

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/310581993>

Breeding season microhabitat use by Cerulean Warbler (*Setophaga cerulea*) in an experimentally-managed forest

Article in *Forest Ecology and Management* · November 2016

DOI: 10.1016/j.foreco.2016.11.008

CITATIONS

2

READS

83

2 authors:



Claire Nemes

University of Maryland Center for Environmental Science

4 PUBLICATIONS 8 CITATIONS

[SEE PROFILE](#)



Kamal Islam

Ball State University

24 PUBLICATIONS 131 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Hawaii Bird Ecology - Non-native species [View project](#)



Breeding season microhabitat use by Cerulean Warbler (*Setophaga cerulea*) in an experimentally-managed forest [☆]



Claire E. Nemes, Kamal Islam ^{*}

Department of Biology, Ball State University, Muncie, IN 47306-0440, USA

ARTICLE INFO

Article history:

Received 29 February 2016
Received in revised form 6 November 2016
Accepted 7 November 2016
Available online 17 November 2016

Keywords:

Cerulean Warbler
Hardwood Ecosystem Experiment
Microhabitat
Nest patch
Territory
Nest success

ABSTRACT

Cerulean Warbler (*Setophaga cerulea*) populations have undergone significant declines over the past four decades, and the species is considered state endangered in Indiana. These migratory songbirds nest in the canopies of mature deciduous forests throughout eastern North America, but local microhabitat preferences vary by geography and scale, and may influence differential nest success rates across the breeding range. Between 2010 and 2015, we searched for nests, mapped out male territories, and monitored nest success in the Hardwood Ecosystem Experiment in central Indiana. We collected data on a variety of microhabitat features at the territory, nest patch, and nest site levels, as well as at non-use points, and evaluated the influence of several characteristics on nest success. We evaluated nest patch and territory attributes using binomial generalized linear models and nest success with a generalized linear mixed-effects model. Cerulean Warblers selected nest patches characterized by taller trees and located on ridges and valleys rather than on mid-slopes, while males selected territories that were located on steeper northeast-facing slopes closer to roadways than random points. Successful nests were placed lower in the nest tree and were found in areas with shorter trees; several features selected by Cerulean Warblers at the nest patch and territory levels were associated with lower nest success rates. As elsewhere in the range, white oak was an important nest tree species. In developing forest management strategies, land managers must strive to balance small-scale microhabitat preferences with the need for regenerating oak-hickory forests to sustain Cerulean Warbler breeding populations.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

The Cerulean Warbler (*Setophaga cerulea*, formerly *Dendroica cerulea*) is a small migratory songbird that has gained increased attention in recent years due to its worrisome population trends. Breeding Bird Survey data indicate that over the past 40 years, populations of the Cerulean Warbler have declined at a rate of nearly 3% per year (Sauer et al., 2011), among the most drastic decreases of any North American songbird. This Neotropical migrant is considered state endangered in Indiana and endangered in Canada; it is classified as vulnerable elsewhere in its range (BirdLife International, 2012; COSEWIC, 2010; Indiana Department of Natural Resources, 2013).

Since Robbins et al. (1992), Hamel (2000), and others first sounded the alarm about the species' decline, there has been a sig-

nificant amount of research devoted to these birds, but many aspects of their life history remain unclear. A number of factors have contributed to population decreases, with habitat loss and degradation on both the breeding and wintering grounds appearing to be the primary causes (Buehler et al., 2013). Cerulean Warbler researchers have posited that changes in habitat across the breeding range have led to a reduction in the availability and quality of nest sites, and therefore, to lower nest success (USFWS, 2006). However, nest success rates vary widely across the breeding range (Boves and Buehler, 2012; Buehler et al., 2008). Some regions, therefore, undoubtedly host source populations, while others may act as ecological sinks for this species, for reasons that are not yet clear.

Determining the relationship between nest and territory placement, nest success, and habitat features at the local level remains an important goal of Cerulean Warbler research and may illuminate the drivers behind differential nest success rates. Unlike many other imperiled species, Cerulean Warblers have been witnessed nesting in a wide variety of tree species and appear to select for different habitat features depending on the geographic location (Boves et al., 2013; Buehler et al., 2013).

[☆] This article is part of the special issue: Long-term forest management experiments in the eastern deciduous forest of North America – select papers from the 20th Central Hardwood Forest Conference, published in the journal Forest Ecology and Management 387, 2017.

^{*} Corresponding author.

E-mail address: kislam@bsu.edu (K. Islam).

Though considered an area-sensitive, mature forest species, most research has shown that Cerulean Warblers are attracted to gaps in the forest canopy when choosing where to place nests and defend territories (Bakermans et al., 2012; Buehler et al., 2013; Hamel, 2000; Oliarnyk and Robertson, 1996; Weakland and Wood, 2005; Wood and Perkins, 2012). However, Barnes et al. (2016) did not find evidence that Cerulean Warbler occurrence or density were related to canopy gaps in south-central Indiana. Other features associated with territory placement and nest locations were also found to vary across the range; for example, females in the Appalachians selected nest patches with more understory cover (Boves et al., 2013), while those in Ontario had more mid-story cover (Jones et al., 2001).

Nest "site" describes the size and species of the nest tree, while nest "patch" refers to the habitat characteristics in the immediate vicinity of the nest tree, such as aspect or vegetation density. Demographic measures such as daily nest survival, nest success, and fecundity vary and are likely influenced by microhabitat (Bakermans et al., 2012; Martin, 1998; Martin and Roper, 1988; but see Rodewald and Yahner, 2001). Differences in these microhabitat features at the nest site and patch levels may, in whole or in part, lead to the lower nest success rates in southern Indiana in comparison to the core of the breeding range in the Appalachian Mountains (Buehler et al., 2008; Roth and Islam, 2008).

Despite several site-specific differences in nesting and territory habitat, studies across the range have consistently supported the species' preference for white oak (*Quercus alba*) for both nesting and foraging (Barnes et al., 2016; Boves et al., 2013; Newell and Rodewald, 2011; Roth and Islam, 2008; Wagner and Islam, 2014; Weakland and Wood, 2005), while avoiding red maple (*Acer rubrum*) and northern red oak (*Quercus rubra*) for nesting (Bakermans and Rodewald, 2009; Boves et al., 2013; Newell and Rodewald, 2011; Wagner and Islam, 2014). In comparison with other tree species, oaks are relatively slow growing. When first germinating they tolerate shade, but in order to reach maturity they require canopy disturbances to allow sunlight to reach the forest floor and "release" sapling growth (Carman, 2013). Historically, weather events and fires (both naturally-occurring and those intentionally started by Native Americans) provided sources of disturbance that allowed oak regeneration in the Central Hardwood Forest Region. However, modern-day fire suppression and forest management strategies have resulted in poor oak recruitment (Abrams, 2003; Carman, 2013; Fralish, 2003; Jenkins, 2013). Uneven-aged management techniques, including single-tree selection, are widely employed on public lands in Indiana; however, research indicates that this type of harvesting results in less diverse species composition and does not allow for significant oak regeneration (Jenkins and Parker, 1998). If uneven-aged management continues to be practiced exclusively, southern Indiana state forests may in time become dominated by fast-growing, shade-tolerant species such as American beech (*Fagus grandifolia*) and maple (*Acer* sp.). This will result in the loss of ecologically and economically valuable oaks and hickories (Carman, 2013), species upon which Cerulean Warblers rely for nesting. In contrast, even-aged techniques, such as shelterwood and clearcutting methods, may favor oak regeneration (Iverson et al., 2008; Jenkins and Parker, 1998), particularly if they are coupled with prescribed burns and provided there is a sufficient soil seed bank or coppiced stumps to allow regrowth of the desired species.

We investigated the influence of even- and uneven-aged management practices on Cerulean Warbler habitat use. Varying forest management practices within our study could result in Cerulean Warbler microhabitat characteristics that further differ from those found at other sites. Nest placement and the surrounding microhabitat characteristics can potentially have a substantial impact on reproductive success or failure (Martin and Roper, 1988;

Martin, 1998). As such, this research was designed to determine the specific habitat features associated with Cerulean Warbler nest patches, territories, and nest success rates in this region of the state, which may help forest managers better understand the potential impacts of local timber harvesting on this species.

Our primary research objectives were (1) to determine microhabitat characteristics at the nest patch level (in the immediate vicinity of the nest) and compare them with nearby non-nest locations, (2) to compare microhabitat characteristics of male territories with randomly sampled non-use locations outside of the territory, and (3) to ascertain which nest patch and nest site characteristics are the best predictors of Cerulean Warbler nest success.

2. Methods

2.1. Study area

All research was conducted within the experimental plots of the Hardwood Ecosystem Experiment (HEE), located at 39°14'N, 86°22'W. This project, initiated in 2006, is a 100-year study designed to investigate the impacts of timber management practices on the ecosystems of Morgan-Monroe and Yellowwood state forests in Brown, Morgan, and Monroe counties in the Central Hardwoods Ecoregion of Indiana. The HEE is a collaborative effort between numerous stakeholders, including state agencies, non-profit organizations, and local universities (Swihart et al., 2013). The forest type is primarily oak-hickory (*Quercus-Carya*), with sugar maple (*Acer saccharum*), tulip tree (*Liriodendron tulipifera*), American beech, and white ash (*Fraxinus americana*) also common. Due to the erosion process characteristic of this area, the terrain is very hilly, frequently steep, and bisected by intermittent small streams that drain into larger ones (Homoya et al., 1985).

The HEE study site consists of nine experimental plots, ranging from 303 to 483 ha in size, scattered throughout the two state forests (Fig. 1). The nine units each consist of a core research area within which management activities take place. Adaptive management strategies will be employed for the 100-year duration of the HEE and intend to regenerate 20% of the harvested research core every 20 years. Each unit was randomly assigned to one of three management strategies: uneven-aged harvest, even-aged harvest, or control. The initial round of timber harvesting was completed during the fall and winter of 2008–2009 (Kalb and Mycroft, 2013).

Control cores (units 2, 4, and 5) undergo no logging or prescribed fire treatments for the duration of the experiment (Fig. 1). Even-aged units (3, 6, and 9) receive shelterwood and clearcut harvests to produce even-aged forest stands. Two harvest areas in each unit were assigned shelterwood cuts, a three-stage process occurring over a period of approximately 20 years that is designed to promote regeneration of oak and hickory species. The other two areas in the even-aged units receive clear cutting, which involves the removal of large (>30.48 cm DBH) trees in the harvest area; mid-sized oaks and hickories are coppiced to allow re-sprouting from the stumps (Kalb and Mycroft, 2013). Prescribed burns will also be conducted in portions of the even-aged research cores. The uneven-aged units (1, 7, and 8) receive eight patch cuts of varying sizes, which are similar to clearcuts but smaller in scale. Single-tree selection harvests are also conducted in the research core (Kalb and Mycroft, 2013). Such uneven-aged treatments most closely approximate the current timber harvest strategies in Indiana state forests, where group and single-tree selection methods applied on 15–25 year cutting cycles are common (Swihart et al., 2013). A 150 m buffer area surrounds each research core and is managed according to current Indiana Department of Forestry strategies with the intention of minimizing harvest effects in each of the units (Kalb and Mycroft, 2013). Each unit is also overlain

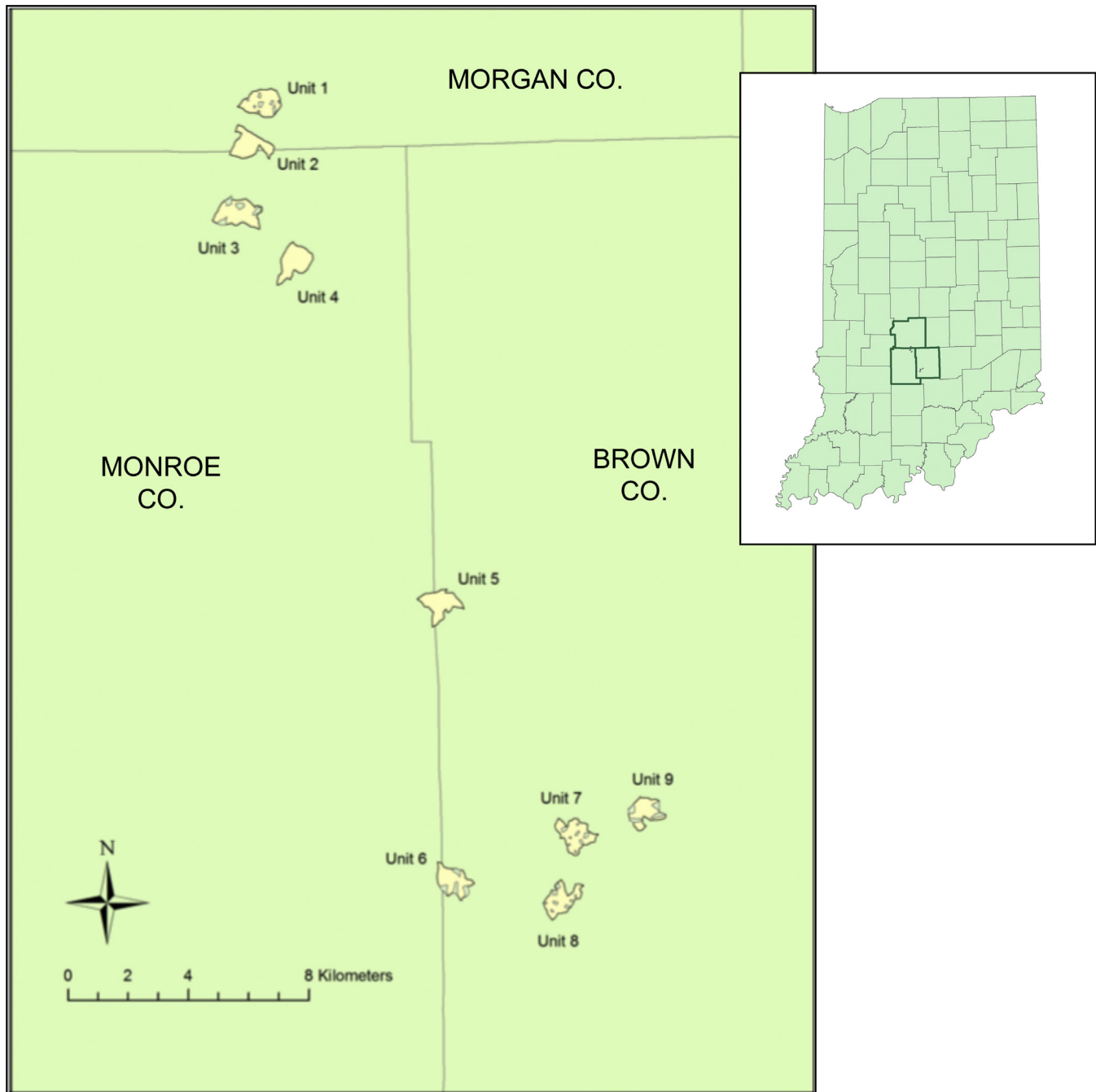


Fig. 1. Map showing locations and relative sizes of the nine experimental units in the Hardwood Ecosystem Experiment. Inset: locations of Morgan, Monroe, and Brown counties in south-central Indiana.

with a point count grid, with points located at 200 m intervals in a 7×7 pattern. This distance serves to minimize the chance of double-counting the same individual bird during aural point counts because male Cerulean Warblers typically broadcast their song to a distance of 95–100 m (Hamel et al., 2009; Jones et al., 2000).

2.2. Territory demarcation

Between 2011 and 2015, 100 m fixed-radius point count surveys for Cerulean Warblers were conducted in each HEE unit according to the methods outlined in Islam et al. (2013). Surveyors recorded the cardinal direction and estimated distance of all singing males detected during the 5-min count period, then revisited

these locations in order to perform territory mapping using methods similar to those described in Roth and Islam (2007) and Falls (1981). The majority of mapping efforts were conducted in late May and throughout June of each year; at this point in the breeding season, all singing males were assumed to be local breeders rather than migrants. At each location where a singing male was detected, all trees in which the focal male was observed singing were flagged. Each tree's species and coordinates were recorded using a handheld Global Positioning System (GPS) unit (Garmin GPSMap 62S). A minimum of 5 trees (but generally 8 or more) were marked for each male. Mapping was often completed in one day, but for many individuals a sufficient number of locations was not obtained on one visit and mapping was continued on subsequent occasions. Song perch tree coordinates were used

to generate territory polygons using ArcMap's Minimum Bounding Geometry: Convex Hull function (ESRI, 2015).

2.3. Nest searching and monitoring

Between 2011 and 2015, observers searched for Cerulean Warbler nests within the HEE units by observing nesting behavior of adult birds. Because nests are small, well camouflaged, and located high in the forest canopy (at an average height of 18.9 m in our study area), they can be extremely challenging to find despite intensive efforts. As Cerulean Warblers arrive at our study sites in Indiana during mid to late April, nest searching generally commenced in the last week of April or first week of May and continued throughout the breeding season.

All nests were monitored using a tripod-mounted 82 mm Nikon Prostaff spotting scope with 20–60× zoom. During the early nest stages, nests were monitored every 2–3 days; the frequency of visits increased as the estimated date of fledging approached to maximize the chance of observing the chicks' departure. Information such as date and time of discovery, estimated nest stage (construction, incubation, brooding, feeding, or fledging), and number of chicks (if hatched) was recorded. If no activity was observed at the nest, it was revisited on two more occasions before concluding that it had failed. Nest site and patch data were collected after the nest was no longer active to minimize the possibility of disturbing the birds or attracting the attention of predators.

2.4. Microhabitat sampling overview

A 0.04 ha (11.3 m-radius) circular plot was used to sample microhabitat data at different levels (James and Shugart, 1970). Data were collected at the geometric center of male territories, calculated using the Center-to-Point tool in ArcGIS (ESRI, 2015). For each territory point, we generated a paired random non-use point in the same experimental unit for comparison, ensuring that these did not fall within 50 m of any Cerulean Warbler territories mapped in the current or previous years.

Microhabitat data were assessed within sample plots centered directly underneath each Cerulean Warbler nest, referred to hereafter as the “nest patch” level. Microhabitat data were also assessed at a second non-nest location in a randomly generated compass direction, 50 m away from the nest. This second location was assumed to be close enough to fall within the male's territory but, hypothetically, represented a site that was not chosen for nesting (Dearborn and Sanchez, 2001; Newell and Rodewald, 2011). In instances when the non-nest location fell within a known territory, a random-numbers generator was used to determine a new, alternative compass direction. Since we only began collecting nest patch-level data in 2014, we returned to the locations of nests found in 2011–2013 and sampled patch data for them in 2014. Although there is a possibility that some microhabitat characteristics may have changed in years between the original nesting attempt and when the patch was surveyed, abiotic components such as slope, aspect, and distance to landscape features remain constant. Furthermore, no measurements of herbaceous vegetation, which were assumed to vary more than woody vegetation on a yearly basis, were included in the models. Microhabitat data for all 90 non-nest locations were sampled in 2015. Microhabitat data describing the nest site (characteristics such as nest height and nest tree species) were collected during the same season that the nest was found.

2.5. Microhabitat sampling measurements

Height of the tallest tree in each quadrant of the circle (NE, SE, SW, and NW) was measured using a Nikon laser rangefinder.

Means of these four values were calculated so that each survey circle had a single “Tallest Tree” value, a relative indicator of canopy height. Diameter at breast height (DBH) was recorded for all trees >10 cm in the microhabitat plot. Trees and other woody plants within 5 m of the center (0.008 ha) and under 10 cm DBH were counted, identified to species, and recorded as “shrubs.” Presence or absence of grapevine, an important nesting material for this species, was also recorded (Buehler et al., 2013). Because roads in the state forests create breaks in the canopy that Cerulean Warblers may find attractive, distance to roadway (in meters) for each point was calculated in ArcGIS 10.2 (ESRI, 2015). Cerulean Warblers will use both dry upland slopes and wet bottomland forests for nesting (Buehler et al., 2013; Hamel, 2000; Rosenberg et al., 2000); therefore, we calculated distance to the nearest stream (in meters). Road, stream, and harvest data layers were obtained courtesy of the Indiana Department of Natural Resources (IDNR).

The topographic position of each microhabitat survey plot was identified with ArcGIS using the Topographic Position Index extension developed by Jenness Enterprises (2006). A Digital Elevation Model (DEM) raster was obtained from the United States Geological Survey 2011 National Land Cover Database (Homer et al., 2015). This raster was reclassified into three topographic categories: V (valley), M (mid-slope), or R (ridgetop); each survey point was determined to fall into one of these groups. No point fell exactly on the middle value between two categories. The accuracy of these classifications was verified by comparing with known positions of several nests.

Slope values (percent) were recorded in the field using a Suunto clinometer. Uphill and downhill slopes were recorded separately, and the two readings were averaged for use in the analysis. Aspect (0–359°) was determined using a Suunto compass. Prior to analysis, Beers' transformation was used to convert all compass aspect values, using the formula = $\cos(45 - [\text{measured aspect}]) + 1$. This assigns a higher weight to sites on more productive northeastern-facing slopes (45°) than those on less productive southwestern slopes (Beers et al., 1966).

2.6. Statistical analysis

To analyze microhabitat differences at the nest patch and territory levels, we employed binomial generalized linear models (GLM), a suitable modeling technique when response variables do not follow a normal error distribution. Presence (1) or absence (0) of a nest was used as the response variable in the first analysis, and presence or absence of a territory was the response variable in the second analysis. We evaluated the influence of nine covariates on nest site and territory selection (Table 1). The most parsimonious model was selected based on Akaike's Information Criterion corrected for small sample sizes (AICc) to prevent overfitting of the model. Models with a $\Delta\text{AICc} < 2.0$ were considered equally plausible (Burnham and Anderson, 2002). All statistical analyses were performed using the program R (R Core Team, 2015). Model averaging, using the AICmodavg package (Mazerolle, 2015) and the MuMIn package (Bartoń, 2015), was conducted when more than one model was selected based on AICc. We used the model-averaged coefficients to generate predictions of nest presence or territory presence based on each covariate in the candidate models. Means and 95% confidence intervals were then plotted. Prior to conducting the GLMs, we tested for collinearity (Pearson's $|r| > 0.3$) among the variables in the datasets using the Hmisc package in R (Harrell, 2015). In the nest patch and territory datasets, mean tallest tree height was positively correlated with mean DBH ($r = 0.38$ and $r = 0.45$, respectively); hence, only the former was used in these models. Significant covariates were plotted using the package ggplot2 (Wickham, 2009).

To determine the influence of nest patch microhabitat and nest site variables on nest success, we used a generalized linear mixed-effects model (GLMM) through the lme4 package in R (Bates et al., 2015). Year was included as a random effect to account for variation in Cerulean Warbler nest success rates between years.

Table 1

Variables included in the microhabitat models. The nest patch model included mean tallest tree height, percent slope, percent canopy cover, number of shrubs/small trees, distance to nearest road, and topographic position. The territory model included mean tallest tree height, percent slope, Beers' aspect, presence of grapevine, percent canopy cover, number of shrubs/small trees, distance to nearest road, and topographic position. The nest success model consisted of mean tallest tree height, number of shrubs, percent canopy cover, distance to nearest road, height of nest tree, white oak vs. non-white oak, and forest management type.

| Variable name | Description |
|---------------|--|
| TALL | Height (m) of tallest tree in each of four quadrants, averaged |
| CANOPY | Mean percent canopy cover in the survey circle (average of 20 measurements) |
| SLOPE | Average of two slope readings (uphill and downhill from center of circle), percent |
| BEERS | Beers' aspect (0–2) |
| GRAPE | Presence or absence of grapevine in the survey circle (presence = 1, absence = 0) |
| SHRUB | Number of shrubs and trees <10 cm DBH |
| DISTROAD | Distance (m) from center of survey circle to nearest road (paved or gravel) |
| TPI | Topographic position index (R = ridgetop, M = mid-slope, V = valley) |
| QUAL | Nest occurred in a white oak tree (1) versus non-white oak (0) |
| NESTHT | Height of nest tree (m) |
| MGMT | Forest management type (E = even-aged, U = uneven-aged, C = control) |

As above, we first tested for collinearity among the variables, i.e. those with a Pearson's $|r| > 0.3$. Beers' aspect was omitted from the model because too many Cerulean Warbler nests were located in areas with a flat aspect (for example, in a streambed or stream valley) and therefore, were not assigned any Beers' aspect value. We examined the influence of seven remaining variables on Cerulean Warbler nest success (Table 1). Because the GLMM has difficulty comparing covariates on very different scales, continuous variables were re-scaled to z-scores prior to analysis (Sokal and Rohlf, 1995). Model averaging was conducted when covariates were included in multiple component models.

Microhabitat surveys were not conducted at random non-use points in 2013 owing to time constraints and fieldwork logistics; therefore, 2013 was excluded from the territory microhabitat analysis, and years included were 2012, 2014, and 2015 (n territories = 158). Out of 93 nests discovered between 2011 and 2015, 90 nests (paired with 90 non-nest points) were used for evaluation of influential parameters on nest success.

3. Results

3.1. Overview

Between 2011 and 2015, 93 Cerulean Warbler nests were found at our study sites in south-central Indiana (Fig. 2). Of these, nearly half were located in species of the white oak group (*Quercus alba*, *Q. montana* (*prinus*), or *Q. muhlenbergii*), with white oaks (*Q. alba*) comprising the vast majority of nest trees ($n = 37$). Smaller numbers of Cerulean Warbler nests were found in a variety of other species (see Fig. 2 for detailed information). Tree species use appeared to vary somewhat by year; for example, from 2011 to 2014 only two nests were discovered in American sycamores

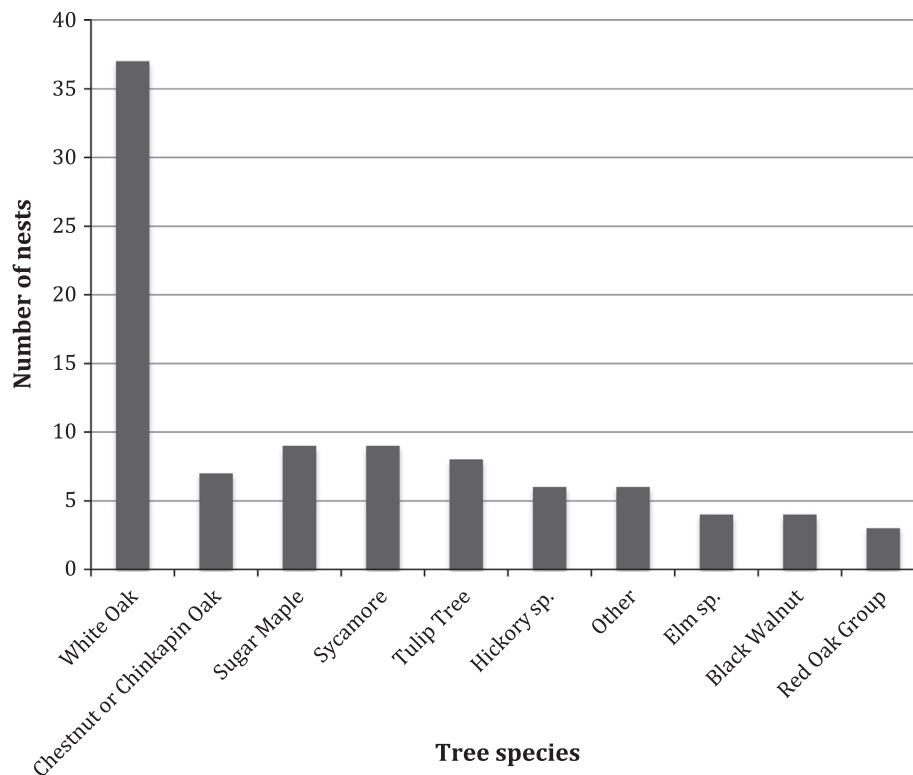


Fig. 2. Tree species in which Cerulean Warbler nests were found, 2011–2015 (n nests = 93). "Hickory sp." includes *Carya glabra* (pignut hickory) and *C. ovata* (shagbark hickory). "Elm sp." includes *Ulmus rubra* (slippery or red elm) and *U. americana* (American elm). "Red Oak Group" includes *Quercus velutina* (black oak) and *Q. rubra* (Northern red oak). "Other" consists of species in which only one or two nests were found during the entire study period. This includes basswood (*Tilia americana*, $n = 2$), American beech (*Fagus grandifolia*, $n = 1$), ash (*Fraxinus* sp., $n = 1$), black tupelo (*Nyssa sylvatica*, $n = 1$), and sassafras (*Sassafras albidum*, $n = 1$).

Table 2

Nest patch component models with $\Delta AICc$ values and weights for nest patch selection. Models with $\Delta AICc < 2$ are considered equally plausible; the null model is included for comparison.

| Component models | AICc | $\Delta AICc$ | Weight |
|--|--------|---------------|--------|
| Distance to road + mean tallest tree height | 231.25 | 0.00 | 0.31 |
| Mean tallest tree height | 231.96 | 0.70 | 0.22 |
| Canopy + distance to road + mean tallest tree height | 232.48 | 1.22 | 0.17 |
| Distance to road + slope + mean tallest tree height | 232.64 | 1.38 | 0.16 |
| Distance to road + slope + mean tallest tree height + topographic position | 232.81 | 1.55 | 0.14 |
| (Null) | 247.39 | 16.14 | 0.00 |

(*Platanus occidentalis*), while in 2015, 7 nests out of 21 were in sycamores. Nests were found in all forest management types and in all of the nine HEE units except Unit 1 (a control unit). More nests were found in even-aged units ($n = 43$) than in uneven-aged ($n = 34$) or control units ($n = 13$), despite intensive searching in all management types.

Over the five-year period, mean nest tree DBH was 44.19 cm ($SE \pm 1.64$) and mean nest height was 18.86 m ($SE \pm 0.49$) in the study area. Mean nest tree height was 25.83 m ($SE \pm 0.51$), and mean orientation of the nest relative to the trunk was 171.24 degrees ($SE \pm 10.78$). Mean distance from nest to trunk was 4.80 m ($SE \pm 0.3$).

3.2. Nest patch

Analysis of the microhabitat covariates at the nest patch vs. nearby non-nest points produced five equally plausible models with a $\Delta AICc < 2.0$ (Table 2). Mean tallest tree height was the most important covariate, appearing in all five models (Table 3), indicating that Cerulean Warbler nest patches were found in forest stands with taller trees (Fig. 3). Nests were also located closer to roads, on steeper slopes, and in stands with a higher percentage of canopy cover than non-use points; however, these covariates had 95% CIs that overlapped zero and thus were not considered significant (Table 3). The reference topographic position of mid-slope was different from 0 and nests were found more often on ridges and in valleys than on mid-slopes, but the three positions were not considered to be significantly different from one another (Fig. 4). Only plots of significant variables are shown for the nest patch and territory models.

3.3. Territory

Analysis of microhabitat variables at the territory center versus random points produced ten equally plausible models (Table 4). Beers' aspect and distance to road were each included in all ten models and showed 95% CIs that did not overlap 0; percent slope

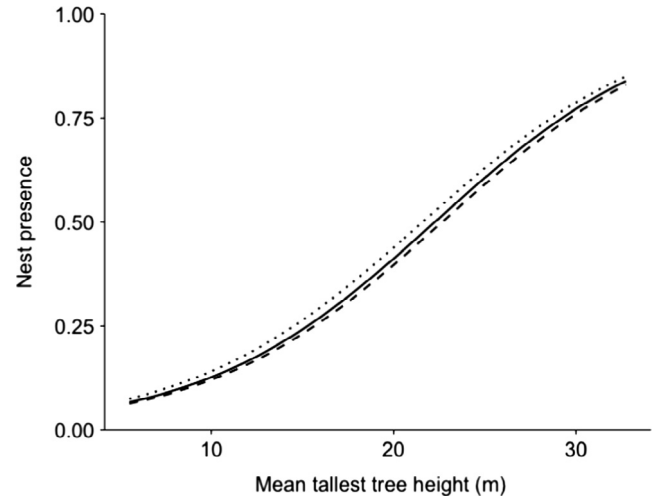


Fig. 3. Model-averaged prediction for influence of mean tallest tree height on nest presence at each of the three different topographic positions, 2011–2015. The solid line represents nests on ridges, the dotted line represents mid-slope nests, and the dashed line represents valley nests. For clarity, standard error is not depicted in this figure but values are listed in Table 3.

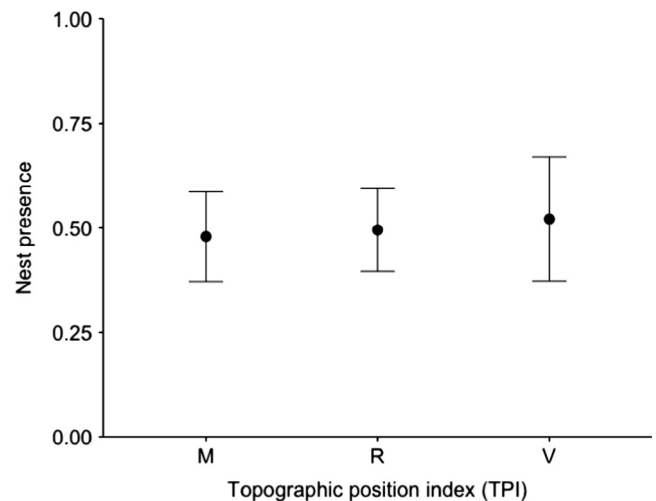


Fig. 4. Model-averaged prediction for influence of topographic position on nest presence, 2011–2015. M = nests on mid-slopes, R = nests on ridges, and V = nests in valleys. Standard error bars are shown.

Table 3

Model-averaged coefficients (estimates) for nest patch model. Topographic position is a categorical variable and therefore coefficient estimates of nest presence for each category (ridge, mid-slope, and valley) are presented separately; relative variable importance of topographic position (all categories) is 0.14. Covariates that are significant at the 95% confidence level are marked with an asterisk (*).

| Model-averaged coefficients | Estimate | Std. error | Adjusted std. error | Relative variable importance | N containing models | 95% CI lower bound | 95% CI upper bound |
|-----------------------------|----------|------------|---------------------|------------------------------|---------------------|--------------------|--------------------|
| Mean tallest tree height* | 0.1551 | 0.0400 | 0.0403 | 1.00 | 5 | 0.0761 | 0.2340 |
| Distance to road | -0.0024 | 0.0014 | 0.0014 | 0.78 | 4 | -0.0050 | 0.0003 |
| Slope | 0.0123 | 0.0110 | 0.0111 | 0.30 | 2 | -0.0094 | 0.0341 |
| Canopy cover | 1.4000 | 1.5061 | 1.5167 | 0.17 | 1 | -1.5726 | 4.3727 |
| Topographic position | | | | | | | |
| - Mid-slope* | -3.5258 | 1.0931 | 1.0997 | | | -5.6811 | -1.3704 |
| - Ridge | 0.3467 | 0.4297 | 0.4327 | 0.14 | 1 | -0.5014 | 1.1949 |
| - Valley | 0.9298 | 0.4726 | 0.4759 | | | -0.0031 | 1.8626 |

was also a significant covariate (Table 5). Beers' aspect was positively correlated with territory presence (Fig. 5); hence, territories were more often located on northeast-facing slopes. In comparison with randomly sampled points, territories were located in closer

Table 4
Territory component models with $\Delta AICc$ values and weights for territory selection. Models with $\Delta AICc < 2$ are considered equally plausible; the null model is included for comparison.

| Territory component models | AICc | $\Delta AICc$ | Weight |
|--|--------|---------------|--------|
| Beers' aspect + distance to road + slope + mean tallest tree height | 346.36 | 0 | 0.15 |
| Beers' aspect + canopy + distance to road + slope + mean tallest tree height | 346.37 | 0.02 | 0.15 |
| Beers' aspect + canopy + distance to road + slope | 346.54 | 0.18 | 0.14 |
| Beers' aspect + canopy + distance to road + shrub + slope + mean tallest tree height | 346.86 | 0.5 | 0.12 |
| Beers' aspect + distance to road + slope | 347.31 | 0.96 | 0.1 |
| Beers' aspect + canopy + distance to road + shrub + slope | 347.56 | 1.2 | 0.08 |
| Beers' aspect + distance to road + shrub + slope + mean tallest tree height | 347.77 | 1.41 | 0.08 |
| Beers' aspect + canopy distance to road + grapevine + slope + mean tallest tree height | 348.19 | 1.83 | 0.06 |
| Beers' aspect + canopy + distance to road + mean tallest tree height | 348.3 | 1.94 | 0.06 |
| Beers' aspect + distance to road + grapevine + slope + mean tallest tree height | 348.32 | 1.96 | 0.06 |
| (Null) | 371.85 | 25.5 | 0.00 |

Table 5
Model-averaged coefficients for territory selection model. The "estimate" coefficient column describes the magnitude and direction of the relationship between each covariate and territory presence. Covariates that are significant at the 95% confidence level are marked with an asterisk (*).

| Model-averaged coefficients | Estimate | Std. error | Adjusted std. error | Relative variable importance | N containing models | 95% CI lower bound | 95% CI upper bound |
|-----------------------------|----------|------------|---------------------|------------------------------|---------------------|--------------------|--------------------|
| Beers' aspect* | 0.5997 | 0.1822 | 0.1830 | 1.00 | 10 | 0.241 | 0.958 |
| Distance to road* | -0.0049 | 0.0013 | 0.0014 | 1.00 | 10 | -0.008 | -0.002 |
| Slope* | 0.0247 | 0.0118 | 0.0118 | 0.94 | 9 | 0.002 | 0.048 |
| Mean tallest tree height | 0.0495 | 0.0301 | 0.0302 | 0.68 | 7 | -0.010 | 0.109 |
| Canopy | 1.7410 | 1.0892 | 1.0941 | 0.62 | 6 | -0.403 | 3.885 |
| Number of shrubs | 0.0032 | 0.0030 | 0.0030 | 0.28 | 3 | -0.003 | 0.009 |
| Presence of grapevine | 0.1291 | 0.2849 | 0.286 | 0.12 | 2 | -0.432 | 0.690 |

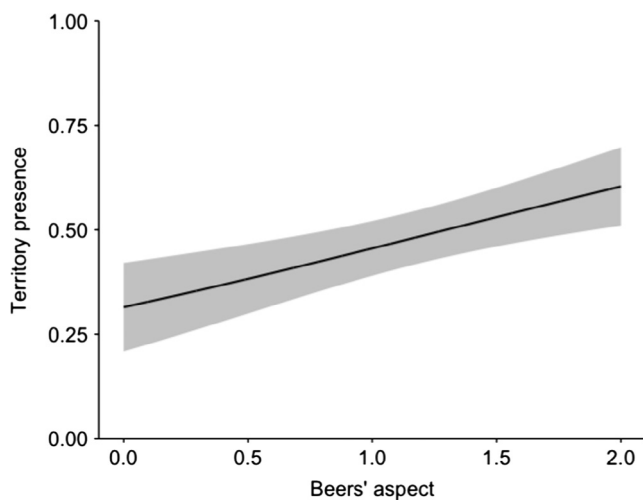


Fig. 5. Model-averaged prediction for influence of Beers' aspect on territory presence in 2012, 2014, and 2015. Beers aspect ranges from 0 (perfectly southwest-facing slopes) to 2 (perfectly northeast-facing slopes). The closer that Beers' aspect is to 2.0, the more northeasterly the slope. The shaded gray area represents 95% confidence intervals.

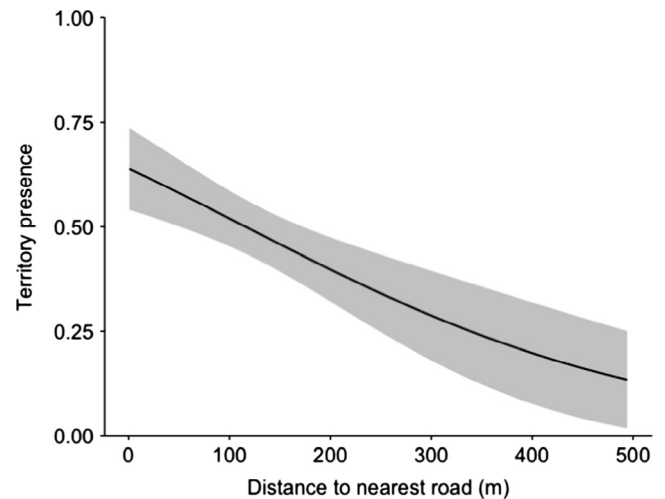


Fig. 6. Model-averaged prediction for influence of distance to roadway on territory presence in 2012, 2014, and 2015. Increased territory presence is correlated with decreasing distance to the nearest road. The shaded gray area represents 95% confidence intervals.

proximity to roads (Fig. 6) and on steeper slopes (Fig. 7). The territory selection model showed weak support (95% CIs overlapping zero) for several additional covariates: territories were located in areas with greater mean tallest tree height, a higher percentage of canopy cover, more shrubs and small trees, and more grapevine.

Of the 158 territories mapped during 2012, 2014, and 2015, 43 were located in control units, 49 were in uneven-aged units, and 66 were in even-aged units. Mean male territory size in Morgan-Monroe and Yellowwood state forests was 0.28 ha, which is similar to other sites in Indiana (Islam et al., 2013; Islam and Basile, 2002; Islam and Roth, 2004) but much smaller than territory sizes of

1–2 ha in Ohio (Newell and Rodewald, 2011) or 1.4 ha in Ontario (Oliarnyk and Robertson, 1996).

3.4. Nest success

Modeling of the variables influencing nest success resulted in 12 candidate models with a $\Delta AICc$ value of under 2.00 (Table 6). Two of these variables, mean tallest tree height and nest height, were each included in 10 of the 12 models and were considered significant based on the 95% CIs (Table 7). Nest height was negatively correlated with nest success, indicating that nests located lower in trees had a higher probability of survival. Nest success

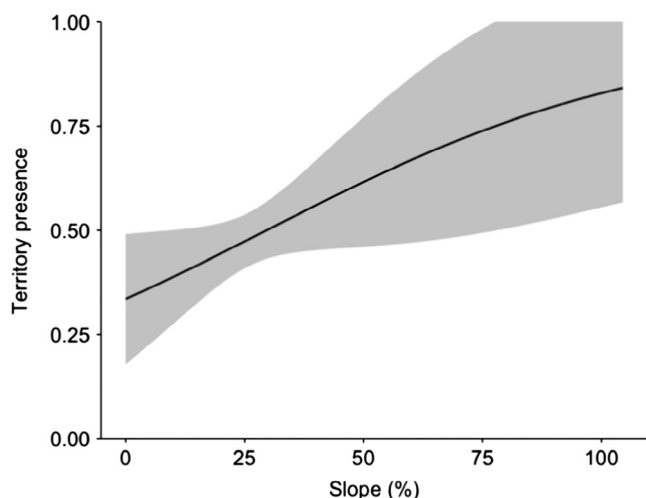


Fig. 7. Model-averaged prediction for influence of percent slope on territory presence in 2012, 2014, and 2015. Greater percent slope (steeper grades) are associated with increased territory presence. The shaded gray area represents 95% confidence intervals.

was lower in areas that had a greater mean tallest tree height. The model showed only weak support (95% CIs overlapped 0) for the influence of several other covariates on Cerulean Warbler nest success: success was higher when nests were located farther from roads and in stands with higher canopy cover; it was lower for nests in white oaks. Nest success was higher in the control units than the even- and uneven-aged units, though the management types were not significantly different from one another.

Table 6

Nest success component models with $\Delta AICc$ values and weights for territory selection. Models with $\Delta AICc < 2$ are considered equally plausible; the null model is included for comparison.

| Nest success component models | AICc | $\Delta AICc$ | Weight |
|---|--------|---------------|--------|
| Distance to road + nest height + mean tallest tree height | 157.36 | 0 | 0.15 |
| Nest height + mean tallest tree height | 157.59 | 0.22 | 0.13 |
| Distance to road + nest height + white oak + mean tallest tree height | 157.82 | 0.45 | 0.12 |
| Distance to road + management type + nest height + white oak + mean tallest tree height | 158.05 | 0.69 | 0.11 |
| Nest height + white oak + mean tallest tree height | 158.64 | 1.27 | 0.08 |
| Canopy + nest height + mean tallest tree height | 159.05 | 1.69 | 0.06 |
| Management type + white oak + mean tallest tree height | 159.13 | 1.76 | 0.06 |
| Management type + nest height + white oak + mean tallest tree height | 159.15 | 1.79 | 0.06 |
| Canopy + distance to road + nest height + white oak + mean tallest tree height | 159.18 | 1.82 | 0.06 |
| Canopy + distance to road + nest height + mean tallest tree height | 159.25 | 1.89 | 0.06 |
| Nest height | 159.28 | 1.91 | 0.06 |
| Distance to road + management + nest height + mean tallest tree height | 159.31 | 1.94 | 0.06 |
| (Null) | 164.59 | 7.23 | 0.00 |

Table 7

Model-averaged coefficients for the nest success model. The “estimate” coefficient column describes the magnitude and direction of the relationship between each covariate and nest success. Covariates that are significant at the 95% confidence level are marked with an asterisk (*).

| Model-averaged coefficients | Estimate | Std. error | Adjusted std. error | Relative variable importance | N containing models | 95% CI lower bound | 95% CI upper bound |
|-----------------------------|----------|------------|---------------------|------------------------------|---------------------|--------------------|--------------------|
| Distance to road | 0.3180 | 0.2049 | 0.2082 | 0.99 | 10 | -0.09008665 | 0.72607713 |
| Nest height* | -0.5201 | 0.1891 | 0.1923 | 0.94 | 10 | -0.89693128 | -0.14330789 |
| Mean tallest tree height* | -0.5078 | 0.248 | 0.2517 | 0.55 | 5 | -1.00113881 | -0.01454671 |
| Nest in white oak | -0.5747 | 0.403 | 0.4093 | 0.48 | 6 | -1.37687776 | 0.22740045 |
| Forest management type | | | | 0.19 | 3 | | |
| - Control* | 2.5962 | 0.6027 | 0.6070 | - | - | 1.40638732 | 3.78594385 |
| - Even-aged | -1.1663 | 0.6101 | 0.6205 | - | - | -2.38237186 | 0.0497988 |
| - Uneven-aged | -0.9684 | 0.6204 | 0.6309 | - | - | -2.20501971 | 0.26822695 |
| Canopy | 0.1583 | 0.1847 | 0.1878 | 0.20 | 3 | -0.20975782 | 0.52637066 |

4. Discussion

4.1. Territory and nest patch characteristics

Cerulean Warblers at our study site selected many of the same characteristics when choosing where to locate their territories and nests. Both nest patches and territories were situated closer to roads and found on steeper slopes when compared with non-use locations. In Morgan-Monroe and Yellowwood state forests, the majority of roads are small, graveled, and not accessible by public vehicular traffic; many of them function as hiking trails and/or logging roads. These minor roads may produce breaks in the canopy that are attractive to breeding Cerulean Warblers but do not result in a “hard” habitat edge. Such features may create structural conditions that emulate natural canopy gaps resulting from tree fall and other disturbances in mature forests (Barnes et al., 2016; Hamel, 2000; Rosenberg et al., 2000). Steeper slopes, as posited by Barnes et al. (2016), can produce a heterogeneous canopy structure that likewise appeals to Cerulean Warblers.

The association between Cerulean Warbler nests and canopy gaps has been well documented in the literature (Jones et al., 2001; Oliarnyk and Robertson, 1996; Rogers, 2006; Wagner and Islam, 2014). In Ontario, a majority of nests were located in close proximity to canopy gaps (Oliarnyk and Robertson, 1996), and Boves et al. (2013) found that nest patches in the Appalachians were also located in areas that had characteristics of small-scale canopy disturbances. A previous study of Cerulean Warbler territories in the HEE found similar results, with territories lying closer to roads and streams that could produce canopy gaps (Kaminski and Islam, 2013). Territories were found in close proximity to roads in West Virginia (Weakland and Wood, 2005); elsewhere in the Appalachian Mountains and in Ontario, territories were also found

near other types of canopy gaps, both manmade and naturally occurring (Barg et al., 2006; Boves et al., 2013; Oliarnyk and Robertson, 1996; Perkins and Wood, 2014).

Birds may derive a number of benefits from the conditions associated with canopy gaps. The increased light penetration, higher soil moisture, and greater nutrient levels in such areas can result in greater vegetative productivity and, by extension, an increase in prey availability (Muscolo et al., 2014). Cerulean Warblers have been observed foraging for prey on branches near the edges of forest gaps (George, 2009), and numerous insectivorous bird species were found to utilize gaps in Illinois, indicating that they can provide improved foraging opportunities for these species (Blake and Hoppes, 1986). Cerulean Warblers whose nests are located closer to gaps may thus be able to expend less energy traveling between foraging sites and collect more prey items to feed their offspring, increasing the possibility of reproductive success.

Both nest patches and territories had a higher mean tallest tree height than non-use points, though this was only significant at the nest patch level. This indicates selection for forest stands that have higher canopies and larger trees overall, since tallest tree height and DBH were found to be correlated at both levels (Pearson's $r = 0.38$ for nest patches and $r = 0.45$ for territories). This supports the well-established finding that Cerulean Warblers select areas with large trees when choosing breeding habitat (Boves et al., 2013; Hartman et al., 2009; Jones et al., 2001). Male Cerulean Warbler territories also had higher numbers of shrubs and trees under 10 cm DBH than random points, indicating a denser understory. In concert with the high mean tallest tree height value, this suggests that males are selecting stands with more uneven-aged characteristics.

While slope aspect was not included as one of the input variables in the nest patch or success models, aspect was found to influence Cerulean Warbler territory placement. Beers' aspect values of 2 represent slopes facing 45° , e.g. northeast-facing slopes (Beers et al., 1966). Male territories were frequently located on more northeasterly-facing slopes than were random points. Similar results were found in previous studies in Indiana; male territories were found on eastern slopes (Kaminski and Islam, 2013) and higher-use areas were located primarily on north to southeast-facing slopes (Barnes et al., 2016). This pattern has been reported from Cerulean Warbler territories elsewhere in their range as well (Boves et al., 2013; Oliarnyk and Robertson, 1996).

Birds may receive a number of benefits from breeding on northeast slopes. In the northern hemisphere, northeast-facing slopes receive less solar radiation and are thus cooler and retain more moisture than southwest slopes. This, in turn, contributes to greater productivity and higher plant growth rates on slopes with more northeasterly aspects (Beers et al., 1966; Fekedulegn et al., 2003; Fekedulegn et al., 2004; Fralish, 1994). This increased productivity may be attractive to male Cerulean Warblers if it promotes better foraging and nest concealment opportunities for the territorial male and his prospective mate. In particular, trees on northeast slopes leaf out earlier, which may serve as a cue predicting future prey availability later in the breeding season when parents are feeding nestlings (Marshall and Cooper, 2004). Abundance and size of arthropod prey items such as Lepidopteran larvae can vary throughout the season and may peak relatively early (Feeny, 1970; Marshall and Cooper, 2004); the nutritional content and palatability of leaves may also decrease over time as they develop increased chemical defenses to reduce insect herbivory, resulting in smaller larvae (Feeny, 1970). Earlier leaf-out phenology may also serve to conceal nests from the attentions of predators and brood parasites such as Brown-headed Cowbirds (*Molothrus ater*). Hence, northeast slopes may convey improved reproductive success for Cerulean Warblers.

Topographic position also influenced nest patch location; nests were more frequently found on either ridges or in valleys, and occurred comparatively less often on mid-slopes. This is consistent with Cerulean Warbler habitat use elsewhere in the range; the species is often found either on ridge tops or in lowland riparian areas (Buehler et al., 2013). Territory placement was not found to be related to topographic position, perhaps because a single male's territory may span several positions; for example, he may defend trees both in a stream valley and on the adjacent slope. Within a territory, females may decide where to build their nests at least partially on the basis of topography. As noted by Barnes et al. (2016), the heterogeneous structure and effective canopy gaps produced by steep slopes, a feature to which Cerulean Warblers are evidently attracted, may be amplified on ridges or on steep slopes adjacent to stream valleys. Females may therefore prefer to nest in valleys or on ridges if the resulting gaps produce increased access to prey, as discussed above.

Both Cerulean Warbler nest patches and territories were found to have a higher percentage of canopy cover than non-use points. At the territory level, this contrasts with the findings of Bakermans and Rodewald (2009), who recorded higher Cerulean Warbler densities in forest stands with open canopy structure. However, male territories in Ontario had high, dense canopies (Jones et al., 2001), and Barnes et al. (2016) determined that higher use areas in Indiana were characterized by a more homogeneous canopy structure without large gaps. Female Cerulean Warblers in the Appalachians selected nest patches with lower mid-story cover (Boves et al., 2013), while nest patches in Ontario were characterized by a denser upper canopy (Jones et al., 2001). Boves et al. (2013) determined that males in less-forested landscapes defended territories with more mature forest attributes, including higher canopy closure; the same pattern could potentially apply in southern Indiana.

Mean nest tree DBH in southern Indiana over the five-year period was almost identical to nest tree DBH in the Appalachian Mountains of Tennessee, which had a mean DBH of 44.0 cm (Boves et al., 2013). Mean nest height in Indiana likewise fell within the range of values reported from Tennessee (18–23 m, Boves et al., 2013) and Michigan (19–20 m, Rogers, 2006) but was considerably higher than nest heights in Ontario (mean of 11.8 m, Oliarnyk and Robertson, 2006). At our study site, mean nest tree height was 25.83 m ($SE \pm 0.51$) and nests tended to be positioned south or southeast relative to the trunk of the tree.

Cerulean Warblers at our site showed a clear preference for white oaks as nest trees; this reinforces the findings of Wagner and Islam (2014), who found that Cerulean Warblers in the HEE nest in white oaks more often than would be expected based on their availability on the landscape. Historically, oaks and hickories were dominant species in the Indiana landscape prior to European settlement (Abrams, 2003; Jenkins, 2013). However, nests were also found in a variety of other tree species over the five-year period; the next most-frequently used species included sugar maple, American sycamore, and tulip tree. Preference for white oaks and other species may be related to prey availability; several researchers have recorded Cerulean Warblers preferentially foraging in white oaks (George, 2009; MacNeil, 2010), and Wagner and Islam (2014) found that Lepidopteran larvae were more abundant on oaks and hickories in comparison with other tree species.

4.2. Nest success

Mayfield nest success rates at the HEE in southern Indiana varied from year to year, ranging from 11.0% in 2012 to 34.7% in 2014 (Mayfield, 1961). Mean success over the period 2012–2015 was 24.7%. Despite the tendency of Cerulean Warblers to select nest patches and territories closer to roads, nests located farther

from roads were more successful than those nearby. This may be due to increasing edge effects closer to roads, such as higher rates of predation or brood parasitism (Buehler et al., 2013; Swihart et al., 2013). Cerulean Warblers may be attracted to the canopy gaps and attendant heterogeneous vegetation structure created by roads, but if females place their nests in these areas they may suffer reduced reproductive fitness as a result. Likewise, although both nest patches and territories were characterized by a greater mean tallest tree height (areas with a higher canopy and/or larger trees overall), this variable was related to decreased nest success.

Nest height was also negatively correlated with nest success. Though nest heights in the HEE typically fall in the range of 18–20 m, lower nests were more likely to successfully produce one or more fledglings during the 2011–2015 period. Nests constructed lower in the canopy may be better concealed from aerial predators such as corvids, woodpeckers, and raptors (Auer et al., 2013; Buehler et al., 2013). They may also be less exposed to the elements; severe weather events such as torrential rain, high winds, or drought likely contribute to nest failures, and lower nests may be more sheltered from the effects of weather by a more substantial canopy above. Greater canopy cover was associated with increased nest success, though this relationship was weak.

Interestingly, although female Cerulean Warblers often preferred white oaks as nest trees, nests in white oaks were more likely to fail (though the 95% CI did not indicate significance). Cerulean Warblers at our study site also used a wide variety of other nest tree species (Fig. 2), making it difficult to draw conclusions about structural and foliage characteristics that may contribute to nest success. In the HEE, white oaks are associated with ridges and south-facing slopes (Kalb and Mycroft, 2013). While we were unable to test the influence of aspect on nest success, white oaks on more xeric southwestern slopes might experience less productivity in comparison with other tree species found more frequently on northeast-facing slopes, for the reasons described previously. It is also possible that we failed to include other ecological features associated with white oaks as possible explanatory variables in the model. White oaks tend to leaf out later in the spring than a number of other species (Polgar and Primack, 2011), meaning that Cerulean Warblers nesting in white oaks early in the breeding season may experience less concealment and potentially higher rates of failure.

Cerulean Warbler nests located in control units were somewhat more likely to succeed than those in even- or uneven-aged units, although this effect was not significant overall. Large harvest openings such as those found in the even- and uneven-aged units may create abrupt transitions that increase the likelihood of edge effects, such as higher rates of predation and brood parasitism (Andren and Angelstam, 1988; Paton, 1994).

4.3. Conservation and management implications

Land managers who wish to manage habitat for Cerulean Warblers in south-central Indiana state forests must be willing to consider the microhabitat preferences of local populations. In the Hardwood Ecosystem Experiment, Cerulean Warblers appear to make use of areas with taller, larger trees when establishing territories and situating their nests. In addition, male territories have more shrubs and small trees in the understory, which is consistent with growth of shade-tolerant shrub and tree species in the understories of uneven-aged stands. Certain uneven-aged management strategies, which are currently practiced throughout much of the Indiana state forest system, may therefore provide favorable conditions for Cerulean Warbler territories.

Male Cerulean Warbler territories were located on steep, northeast-facing slopes, which have high productivity, and the topographic variation produces a heterogeneous canopy structure

to which birds may be attracted (Barnes et al., 2016). To preserve good-quality habitat for territorial males, harvests that create large openings should be minimized on these slopes where possible. However, certain features preferred by Cerulean Warblers at the territory level were determined to negatively impact nest success. For example, both territories and nests were located closer to roadways on average; nests in close proximity to roads were more likely to fail, though this effect was not found to be significant. Promoting stands of relatively tall trees may provide attractive habitat for both nesting females and territorial males, who preferred taller, larger trees. However, nest success was higher in areas that had somewhat shorter, smaller trees overall. Even-aged management techniques can potentially result in stands of shorter trees, though such areas might then be less appealing to nesting females and territorial males.

In this study, we examined nest success (from laying to fledging) but did not attempt to estimate survival rates at other life stages. It is possible that features associated with a decreased chance of survival in the nesting phase may benefit Cerulean Warblers during the post-fledging period or thereafter. For example, lower nests may have a greater probability of producing fledglings, but higher nests could allow recent fledglings (who are relatively weak fliers) to remain out of reach of terrestrial predators during that vulnerable period in their life cycle. As they regenerate, even-aged harvests such as clearcuts could potentially provide valuable post-fledging habitat for mature forest dependent species such as Cerulean Warblers, a benefit supported by the literature (Vitz and Rodewald, 2006, 2010).

Cerulean Warblers may prefer characteristics associated with uneven-aged timber harvests for their territories, but land managers must balance this preference with the need to encourage regeneration of oak-hickory forests. Oaks are generally slow-growing, moderately shade-intolerant species, and the heavy reliance upon uneven-aged management frequently does not permit sufficient recruitment of oaks. Likewise, control areas (with no harvests or prescribed burns) may not experience enough disturbance to allow oak regeneration. Even-aged harvests such as clearcuts and shelterwoods can potentially provide adequate habitat for mature forest breeders during the initial cuts while allowing oak regeneration (Newell and Rodewald, 2012). Uneven-aged techniques that create larger openings, such as the patch cuts at the HEE, may also be valuable. As elsewhere in their range, it is clear that Cerulean Warblers in our area rely heavily upon white oak group species for their nest trees. Hence, any long-term forest management plan to benefit these birds must take into consideration the need for oak regeneration.

Acknowledgments

This paper is a contribution of the Hardwood Ecosystem Experiment, a partnership of the Indiana Department of Natural Resources, Purdue University, Ball State University, Indiana State University, Drake University, and The Nature Conservancy. Our research was funded from grants from the Indiana Department of Natural Resources through Purdue University, Ball State University, U.S. Fish and Wildlife Service, Amos W. Butler Audubon Society, Garden Club of America, and the Ball State University chapter of Sigma Xi and we thank them for their financial support of this research. We are especially grateful to Alice Besterman, Clayton Delancey, Ben Duke, Sarah Fischer, Zachary Jameson, and Danny Pirtle for assistance with data collection and to Sasha Auer and Kevin Barnes for help with all aspects of field research. HEE staff Andy Meier, Patrick Ma, and Jeff Riegel helped with identification challenges and offered additional support. Jason Doll provided invaluable assistance with statistical analysis. David LeBlanc provided helpful insights into Indiana forestry practices. This

manuscript benefitted greatly from the comments of Scott Haulton and three anonymous reviewers.

References

- Abrams, M.D., 2003. Where has all the white oak gone? *Bioscience* 53, 927–939.
- Andren, H., Angelstam, P., 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69, 544–547.
- Auer, S.A., Islam, K., Barnes, K.W., Brown, J.A., 2013. Documentation of predation of a nestling Cerulean Warbler by a Red-bellied Woodpecker. *Wilson J. Ornithol.* 152, 642–646.
- Bakermans, M.H., Rodewald, A.D., 2009. Think globally, manage locally: the importance of steady-state forest features for a declining songbird. *For. Ecol. Manage.* 258, 224–232.
- Bakermans, M.H., Rodewald, A.D., Vitz, A.C., 2012. Influence of forest structure on density and nest success of mature forest birds in managed landscapes. *J. Wildlife Manage.* 76, 1225–1234. <http://dx.doi.org/10.1002/jwmg.349>.
- Barg, J.J., Aiama, D.M., Jones, J., Robertson, R.J., 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). *Auk* 123, 795–806.
- Barnes, K.W., Auer, S.A., Islam, K., 2016. Integrating LIDAR-derived canopy structure into Cerulean Warbler habitat models. *J. Wildlife Manage.* 80, 101–116.
- Bartoń, K., 2015. MuMIn: Multi-Model Inference. R package version 15.1. <<http://CRAN.R-project.org/package=MuMIn>>.
- Bates, M.M.D., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-9. <<https://CRAN.R-project.org/package=lme4>>.
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Notes and observations: aspect transformation in site productivity research. *J. Forest.* 64, 691–692.
- BirdLife International, 2012. *Dendroica cerulea*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 20 December 2014.
- Blake, J.G., Hoppes, W.G., 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. *Auk* 103, 328–340.
- Boves, T.J., Buehler, D.A., 2012. Breeding biology, behavior, and ecology of *Setophaga cerulea* in the Cumberland Mountains, Tennessee. *Southeast. Nat.* 11, 319–330.
- Boves, T.J., Buehler, D.A., Sheehan, J., Wood, P.B., Rodewald, A.D., Larkin, J.L., Keyser, P.D., Newell, F.L., Evans, A., George, G.A., Wigley, T.B., 2013. Spatial variation in breeding habitat selection by Cerulean Warblers (*Setophaga cerulea*) throughout the Appalachian Mountains. *Auk* 130, 46–59.
- Buehler, D.A., Giocomo, J.J., Jones, J., Hamel, P.B., Rogers, C.M., Beachy, T.A., Varble, D. W., Nicholson, C.P., Roth, K.L., Barg, J., Robertson, R.J., Robb, J.R., Islam, K., 2008. Cerulean warbler reproduction, survival, and models of population decline. *J. Wildlife Manage.* 72, 46–653.
- Buehler, D.A., Hamel, P.B., Boves, T., 2013. Cerulean Warbler (*Setophaga cerulea*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 511. Academy of Natural Sciences, American Ornithologists' Union, Philadelphia, Washington, DC.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Carman, S.F., 2013. Indiana forest management history and practices. In: Swihart, R. K., Saunders, M.R., Kalb, R.A., Haulton, S.G., Michler, C.H. (Eds.), *The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 12–23. Gen. Tech. Rep. NRS-P-108.
- COSEWIC, 2010. COSEWIC Assessment and Status Report on the Cerulean Warbler *Dendroica Cerulea* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, CAN.
- Dearborn, D.C., Sanchez, L.L., 2001. Do Golden-cheeked Warblers select nest locations on the basis of patch vegetation? *Auk* 118, 1052–1057.
- ESRI, 2015. ArcGIS Desktop 10.2. Environmental Systems Research Institute, Redlands, CA.
- Falls, J.B., 1981. Mapping territories with playback: an accurate census method for songbirds. *Stud. Avian Biol.* 6, 86–91.
- Feeny, P., 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51, 565–581.
- Fekedulegn, D., Colbert, J.J., Rentch, J.S., Gottschalk, K.W., 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. *Castanea* 69, 92–108.
- Fekedulegn, D., Hicks Jr., R.R., Colbert, J.J., 2003. Influence of topographic aspect, precipitation, and drought on radial growth of four major tree species in an Appalachian watershed. *For. Ecol. Manage.* 177, 409–425.
- Fralish, J.S., 1994. The effect of site environment on forest productivity in the Illinois Shawnee Hills. *Ecol. Appl.* 4, 134–143.
- Fralish, J.S., 2003. The central hardwood forest: its boundaries and physiographic provinces. In: Van Samsbeek, J.W., Dawson, J.O., Ponder, F., Jr., Loewenstein, E.F., Fralish, J.S. (Eds.), *Proceedings, 13th Central Hardwood Forest Conference; 2002 April 1–3; Urbana, IL*. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN, p. 565. Gen. Tech. Rep. NC-234.
- George, G.A., 2009. Foraging ecology of male Cerulean Warblers and other neotropical migrants. Dissertation, West Virginia University, Morgantown, USA.
- Hamel, P.B., 2000. Cerulean Warbler Status Assessment. U.S. Fish and Wildlife Service, Fort Snelling, MN.
- Hamel, P.B., Welton, M.J., Smith III, C.G., Ford, R.P., 2009. Test of Partners in Flight effective detection distance for Cerulean Warbler. pp. 328–333. In: Rich, T.D., Arizmendi, C., Demarest, D.W., Thompson, C. (Eds.), *Tundra to Tropics: Connecting Birds, Habitats, and People*. Proceedings of the 4th International Partners in Flight Conference 13–16 February 2008, McAllen, TX. American Press, University of Texas-Pan, Edinburg (TX). 712.
- Harrell Jr., F.E., 2015. Hmisc: Harrell Miscellaneous. R package version 3.16-0. <<http://CRAN.R-project.org/package=Hmisc>>.
- Hartman, P.J., Maehr, D.S., Larkin, J.L., 2009. Habitat selection by Cerulean Warblers in eastern Kentucky. *Wilson J. Ornithol.* 121, 469–475.
- Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D., Megown, K., 2015. Completion of the 2011 National Land Cover Database for the coterminous United States – representing a decade of land cover change information. *Photogram. Eng. Rem. Sens.* 81, 345–354.
- Homoya, M.A., Abrell, D.B., Aldrich, J.R., Post, T.W., 1985. The natural regions of Indiana. *Proc. Indiana Acad. Sci.* 94, 245–268.
- Indiana Department of Natural Resources, 2013. Indiana county endangered, threatened, and rare species list, County: Brown <http://www.in.gov/dnr/naturepreserve/files/np_brown.pdf>. accessed 14 April 2015.
- Islam, K., Kaminski, K.J., MacNeil, M.M., Young, L.P., 2013. The Cerulean Warbler in Morgan-Monroe and Yellowwood State Forests, Indiana: Pre-treatment Data on Abundance and Spatial Characteristics of Territories. Pages 61–77. In: Swihart, Robert K., Saunders, Michael R., Kalb, Rebecca A., Haulton, G.Scott, Michler, Charles H. (Eds.), *The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, p. 350. Gen. Tech. Rep. NRS-P-108.
- Islam, K., Roth, K.L., 2004. Habitat Selection and Reproductive Success of Cerulean Warblers in Southern Indiana. Final Report submitted to U.S. Fish & Wildlife Service, Fort Snelling, MN, December 2004. Department of Biology Technical Report No. 4, Ball State University, Muncie, Indiana 51 p.
- Islam, K., Basile, C., 2002. Relative Abundance and Habitat Selection of Cerulean Warblers in Southern Indiana. Final Report submitted to U.S. Fish & Wildlife Service, Fort Snelling, MN, December 2002. Department of Biology Technical Report No. 1, Ball State University, Muncie, Indiana, 76 p.
- Iverson, L.R., Hutchinson, T.F., Prasad, A.M., Peters, M.P., 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *For. Ecol. Manage.* 255, 3035–3050.
- James, F.C., Shugart Jr., H.H., 1970. A quantitative method of habitat description. *Audubon Field Notes* 24, 727–736.
- Jenkins, M.A., 2013. The history of human disturbance in forest ecosystems of southern Indiana. In: Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, S.G., Michler, C.H. (Eds.), *The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 2–11. Gen. Tech. Rep. NRS-P-108.
- Jenkins, M.A., Parker, J.R., 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana state forests. *For. Ecol. Manage.* 109, 57–74.
- Jenness, J., 2006. Topographic Position Index (TPI), v.1.2. Jenness Enterprises, Flagstaff, AZ. <http://www.jennessent.com/downloads/TPI_Documentation_online.pdf>.
- Jones, J., DeBruyn, R.D., Barg, J.J., Robertson, R.J., 2001. Assessing the effects of natural disturbance on a Neotropical migrant songbird. *Ecology* 82, 2628–2635.
- Jones, J., McLeish, W.J., Robertson, R.J., 2000. Density influences census technique accuracy for Cerulean Warblers in eastern Ontario. *J. Field Ornithol.* 71, 46–56.
- Kalb, R.A., Mycroft, C.J., 2013. The Hardwood Ecosystem Experiment: goals, design, and implementation. The history of human disturbance in forest ecosystems of southern Indiana. In: Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, S.G., Michler, C.H. (Eds.), *The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp. 36–57. Gen. Tech. Rep. NRS-P-108.
- Kaminski, K.J., Islam, K., 2013. Effects of forest treatments on abundance and spatial characteristics of Cerulean Warbler territories. *Am. Midl. Nat.* 170, 111–120.
- MacNeil, M.M., 2010. Does Timber Harvesting Affect Cerulean Warbler Foraging Ecology? Thesis. Ball State University, Indiana, USA.
- Marshall, M.R., Cooper, R.J., 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology* 85, 432–445.
- Martin, T.E., 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79, 656–670.
- Martin, T.E., Roper, J.J., 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90, 51–57.
- Mayfield, H., 1961. Nesting success calculated from exposure. *Wilson Bull.* 73, 255–261.
- Mazerolle, M.J., 2015. AICcmodavg: Model selection and multimodel inference based on (QAICc). R package version 2.0-3. <<http://CRAN.R-project.org/package=AICcmodavg>>.
- Muscolo, A., Bagnato, S., Sidari, M., Mercurio, R., 2014. A review of the roles of forest canopy gaps. *J. Forest. Res.* 25, 725–736.
- Newell, F.L., Rodewald, A.D., 2011. Role of topography, canopy structure, and floristics in nest-site selection and nesting success of canopy songbirds. *For. Ecol. Manage.* 262, 739–749.
- Newell, F.L., Rodewald, A.D., 2012. Management for oak regeneration: short-term effects on the bird community and suitability of shelterwood harvests for canopy songbirds. *J. Wildlife Manage.* 76, 683–693.
- Oliarnyk, C.J., Robertson, R.J., 1996. Breeding behavior and reproductive success of cerulean warblers in southeastern Ontario. *Wilson Bull.* 108, 673–684.

- Paton, P.W.C., 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv. Biol.* 8, 17–26.
- Perkins, K.A., Wood, P.B., 2014. Selection of forest canopy gaps by male Cerulean Warblers in West Virginia. *Wilson J. Ornithol.* 126, 288–297.
- Polgar, C.A., Primack, R.B., 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytol.* 191, 926–941.
- R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- Robbins, C.S., Fitzpatrick, J.W., Hamel, P.B., 1992. A warbler in trouble: *Dendroica cerulea*. In: Hagan III, J.M., Johnston, D.W. (Eds.), *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, D.C. pp. 549–62.
- Rodewald, A.D., Yahner, R.H., 2001. Avian nesting success in forested landscapes: influence of landscape composition, stand and nest-patch microhabitat, and biotic interactions. *Auk* 118, 1018–1028.
- Rogers, C.M., 2006. Nesting success and breeding biology of Cerulean Warblers in Michigan. *Wilson J. Ornithol.* 118, 145–151.
- Rosenberg, K.V., Barker, S.E., Rohrbaugh, R.W., 2000. An Atlas of Cerulean Warbler Populations. Cornell Laboratory of Ornithology, Ithaca, New York, NY.
- Roth, K.L., Islam, K., 2007. Do Cerulean Warblers (*Dendroica cerulea*) exhibit clustered territoriality? *Am. Midl. Nat.* 157, 345–355.
- Roth, K.L., Islam, K., 2008. Habitat selection and reproductive success of Cerulean Warblers in Indiana. *Wilson J. Ornithol.* 120, 105–110.
- Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, Jr., D.J., Link, W.A., 2011. The North American breeding bird survey, results and analysis 1966–2010. USGS Patuxent Wildlife Research Center, Laurel, MD. <<http://www.pwrc.usgs.gov/bba>>.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York. 887 p.
- Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, S.G., Michler, C.H. (Eds.), 2013. *The Hardwood Ecosystem Experiment: a framework for studying responses to forest management*. Gen. Tech. Rep. NRS-P-108. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 350 p.
- U.S. Fish and Wildlife Service (USFWS), 2006. *Cerulean Warbler Risk Assessment and Conservation Planning Workshop*. National Conservation Training Center, Shepardsville, WV.
- Vitz, A.C., Rodewald, A.D., 2006. Can regenerating clearcuts benefit mature-forest songbirds? An examination of post-breeding ecology. *Biol. Conserv.* 127, 477–486.
- Vitz, A.C., Rodewald, A.D., 2010. Movements of fledgling ovenbirds (*Seiurus aurocapilla*) and worm-eating warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *Auk* 127, 364–373.
- Wagner, J., Islam, K., 2014. Nest-site selection and breeding ecology of the Cerulean Warbler in southern Indiana. *Northeast. Natural.* 21, 515–528.
- Weakland, C.A., Wood, P.B., 2005. Cerulean Warbler (*Dendroica cerulea*) microhabitat and landscape-level habitat characteristics in southern West Virginia. *Auk* 122, 407–508.
- Wickham, H., 2009. ggplot2: elegant graphics for data analysis. R package version 2.0-3. <<http://CRAN.R-project.org/package=ggplot2>>.
- Wood, P.B., Perkins, K.A., 2012. Behavioral activities of male Cerulean Warblers in relation to habitat characteristics. *Wilson J. Ornithol.* 124, 497–505.