CERULEAN WARBLER TERRITORY SIZE IS INFLUENCED BY PREY–RICH TREE ABUNDANCE

Jennifer R. Wagner[1,2] and **Kamal Islam**:   Department of Biology, Ball State University, Muncie, IN 47306 USA

Keith Summerville: Department of Environmental Science and Policy, Drake University, Des Moines, IA 50311 USA

ABSTRACT.   Food availability has far-reaching implications for the breeding success of birds and may be a limiting resource affecting populations. Many birds, such as the Cerulean Warbler (*Setophaga cerulea*), defend territories for foraging purposes, and the size of their territory is likely to vary with an area's potential for foraging. This study investigated the abundance of prey in various trees (white oak group [*Quercus alba* L. and *Q. prinus* L.], hickories [*Carya* spp.], and sugar maples [*Acer saccharum* Marshall]) to understand the relationship between prey availability, tree species, and territory size. Relative prey abundance using caterpillar frass (droppings) was calculated. Estimated basal area of the various tree groups within each territory was used to determine whether Cerulean Warbler territory size is predicted by prey-rich trees. The white oak group and hickory group dropped almost double the amount of frass compared to sugar maples, suggesting that the former groups may provide more prey to foraging Cerulean Warblers. Territory size ($n = 51$) was negatively correlated with the basal area of trees in the white oak group, positively correlated to the basal area of the sugar maple group, yet no relationship to hickory or total tree basal area (combined tree types) was found. Therefore, Cerulean Warblers may adjust territory size based on an awareness of the prey-productivity of different tree taxa.

Keywords: Avian, foraging habitat, frass collection, prey, *Setophaga cerulea*, territory size

INTRODUCTION

Food availability has far-reaching implications for the breeding success of avian species, as it affects egg production (Drent & Daan 1980; Perrins 1996), ultimate clutch size (Perrins & McCleery 1989; Aparicio 1994; Robertson 2009), number of broods (Nagy & Holmes 2005), the condition of nestlings (Herring et al. 2011), and the survival of fledglings (Martin 1987). Although some have argued that prey is a superabundant resource (Fretwell 1972; Wiens 1977) and has not contributed to the decline of Neotropical migrants (Rappole & McDonald 1994), there are hundreds of studies, both theoretical and experimental, that have demonstrated the limitations in prey during the avian breeding season (reviewed in Martin 1987) and the importance of vegetative structure in supporting ample prey resources (e.g., van Balen 1973).

Many birds defend territories during the breeding season to maximize foraging capacity (Hinde 1956; Brown 1969) and, therefore, territory size should maximize resource exploitation while minimizing defense-related energy expenditure (Hixon 1980). Territorial birds may use environmental cues that enable the selection of quality habitat (Brown 1964; Fretwell & Lucas 1970; Wiens 1977; Davies 1980; Chalfoun & Martin 2007). For example, food availability has been found to influence territory selection (Stenger 1958; Myers et al. 1979; Smith & Shugart 1987; Marshall & Cooper 2004) and breeding performance (Seki & Takano 1998; Nagy & Holmes 2005).

Because food is crucial to successful reproduction, we sought to understand its importance to the rapidly declining Cerulean Warbler (*Setophaga cerulea*) (Robbins et al. 1992; Hamel 2000; Sauer et al. 2008). Cerulean Warblers primarily forage in hickories (*Carya* spp.; Gabbe et al. 2002), chestnut and white oaks (*Quercus prinus* L. and *Q. alba* L.; George 2009; MacNeil 2010), and sugar maples (*Acer saccharum* Marshall; George 2009). Cerulean Warblers glean insects from foliage (Buehler

[1] *Current address:* Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061 USA.
[2] *Corresponding author:* Jennifer Wagner; 845-536-3285; e-mail: wagnerjr@vt.edu.

et al. 2013) and their adult diet consists primarily of lepidopteran larvae and homopterans (Sample et al. 1993; Buehler et al. 2013). Although little is known about the nestling diet (Wagner 2012, Auer et al. In Press), Lepidoptera larvae (caterpillars), in particular, are a large and energetically profitable food source for nestlings as they have little chitin, making them highly digestible to birds (Bernays 1986; Bell 1990). Additionally, the majority of caterpillars are defoliators, making them readily available to gleaners like the Cerulean Warbler (MacArthur 1959; Holmes & Schultz 1988).

Due to the importance of caterpillars as an excellent food source, hatching of insectivorous birds is synchronized with a peak in insect prey abundance (Lack 1968; Visser et al. 2006; García-Navas & Sanz 2011). The importance is exemplified by recent work from the Netherlands; climatic cues have been associated with asynchrony in peak caterpillar abundance of the winter moth (*Operophtera brumata* L.) and energy demands of the Great Tit (*Parus major* L.), which has contributed to a decline in fledgling number and weight (Visser et al. 2006). Therefore, synchronizing reproduction and/or raising offspring in areas with ample resources are imperative.

No study has yet investigated Cerulean Warbler territory selection in relation to prey availability. The objective of this study was twofold. First, to determine which tree groups (categories described below) contain the greatest amount of caterpillars, an optimal prey item, during the avian breeding season. This was measured through caterpillar frass (droppings), which is highly correlated to caterpillar abundance (Seki & Takano 1998) and, therefore, is useful for comparing relative prey abundances (van Balen 1973; Zandt 1994). Second, tree surveys were conducted throughout all territories and post-hoc analyses were performed to determine if basal area of prey-rich trees (i.e., those with the greatest frass drop) was a useful predictor of territory size. We hypothesized that areas with a greater abundance of prey-rich trees would be deemed of higher quality by the Cerulean Warbler males and, therefore, would necessitate the defense of a smaller area for the territory compared with males in areas with a lower abundance of prey–rich trees.

METHODS

Study area.—This study was conducted from May to July 2011, in Morgan–Monroe (~9,700 ha; 39° 19′ N, 86° 24′ W) and Yellowwood (~9,500 ha; 39° 11′ N, 86° 19′ W) State Forests in Morgan, Monroe, and Brown counties, Indiana. Both forests are within the Brown County Hills region (Homoya et al. 1984), with wet-mesic bottomlands dominated by sugar maple, American sycamore (*Platanus occidentalis* L.), and American beech (*Fagus grandifolia* Ehrh.) and mesic slopes dominated by sugar maple, tulip poplar (*Liriodendron tulipifera* L.), American beech, and northern red oak (*Quercus rubra* L.). Dry mesic slopes are dominated by white oak (*Quercus alba* L.) (Jenkins et al. 2004). The research was conducted on nine study sites, selected by the Hardwood Ecosystem Experiment (HEE) to study faunal response to silviculture (Swihart et al. 2013). For testing the questions in this study, vegetation was sampled at the scale of the territory, and thus we consider the landscape-scale silvicultural practices to be reflected in the analysis of basal area.

Avian territory delineation and vegetation sampling.—Male Cerulean Warblers were located using point count surveys in May 2011 conducted between 0600 to 1030 hr Eastern Standard Time at each of the nine HEE study sites (Jones & Islam 2006; Wagner & Islam 2014). We conducted 1–3 site revisits at areas where Cerulean Warblers were detected and demarcated territories. If a male was not apparent on a revisit, playback was used to elicit a territorial song (Falls 1981). We located singing males and recorded GPS locations of perch trees (range = 5–17 per male). Territories were typically demarcated during a single visit. However, if a bird was minimally active on the first visit, we revisited it a second time to demarcate the minimum number of trees. GPS coordinates were used to produce minimum convex polygons in ArcMap (ArcGIS 10.0, ESRI 2010).

To determine basal area (BA) of mature trees in each territory, we identified the centroid of the territory as the cross point of the two longest distances across each territory (in ArcGIS 10.0). At the centroid, an 11.3 m radius vegetation plot (0.04 ha, James & Shugart 1970) was established. Species and diameter at breast height (DBH) of all trees >10 cm DBH were determined. BA of each tree was calculated as $BA = 0.00007854 \times DBH^2$. To calculate BA

for each tree group, the BA was summed across all trees in the plot. This total basal area was then divided by 0.04 ha (vegetation plot size) to determine the BA in m^2/ha.

Frass collection.—Mass of caterpillar frass (droppings) was used as a proxy for prey abundance. Frass was collected during two sample periods using funnel traps placed below trees within Cerulean Warbler territories. We used low density polyethylene plastic (thickness of 0.05 cm) to form funnels with an overall collection surface of 0.2 m^2 (diameter = 0.5 m). The bottom of the funnel was sealed during the sample period and affixed to a 0.91 m wooden stake (adapted from Liebhold & Elkinton 1988). Two traps were placed below each tree to determine precision of sampling methodology, producing a total collection area of 0.4 m^2 per tree. The first trap was placed at the part of the tree where there was the greatest distance between crown foliage edge and trunk (as estimated visually by J. Wagner). The second trap was placed as close to 180° from this location as possible and both traps were equidistant from the trunk and outer extremities of the crown.

Frass was sampled from 23 trees within a subset of Cerulean Warbler territories, selected because these territories were demarcated early enough within the season to ensure sampling during the period of interest. Four to six randomly selected trees (within the categories of white oak, hickory, or sugar maple) in six territories with two traps per tree were sampled. A stratified random sampling method was used to ensure even sampling of points within territory polygons. Briefly, the territory was divided into concentric circles and a random point was generated within each area to ensure that sampling was distributed throughout the territory. At each random point, the nearest tree of at least 15 cm DBH in any cardinal direction was used as the random tree. This tree size minimum allowed us to sample the vertical stratification of all vegetative strata (midstory and lower- to upper-canopy) because although Cerulean Warblers are high canopy nesters and singers, they do spend time in relatively lower strata during foraging (Barg et al. 2006; Wood & Perkins 2012). The species, height, DBH, and coordinates of the 23 sampled trees were noted.

Frass was collected with a Ziploc bag during a four day period in early June and an eight day period in late June/early July. In the field, large plant matter was removed from the trap.

In the laboratory, reduced mm paper was used to sort only frass pellets larger than 0.6 mm, since smaller pellets have a negligible influence on frass mass (Tinbergen 1960) and reduce efficiency. Samples were dried in an oven at 85° C for 24 hr (Tinbergen 1960) and weighed to 0.001 g on an OHAUS Precision Standard TS00D microbalance (Parsippany, New Jersey). The collected masses were summed across both sample periods for each tree to produce a total frass mass. No attempt to identify collected frass to associated Lepidoptera species was made.

Data analysis.—To determine which trees had the greatest prey abundance, we used the sample periods of 6 June to 9 June and 28 June to 6 July 2011. Although we attempted to sample across a wider temporal scale, many rainy days prohibited the collecting of frass samples from all trees during the same dates. We therefore only included dates for which all trees were sampled and during which breeding (nestling and/or fledgling period) was still occurring. We compared total frass mass (mg) from prey-host trees of the categories: hickory spp. (Shagbark [*Carya ovata* (Mill.) K. Koch], pignut [*C. glabra* (Mill.) Sweet], and bitternut [*C. cordiformis* (Wangenh.) K. Koch]; $n = 5$), white oak group (white oak and chestnut oak; $n = 14$), and sugar maple ($n = 4$). Daily frass mass for individual trees was summed across the aforementioned dates, producing a total frass mass for each tree. Data were checked for normality and raw data were used for analyses. Neither height nor DBH significantly affected frass drop and therefore were not used in analyses. A one–way analysis of variance (ANOVA) was used to compare total frass mass between tree groups (Minitab Statistical Software 2013). Fisher's post hoc analysis was used to compare individual group means.

The hypothesis that territory size is influenced by density of prey-rich or prey-poor trees within the territory was tested using linear regressions with territory size as the dependent variable and basal area of the tree category as the independent variable (white oak group, hickory spp., or sugar maples). To meet normality assumptions, territory sizes were log10-transformed (Minitab Statistical Software 2013).

The efficiency and precision of using constructed frass traps was tested by determining whether two traps under the same tree produced unified results. The amount of frass per trap per

day was used to test for differences in frass collection between the two traps of the same tree. Instances where one trap fell over (15/100 samples) were not used in the analysis. We used 75 paired samples, collected from 60 traps under 30 trees (some sampled trees were not used in analyses). The collection of two time periods during 28 June to 6 July 2011 allowed the addition of samples to this test. A paired *t*-test was used to test for differences in frass mass collected per trap (Minitab Statistical Software 2013). All statistical tests were conducted using an α-level of 0.05, however marginal significance (α-level = 0.05–0.10) was considered with post-hoc analysis due to small sample sizes.

RESULTS

The total frass drop (mg; mean $\pm$ SE) produced by each tree category during the sample periods combined was: white oak group (50.9 $\pm$ 5.1), hickory spp. (47.7 $\pm$ 4.7), and sugar maple (27.2 $\pm$ 5.1) (Fig. 1). There was a marginally significant difference in total frass drop during our sample period among the three tree categories ($F_{2,20}$ = 3.23, p = 0.061; Fig. 1). Trees in the white oak group produced more frass than sugar maples (Fisher's LSD: p = 0.020) and hickories tended to produce more frass than sugar maples (Fisher's LSD: p = 0.080).

Average size of the 51 territories analyzed was 2145 $\pm$ 298 m^2 [mean $\pm$ SE] (range 108–10225 m^2) and when analyzed for a relationship to basal area of particular trees, several relationships were found (Table 1). Territory size was negatively correlated to the basal area of trees in the white oak group ($F_{1,49}$ = 5.93, r^2 = 0.108, p = 0.019; Fig. 2) and positively correlated to the basal area of sugar maples ($F_{1,49}$ = 5.43, r^2 = 0.099, p = 0.024; Fig. 3). There was no relationship between territory size and the basal area of hickories or all trees together ($p > 0.05$). These data suggest that territory size is influenced specifically by the density of trees in the white oak group; smaller territories tend to have higher densities of these trees than larger territories. Conversely, larger territories tended to have a greater density of sugar maples.

No difference was found between frass mass collected from traps A and B of the same tree (t_{74} = 0.48, p = 0.63). Thus, one trap per tree may be sufficient for sampling of relative frass drop from tree crowns.
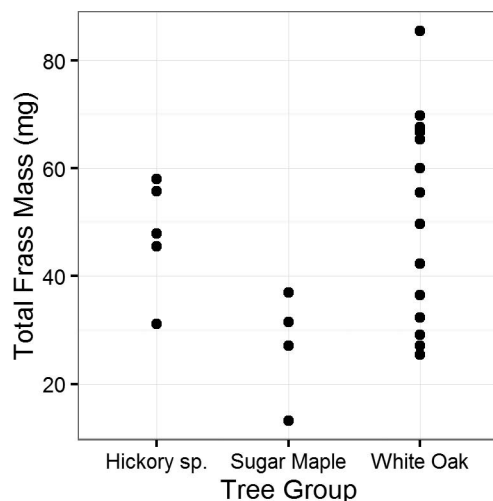

Figure 1.—Amounts of insect frass collected under three taxonomic tree groups, i.e., white oak group, hickories, and sugar maples. Trees were sampled from 6 June to 9 June and 28 June to 6 July 2011.

DISCUSSION

Trees in the white oak group and hickories dropped nearly double the amount of frass compared to sugar maples. The finding that oaks in particular contain a high abundance of insects (specifically Lepidoptera) is consistent with findings from other locations in the eastern deciduous forest (Wagner et al. 1995; Butler & Strazanac 2000a; Summerville et al. 2003) and in Europe (Southwood 1961; Veen et al. 2010). A tree fogging study in Ohio found that oaks tend to support greater species richness and abundance of Lepidoptera than beeches (Summerville et al. 2003). In the Baltic Islands of Sweden, frass biomass was highest (nearly double the mass) from oak species compared with three other deciduous taxa and two coniferous taxa (Veen et al. 2010). In Appalachia, research involving branch clippings produced similar results: white oaks contained ~25% of caterpillar species abundance, whereas maples contained 15% (Butler & Strazanac 2000b). Butler & Strazanac (2000b) also reported caterpillar abundance on hickory and chestnut oak and found that they supported 18% and 17%, respectively. This is somewhat comparable to our finding, as hickories dropped more frass than maples, yet less than trees in the white oak group. Interestingly, Butler & Strazanac (2000b) reported ~25% of caterpillar abundance on trees

Table 1.—Basal area results of each tree group throughout Cerulean Warbler territories in 2011. The "All Trees" category includes the three prior tree groups and any other trees with a diameter at breast height (DBH) >10 cm.

Basal area (m²/ha)			
Territory size (m²)	White oak group	Hickory spp.	Sugar maples	All trees
108	19.72	4.23	0.00	33.92
189	3.77	0.00	0.00	11.81
238	7.88	2.50	3.02	28.74
268	9.10	0.44	0.00	34.77
333	4.01	0.00	2.53	17.81
384	4.02	2.06	0.68	14.59
508	19.28	0.30	0.40	27.10
578	0.00	2.96	6.52	15.98
617	21.69	0.22	0.00	32.52
621	0.00	1.37	0.31	8.31
734	23.73	2.91	0.20	38.19
755	0.00	9.08	0.28	13.81
827	1.71	3.96	1.37	15.85
871	3.63	14.44	1.82	23.27
881	0.00	0.00	0.00	22.69
929	0.00	9.21	0.00	20.15
973	10.78	2.43	4.02	31.04
975	10.02	11.28	0.00	38.14
980	18.70	2.14	0.75	28.74
1050	14.74	0.00	0.20	23.51
1124	0.00	0.00	4.75	18.66
1134	14.28	1.25	2.63	21.70
1185	21.02	0.72	0.00	21.74
1219	16.89	2.00	0.25	21.24
1363	0.00	0.00	0.00	11.98
1475	0.00	0.00	2.55	15.28
1475	0.00	0.00	1.70	15.85
1507	8.77	1.34	3.09	33.99
1540	5.11	3.84	0.00	39.75
1626	9.25	8.20	0.00	17.45
1840	14.19	0.28	4.60	23.77
1938	0.00	3.67	0.00	19.36
2006	19.02	0.00	0.54	29.32
2076	0.00	0.00	4.53	19.69
2144	0.00	0.00	5.19	18.57
2286	0.00	11.11	5.27	21.38
2379	0.00	0.00	6.26	32.45
2385	17.58	0.00	1.65	19.23
2607	0.00	0.00	0.00	30.01
2760	18.95	0.00	2.37	21.33
3413	2.79	5.66	0.23	10.18
3421	0.00	7.93	0.00	12.60
3923	0.00	4.83	1.81	22.01
4189	0.00	0.00	3.06	22.07
4318	0.00	7.48	2.58	22.11
4369	0.00	0.00	0.00	33.47
5335	0.00	0.00	3.62	3.62
5882	0.00	0.00	7.71	35.16
7592	0.00	14.03	0.71	15.40

Table 1.—Continued.

Basal area (m²/ha)			
Territory size (m²)	White oak group	Hickory spp.	Sugar maples	All trees
7826	6.72	2.85	4.11	20.23
10225	0.00	2.84	3.87	20.32

in the red oak group, suggesting that they may support just as high of a food source for insectivorous warblers as the trees in the white oak group, although we did not sample enough trees in that group to make frass comparisons.

We associate the greater frass drop in white oak trees to two non-mutually exclusive mechanisms. Prey was more numerous and/or prey was larger during the collected time periods in trees in the white oak and hickory groups than in sugar maples. Both of these explanations would account for the greater mass of frass drop and contribute to large quantities or individually-large prey items. We excluded frass smaller than 0.6 mm in diameter, and thus excluded the smallest larvae from our samples. Large quantities of small caterpillars may be a substantial food source, particularly if they are clumped together, alleviating foraging effort on the bird (e.g., Naef-Daenzer & Keller 1999). These small frass particles were negligible (~1% of most samples) and the exclusion of the smallest frass was performed uniformly across all sampled trees; however, future studies may consider including this size of frass.

When we analyzed how territory size related to the basal area of tree type within the territory, we found that territory sizes of the Cerulean Warbler had a negative relationship to BA of trees in the white oak group (the most prey-rich trees group) within their territory. Yet, there was no relationship between territory size and the hickory tree group (the next highest prey-rich group). There was a positive relationship with sugar maple BA, and no relationship to total tree BA. To our knowledge, this is the first study to document the finding that trees in the white oak group may have a relationship to Cerulean Warbler territory size, allowing Cerulean Warblers to maintain smaller territories. This finding corroborates field observations, as the Cerulean Warbler is found in high abundance in oak and hickories at our field sites (Barnes et al. 2016) and in other parts of their range (e.g., the Appalachian Mountains, Boves
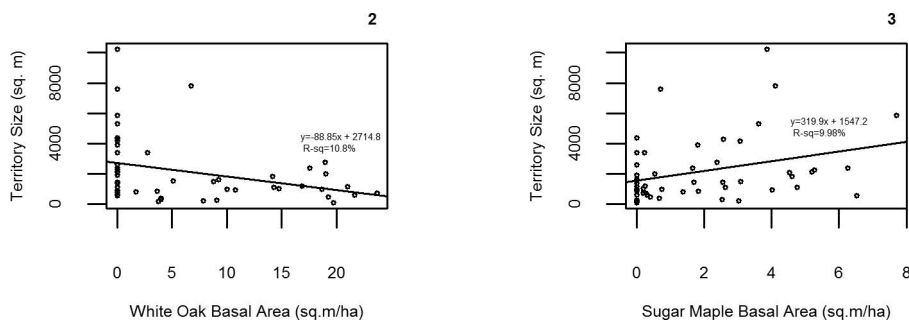
Figures 2 & 3.—The relationship between basal area of white oak and sugar maple trees and the territory size of Cerulean Warblers. 2. Territory size tended to be negatively related to the basal area of trees in the white oak group; 3. Territory size tended to be positively related to the basal area of sugar maples. There was no relationship between territory size and the basal area of hickories or all trees (not shown).

et al. 2013; Wood et al. 2013), while also preferentially selecting oak (and other large trees) as song perches (Jones & Islam 2006). However, when oak is not readily available, Cerulean Warblers will use other tree species for daily activities, such as black cherry (*Prunus serotina* Ehrh.) and black locust (*Robinia pseudoacacia* L.) in West Virginia, American elm (*Ulmus americana* L.) and sycamore in Ohio (Wood et al. 2013), and sugar maple in Ontario, Canada (Oliarnyk & Roberton 1996). However, as discussed above, there may be vast differences in the extent to which these other tree species are able to support an abundant food supply for Cerulean Warblers.

In this study, territory size was used as a proxy for energy expenditure; territory defense is an energetically-demanding task (Walsberg 1983) and adults (especially males) must simultaneously forage for nestlings and provide predation defense. Given the evidence provided here and the foraging selectivity found in other studies (Gabbe et al. 2002; George 2009; MacNeil 2010), it is likely that white oak and hickory-dominated stands may alleviate energetic pressures and support a greater abundance of Cerulean Warblers compared with areas dominated with other trees species (e.g., Barnes et al. 2016). Further, it is plausible that they may have higher reproductive success in oak/hickory-dominated stands compared with areas dominated with other tree species because of the differences in foraging potential necessary for self-maintenance and provisioning of nestlings (e.g., Varble 2006); however, this needs to be studied.

Although it can be beneficial to select territories with a high density of foraging trees, there are at least two mechanisms which may act to reverse the presumed positive impacts of increases in prey. First, due to the quality of prey available in specific tree stands, these areas may be deemed more valuable by conspecifics and thus, male Cerulean Warblers may expend more energy defending their territories. For example, clustering of Cerulean Warbler territories (Roth & Islam 2007; Dibala 2012) has resulted in close territory boundaries and may require ample energy to defend. Second, predator abundance may be influenced by forest tree composition (e.g., Auer et al. 2013). For example, at our project sites, small mammal populations were correlated with mast production of oaks (Kellner et al. 2013) and Eastern chipmunks have caused forced-fledging of nestling Cerulean Warblers in the Appalachian Mountains (Boves 2011).

This study provides the first evidence that Cerulean Warblers seek prey-rich trees, specifically trees in the white oak group, for establishing territory size. Other studies have noted the importance of prey-rich areas, such as an increase in territory number in a black locust grove after a lepidopteran outbreak (Rosenberg et al. 2000) and an apparent increase in successful nests during a cicada outbreak year compared with non-outbreak years (Varble 2006). Future studies with larger sample sizes of prey abundance are warranted to further establish the importance of specific tree stands to this bird species. When compared to trees in the white oak group, we under-sampled maples and hickories for frass. Yet, even with these limited, unbalanced data on frass drop, there is an important suggested difference in prey productivity across the three tree types. Furthermore,

the inverse relationship between oak BA and territory size when we used a large sample of territories suggests that warblers recognize the difference in tree type and adjust territories appropriately. However, this apparent pattern needs further testing with a large, balanced data set which aims to collect frass from the three main tree types within territories during the breeding season.

This study adds to the mounting evidence that the Cerulean Warbler has specific habitat associations and, therefore, may rely on specific tree taxa for their continued existence. This may be important for conservation efforts because studies of eastern deciduous forest structure indicate that mature oak and hickory forests may be succeeded by maple and beech forests (e.g., Saunders & Arseneault 2013). At our project sites, the oak and hickory group comprised older individuals with multiple younger cohorts of other tree species (Saunders and Arseneault 2013). At Kieweg Woods in west-central Indiana, the same trend in tree succession was found whereby sugar maple, American beech, and slippery elm (*Ulmus rubra* Muhl.) dominate the young age classes (Cowell & Hayes 2007). It is understood that human disturbance is the primary cause of forest structure changes, either through the use of specific harvest regimes or forest suppression (Cowell & Hayes 2007; Jenkins 2013). In the future, it will be important to monitor and identify specific forest areas that are crucial to declining insectivorous birds, such as the Cerulean Warbler.

ACKNOWLEDGMENTS

LITERATURE CITED

Aparicio, J.M. 1994. The seasonal decline in clutch size: an experiment with supplementary food in the kestrel, *Falco tinnunculus*. Oikos 71:451–458.

Auer, S.A., K. Islam, K.W. Barnes & J.A. Brown. 2013. Documentation of Red-Bellied Woodpecker predation of a Cerulean Warbler nestling. Wilson Journal of Ornithology 125:642–646.

Auer, S., K. Islam, J.R. Wagner, K.S. Summerville & K. Barnes. 2016. Cerulean warbler nestling diet and adult nest provisioning behaviors in southern Indiana. Wilson Journal of Ornithology. In Press.

Barg, J.J., D.M. Aiama, J. Jones & R.J. Robertson. 2006. Within-territory habitat use and microhabitat selection by male Cerulean Warblers (*Dendroica cerulea*). The Auk 123:795–806.

Barnes, K., K. Islam & S. Auer. 2016. Integrating LIDAR-derived canopy structure into Cerulean Warbler habitat models. Journal of Wildlife Management 80:101–116.

Bell, G.P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies in Avian Biology 13:416–422.

Bernays, E.A. 1986. Evolutionary contrasts in insects: nutritional advantages of holometabolous development. Physiological Entomology 11:377–382.

Boves, T.J. 2011. Multiple responses by Cerulean Warblers to experimental forest disturbance in the Appalachian Mountains. Ph.D. Dissertation, University of Tennessee, Knoxville, Tennessee. 221 pp.

Boves, T.J., D.A. Buehler, P.B. Wood, A.D. Rodewald, J.L. Larkin, P.D. Keyser, G.A. George, J. Sheehan, F.L. Newell & A. Evans. 2013. Spatial variation in breeding habitat selection by Cerulean Warblers throughout the Appalachian Mountains. The Auk 130:46–59.

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76:160–169.

Brown, J.L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bulletin 81:293–329.

Buehler, D.A., P.B. Hamel & T. Boves. 2013. Cerulean Warbler (*Setophaga cerulea*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America. At: http://bna.birds.cornell.edu/bna/species/511 (Accessed 1 November 2015).

Butler, L. & J. Strazanac. 2000a. Macrolepidopteran larvae sampled by tree bands in temperate mesic

and xeric forests in the eastern United States. Proceedings of the Entomological Society of Washington 102:188–197.

Butler, L. & J. Strazanac. 2000b. Occurrence of Lepidoptera on selected host trees in two central Appalachian National Forests. Annals of the Entomological Society of America 93:500–511.

Chalfoun, A.D. & T.E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983–992.

Cowell, C.M. & J.J. Hayes. 2007. Structure, history, dynamics of a mature oak-beech forest in western Indiana. The Journal of the Torrey Botanical Society 134:215–222.

Dibala, R. 2012. Population response of a declining songbird to silviculture: How Cerulean Warbler (*Setophaga cerulea*) territory size and settlement patterns fair in the face of forest disturbance. M.Sc. Thesis, Ball State University, Muncie, Indiana. 110 pp.

Davies, N.B. 1980. The economics of territorial behavior in birds. Ardea 68:63–74.

Drent, R.H & S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

ESRI. 2010. ArcGIS Version 10.0. Redlands, California.

Falls, J.B. 1981. Mapping territories with playback: an accurate census method for songbirds. Studies in Avian Biology 6:86–91.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey. 217 pp.

Fretwell, S.D. & H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Gabbe, A.P., S.K. Robinson & J.D. Brawn. 2002. Tree-species preferences of foraging insectivorous birds: implications for floodplain forest restoration. Conservation Biology 16:462–470.

García-Navas, V. & J.J. Sanz. 2011. The importance of a main dish: nestling diet and foraging behavior in Mediterranean Blue Tits in relation to prey phenology. Oecologia 165:639–649.

George, G.A. 2009. Foraging ecology of male Cerulean Warblers and other neotropical migrants. Ph.D. Dissertation. West Virginia University, Morgantown, West Virginia. 96 pp.

Hamel, P.B. 2000. Cerulean Warbler status assessment. U.S. Department of the Interior, Fish and Wildlife Service, Minneapolis, Minnesota. 137 pp.

Herring, G., M.I. Cook, D.E. Gawlik & E.M. Call. 2011. Food availability is expressed through physiological stress indicators in nestling White Ibis: a food supplementation experiment. Functional Ecology 25:682–690.

Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis 98:340–369.

Hixon, M.A. 1980. Food production and competitor density as the determinants of feeding territory size. American Naturalist 115:510–530.

Holmes, R.T. & J.C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology 66:720–728.

Homoya, M.A., D.B. Abrell, J.R. Aldrich & T.W. Post. 1984. The natural regions of Indiana. Proceedings of the Indiana Academy of Science 94: 245–268.

James, F.C. & H.H. Shugart, Jr. 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. Pp. 2–11. *In* The Hardwood Ecosystem Experiment: a Framework for Studying Responses to Forest Management. (R.K. Swihart, M.R. Saunders, R.A. Kalb, S.G. Haulton & C.H. Michler, Eds.). Gen. Tech. Rep. NRS-P-108. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Jenkins, M.A., C.R. Webster, G.R. Parker & M.A. Spetich. 2004. Coarse woody debris in managed central hardwood forests of Indiana, USA. Forest Science 50:781–792.

Jones, K. & K. Islam. 2006. Selection of song perches by Cerulean Warblers. Proceedings of the Indiana Academy of Science 115:37–43.

Kellner, K.F., N.A. Urban & R.K. Swihart. 2013. Short-term responses of small mammals to timber harvest in the United States Central Hardwood Forest Region. Journal of Wildlife Management 77:1650–1663.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen and Co. Ltd. Oxford.

Liebhold, A.M. & J.S. Elkinton. 1988. Techniques for estimating the density of late-instar Gypsy Moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations using frass drop and frass production measurements. Entomological Society of America 17:382–384.

MacArthur, R.H. 1959. On the breeding distributions patterns of North American migrant birds. The Auk 76:318–325.

MacNeil, M. 2010. Foraging ecology of Cerulean Warblers in southern Indiana. M.Sc. Thesis, Ball State University, Muncie, Indiana. 38 pp.

Marshall, M.R. & R.J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. Ecology 85:432–445.

Martin, T.E. 1987. Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology, Evolution, and Systematics 18:453–487.

Minitab Statistical Software. 2013. Version 17.1.0. Minitab, Inc., State College, Pennsylvania.

Myers, J.P., P.G. Conners & F.A. Pitelka. 1979. Territory size in wintering Sanderlings: the effect

of prey abundance and intruder density. The Auk 96:551–561.

Naef-Daenzer, B. & L.F. Keller. 1999. The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. Journal of Animal Ecology 68:708–718.

Nagy, L.R. & R.T. Holmes. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86:675–81.

Oliarnyk, C.J. & R.J. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. Wilson Bulletin 108:673–684.

Perrins, C.M. & R.H. McCleery. 1989. Laying date and clutch size in the Great Tit. Wilson Journal of Ornithology 101:236–253.

Perrins, C.M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138:2–15.

Rappole, J.H. & M.V. McDonald. 1994. Cause and effect in population declines of migratory birds. The Auk 111:652–660.

Robbins, C.S., J.W. Fitzpatrick & P.B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pp. 549–562. *In* Ecology and Conservation of Neotropical Migrant Landbirds (J.M. Hagan III & D.W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

Robertson, B.A. 2009. The influence of spatio-temporal variation in food availability and nest-predation risk on clutch-size decisions. Condor 111:523–533.

Rosenberg, K.V., S.E. Barker & R.W. Rohrbaugh. 2000. An atlas of Cerulean Warbler populations. Final report to USFWS: 1997-2000 breeding seasons. Cornell Laboratory of Ornithology, Ithaca, New York. 55 pp.

Roth, K. & K. Islam. 2007. Do Cerulean Warblers (*Dendroica cerulea*) exhibit clustered territoriality? American Midland Naturalist 157:345–355.

Sample, B.E., R.J. Cooper & R.C. Whitmore. 1993. Dietary shifts among songbirds from a diflubenzuron-treated forest. Condor 95:616–624.

Sauer, J.R., J.E. Hines & J. Fallon. 2008. The North American Breeding Bird Survey, Results and Analysis 1966–2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center, Laurel, Maryland. At: http://www.mbr-pwrc.usgs.gov/bbs/bbs2007.html (Accessed 1 November 2015).

Saunders, M.R. & J.E. Arseneault. 2013. Pre-treatment analysis of woody vegetation composition and structure on the Hardwood Ecosystem Experiment research units. Pp. 96–125. *In* The Hardwood Ecosystem Experiment: a Framework for Studying Responses to Forest Management. (R.K. Swihart, M.R. Saunders, R.A. Kalb, S.G. Haulton & C.H. Michler, Eds.) Gen. Tech. Rep. NRS-P-108. Newtown Square, PA: U.S.

Department of Agriculture, Forest Service, Northern Research Station. 350 pp.

Seki, S. & H. Takano. 1998. Caterpillar abundance in the territory affects the breeding performance of Great Tit (*Parus major minor*). Oecologia 114:514–521.

Smith, T.M. & H.H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68:695–704.

Southwood, T.R.E. 1961. The number of species of insect associated with various trees. Journal of Animal Ecology 30:1–8.

Stenger, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. The Auk 75:125–140.

Summerville, K.S., T.O. Crist, J.K. Kahn & J.C. Gering. 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. Ecological Entomology 28:747–757.

Swihart, R.K., M.R. Saunders, R.A. Kalb, G. Haulton, G.S., & C.H. Michler (Eds). 2013. The Hardwood Ecosystem Experiment: a Framework for Studying Responses to Forest Management. General Technical Report NRS-P-108. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 350 pp.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie 13:265–343.

van Balen, J.H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. Ardea 61:1–93.

Varble, D. 2006. The effects of periodic cicada emergence on forest birds and the ecology of Cerulean Warblers at Big Oaks National Wildlife Refuge. M.Sc. Thesis, University of Tennessee. Knoxville, Tennessee. 104 pp.

Veen, T., B.C. Sheldon, F.J. Weissing, M.E. Visser, A. Qvarnström & G.-P. Sætre. 2010. Temporal differences in food abundance promote coexistence between two congeneric passerines. Oecologia 162:873–884.

Visser, M.E., L.J.M. Holleman & P. Gienapp. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164–172.

Wagner, D.L., J.W. Peacock, J.L. Carter & S.E. Talley. 1995. Spring caterpillar fauna of oak and blueberry in a Virginia deciduous forest. Annals of the Entomological Society of America 88:416–426.

Wagner, J.R. 2012. Cerulean Warbler population and breeding response to recent silviculture and influences of prey availability on avian nesting ecology. M.Sc. Thesis, Ball State University, Muncie, Indiana. 173 pp.

Wagner, J.R. & K. Islam. 2014. Nest-site selection and breeding ecology of the Cerulean Warbler in southern Indiana. Northeastern Naturalist 21: 515–528.

Walsberg, G.E. 1983. Avian ecological energetics. Pp.161–220. *In* Avian Biology. (D.S. Farner & J.R. King, Eds.). Academic Press, New York, New York.

Wiens, J.A. 1977. On competition and variable environments. American Scientist 65:590–597.

Wood, P.B. & K.A. Perkins. 2012. Behavioral activities of male Cerulean Warblers in relation to habitat characteristics. Wilson Journal of Ornithology 124:497–505.

Wood, P.B., J. Sheehan, P. Keyser, D. Buehler, J. Larkin, A. Rodewald, S. Stoleson, T.B. Wigley, J. Mizel, T. Boves, G. George, M. Bakermans, T. Beachy, A. Evans, M. McDermott, F. Newell, K. Perkins & M. White. 2013. Management guidelines for enhancing Cerulean Warbler breeding habitat in Appalachian hardwood forests. American Bird Conservancy. The Plains, Virginia. 28 pp.

Zandt, H.S. 1994. A comparison of three sampling techniques to estimate the population size of caterpillars in trees. Oecologia 97:399–406.