>Turdus migratorius</i>	Mid–mature
BAEA	Bald Eagle	<i>Haliaeetus leucocephalus</i>	
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	Early–mid
BAWW	Black-and-white Warbler	<i>Mniotilta varia</i>	Mid
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	Early–mid
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	Mature
BDOW	Barred Owl	<i>Strix varia</i>	
BEKI	Belted Kingfisher	<i>Megasceryle alcyon</i>	
BGGN	Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	Early
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	Mid, gap
BHVI	Blue-headed Vireo	<i>Vireo solitarius</i>	Mature
BLBW	Blackburnian Warbler	<i>Setophaga fusca</i>	Mature
BLGR	Blue Grosbeak	<i>Passerina caerulea</i>	Early
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	
BRCR	Brown Creeper	<i>Certhia americana</i>	Mature
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	Early
	Black-throated Blue		Mature
BTBW	Warbler	<i>Setophaga caerulescens</i>	
	Black-throated Green		Mature
BTNW	Warbler	<i>Setophaga virens</i>	
BWHA	Broad-winged Hawk	<i>Buteo platypterus</i>	
BWWA	Blue-winged Warbler	<i>Vermivora cyanoptera</i>	Early
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	Mid
CANG	Canada Goose	<i>Branta canadensis</i>	
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>	Mid
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>	
CERW	Cerulean Warbler	<i>Setophaga cerulea</i>	Mid, gap
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	Early
CHSW	Chimney Swift	<i>Chaetura pelagica</i>	
COGR	Common Grackle	<i>Quiscalus quiscula</i>	
COHA	Cooper's Hawk	<i>Accipiter cooperii</i>	
COLO	Common Loon	<i>Gavia immer</i>	
COME	Common Merganser	<i>Mergus marganser</i>	
CORA	Common Raven	<i>Corvus corax</i>	
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	Early
CSWA	Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	Early
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	Mature
DOWO	Downy Woodpecker	<i>Picoides pubescens</i>	Mid

EABL	Eastern Bluebird	<i>Sialia sialis</i>	Early
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	Early-mid
EATO	Eastern Towhee	<i>Pipilo erythrophthalmus</i>	Early, gap
EAWP	Eastern Wood-pewee	<i>Contopus virens</i>	Mid
EUST	European Starling	<i>Sturnus vulgaris</i>	
EWPW	Eastern Whip-poor-will	<i>Antrostomus vociferus</i>	
FISP	Field Sparrow	<i>Spizella pusilla</i>	Early
GCFL	Great Crested Flycatcher	<i>Myiarchus crinitus</i>	Mid
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	Mature
GHOW	Great Horned Owl	<i>Bubo virginianus</i>	
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	Early-mid
GWWA	Golden-winged Warbler	<i>Vermivora chrysoptera</i>	Early-mid
HAWO	Hairy Woodpecker	<i>Picoides villosus</i>	Mid
HETH	Hermit Thrush	<i>Catharus guttatus</i>	Mature
HOWA	Hooded Warbler	<i>Setophaga citrina</i>	Mature, gap
HOWR	House Wren	<i>Troglodytes aedon</i>	Mid
INBU	Indigo Bunting	<i>Passerina cyanea</i>	Early, gap
KEWA	Kentucky Warbler	<i>Geothlypis formosa</i>	Mid, gap
KILL	Killdeer	<i>Charadrius vociferus</i>	
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	Mid-mature
LOWA	Louisiana Waterthrush	<i>Parkesia motacilla</i>	Mature
MAWA	Magnolia Warbler	<i>Setophaga magnolia</i>	Moderate
MODO	Mourning Dove	<i>Zenaida macroura</i>	Any
MOWA	Mourning Warbler	<i>Geothlypis philadelphia</i>	Early-mid
NAWA	Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Mid
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	Early
NOFL	Northern Flicker	<i>Colaptes auratus</i>	Early
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	Early
NOPA	Northern Parula	<i>Setophaga americana</i>	Mature
OROR	Orchard Oriole	<i>Icterus spurius</i>	Early-mid
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>	Mature
PIWA	Pine Warbler	<i>Setophaga pinus</i>	Mature
PIWO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	Mature
PRAW	Prairie Warbler	<i>Setophaga discolor</i>	Early
PUFI	Purple Finch	<i>Haemorhous purpureus</i>	Mature
PUMA	Purple Martin	<i>Progne subis</i>	
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	Mature
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	
RBWO	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	Mature
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	Mature
RHOW	Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	Mid, gap
RSHA	Red-shouldered Hawk	<i>Buteo lineatus</i>	
RTHA	Red-tailed Hawk	<i>Buteo jamaicensis</i>	
RTHU	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	
RUGR	Ruffed Grouse	<i>Bonasa umbellus</i>	
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	Mature
SOSP	Song Sparrow	<i>Melospiza melodia</i>	Early
SSHA	Sharp-shinned Hawk	<i>Accipiter striatus</i>	
SUTA	Summer Tanager	<i>Piranga rubra</i>	Mature
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	Mature

TEWA	Tennessee Warbler	<i>Oreothlypis peregrina</i>	Mid–mature
TRES	Tree Swallow	<i>Tachycineta bicolor</i>	
TUTI	Tufted Titmouse	<i>Baelophus bicolor</i>	Mid
TUVU	Turkey Vulture	<i>Cathartes aura</i>	
VEER	Veery	<i>Catharus fuscescens</i>	Mature, gap
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	Mid
WEVI	White-eyed Vireo	<i>Vireo griseus</i>	Early
WEWA	Worm-eating Warbler	<i>Helmitheros vermivorus</i>	Mature
WITU	Wild Turkey	<i>Meleagris gallopavo</i>	
WIWA	Wilson's Warbler	<i>Cardellina pusilla</i>	
WIWR	Winter Wren	<i>Troglodytes hiemalis</i>	Mature
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	Mature
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>	Early
YBCU	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	Mature
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	Early
YEWA	Yellow Warbler	<i>Setophaga petechia</i>	Early–mid
YRWA	Yellow-rumped Warbler	<i>Setophaga coronata</i>	Mature
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>	Mature
YTWA	Yellow-throated Warbler	<i>Setophaga dominica</i>	Mature

Appendix B. Tree species common and scientific names sampled at point count stations pre- and post-harvest at 9 study areas

Common name	Scientific name	Code	Pre-harvest	Post-harvest
Allegheny chinquapin	<i>Castanea pumila</i>	ALCH		X
American basswood	<i>Tilia americana</i>	AMBA	X	X
American beech	<i>Fagus grandifolia</i>	AMBE	X	X
American elm	<i>Ulmus americana</i>	AMEL		X
American sycamore	<i>Plantanus occidentalis</i>	AMSY	X	X
Black birch	<i>Betula lenta</i>	BLBI	X	X
Black cherry	<i>Prunus serotina</i>	BLCH	X	X
Black gum	<i>Nyssa sylvatica</i>	BLGU	X	X
Black locust	<i>Robinia pseudoacacia</i>	BLLO	X	X
Black oak	<i>Quercus velutina</i>	BLOA	X	X
Black walnut	<i>Quercus velutina</i>	BLWA	X	X
Chestnut oak	<i>Quercus prinus</i>	CHOA	X	X
Common persimmon	<i>Diospyros virginiana</i>	COPE		X
Cucumber magnolia	<i>Magnolia acuminata</i>	CUMA	X	X
Eastern hemlock	<i>Tsuga canadensis</i>	EAHE	X	X
Eastern redbud	<i>Cercis canadensis</i>	EARE	X	X
Flowering dogwood	<i>Cornus florida</i>	FLDO	X	X
Fraser magnolia	<i>Magnolia fraseri</i>	FRMA		X
Green ash	<i>Fraxinus pennsylvanica</i>	GRAS		X
Ironwood	<i>Ostrya virginiana</i>	IRON	X	X
Mockernut hickory	<i>Carya tomentosa</i>	MOHI	X	X
Mountain laurel	<i>Kalmia latifolia</i>	MOLA	X	X
Mulberry	<i>Morus sp.</i>	MULB	X	
Musclewood	<i>Carpinus caroliniana</i>	MUSC	X	X
Northern red oak	<i>Quercus rubra</i>	NROA	X	X
Pawpaw	<i>Asimina triloba</i>	PAWP		X
Pignut hickory	<i>Carya glabra</i>	PIHI	X	X
Pitch pine	<i>Pinus rigida</i>	PIPI	X	X
Post oak	<i>Quercus stellata</i>	POOA	X	X
Red maple	<i>Acer rubrum</i>	REMA	X	X
Sassafras	<i>Sassafras albidum</i>	SASS	X	X
Scarlet oak	<i>Quercus coccinea</i>	SCOA	X	X
Serviceberry	<i>Amelanchier arborea</i>	SERV	X	X
Shagbark hickory	<i>Carya ovata</i>	SHHI	X	X
Silver maple	<i>Acer saccharinum</i>	SIMA		X
Slippery elm	<i>Ulmus rubra</i>	SLEL	X	X
Sourwood	<i>Oxydendrum arboreum</i>	SOUR	X	X
Striped maple	<i>Acer pensylvanicum</i>	STMA	X	X
Sugar maple	<i>Acer saccharum</i>	SUMA	X	X
Tulip poplar	<i>Liriodendrum tulipifera</i>	TUPO	X	X
Virginia pine	<i>Pinus virginiana</i>	VIPI	X	X
White ash	<i>Fraxinus americana</i>	WHAS	X	X
White oak	<i>Quercus alba</i>	WHOA	X	X
White pine ¹	<i>Pinus strobus</i>	WHPI	X	X
Witch hazel	<i>Hamamelis virginiana</i>	WIHA	X	X
Yellow buckeye	<i>Aesculus flava</i>	YEBU	X	X
		Total	39	45

¹In Pennsylvania only