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The Effects of a Periodic Cicada Emergence on Forest Birds and the Ecology of Cerulean Warblers at Big Oaks National Wildlife Refuge, Indiana

Dustin W. Varble
University of Tennessee, Knoxville

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David A. Buehler, Major Professor

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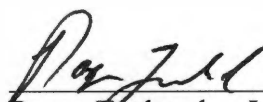
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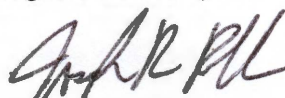
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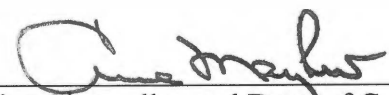
We have read this thesis
and recommend its acceptance:


Frank Van Manen


Roger Tankersley Jr.


Joseph R. Robb

Accepted for the Council:


Vice Chancellor and Dean of Graduate Studies

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Thesis
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The Effects of a Periodic Cicada
Emergence on Forest Birds and the Ecology
of Cerulean Warblers at Big Oaks National
Wildlife Refuge, Indiana

A Thesis
Presented for the
Master of Science Degree
The University of Tennessee, Knoxville

Dustin W. Varble
August 2006

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ABSTRACT

Cerulean Warbler (*Dendroica cerulea*) nests ($n = 53$) were monitored on Big Oaks National Wildlife Refuge in 2004 and 2005 to assess survival rates and to provide breeding habitat data. Mayfield nest success for ceruleans on the refuge was $22.0 \pm 9.6\%$ (2 SE) overall. Fifteen of 53 nests fledged an average of 2.4 ± 0.32 (2 SE) fledglings per nest. Three nests (6% of total) were found parasitized by Brown-headed Cowbirds (*Molothrus ater*), although this should be considered a minimum estimate of parasitism because nests were not checked during incubation. One nest was destroyed during incubation by a Sharp-shinned Hawk (*Accipiter striatus*).

The mean height of cerulean nests was 17.8 ± 1.2 m (2 SE; range = 6.0 – 31.3m). Nests were built in 12 different species of trees; black walnut (*Juglans nigra*) and white oak (*Quercus alba*) were the most common. No habitat characteristics were associated with changes in daily nest survival probability. Daily nest survival also did not differ by temporal characteristics (nest age, stage of nest cycle, or year). Cerulean Warbler breeding habitat differed from random sites. Fewer trees (≥ 3 cm diameter at breast height) and increased woody stem (1-3 cm diameter at breast height) density were associated with cerulean nest sites and nest patches. Nest sites were characterized by having less woody stem density than the nest patch, but tree density did not differ.

Avian nest success, avian consumption of periodic cicadas, and periodic cicada abundance were monitored in 2004 to test the effects of abundant food on nesting ecology. Nests also were monitored in 2005 when periodic cicadas were present in very low numbers. During the 2004 cicada emergence, I estimated that more than 10 million cicadas of 3 different species emerged on the study area and appeared to satiate nest

predators from 23 May–10 June. When analyzed together, nests were more likely to survive during the peak of the periodic cicada emergence than at any other time. The same was true of nests built >1 m above ground. The probability of daily survival of ground nests was unaffected by the periodic cicada emergence. Analysis of Acadian Flycatcher (*Empidonax virescens*), Wood Thrush (*Hylocichla mustelina*), and Cerulean Warbler nests indicated some variation in survival probability over time, but variation in nest survival was not easily distinguishable from a model of constant survival.

Blue Jay (*Cyanocitta cristata*, nest predator) and Brown-headed Cowbird numbers increased on the study plots the year after the cicada emergence. Brood parasitism rates were consistent between years; Wood Thrush nests were the most affected (19% of nests parasitized).

Although cicada emergence appeared to increase nest survival in 2004, increased nest predator populations in 2005 appeared to decrease nest survival rates to below average levels. As a result, the net effect of cicadas on avian populations may be equivocal.

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I. INTRODUCTION

Many species of forest birds have had declining population trends since organized surveys began in 1966 with the North American Breeding Bird Survey (Sauer et al. 2005). Studying avian populations in areas affected by landscape disturbance can show us how, and the degree to which bird populations are affected by human disturbances. I researched a population of forest birds on a forest fragment surrounded by agriculture and urbanization in southeastern Indiana.

Cerulean Warblers breed in mature forests and have been undergoing an estimated annual rate of decline of 4% (Sauer et al. 2005). Ceruleans are declining at one of the greatest annual rates of population declines of any warbler (Robbins et al. 1992). The Cerulean Warbler has been petitioned to be listed as a threatened species and the case is currently under review to determine whether sufficient evidence for listing exists (Salveter 2002). Additional research of Cerulean Warblers may help to clarify the status of their breeding populations, particularly in areas that have been heavily impacted by human disturbances. This research would provide more information to decision makers determining whether listing the species is warranted. By studying a variety of landscapes with varying levels of disturbance, researchers may be able to identify causes of population declines and determine a threshold of human activity that will allow for sustainable populations. This information could then be used to form the basis of management plans for Cerulean Warblers across their breeding range.

Some fragmented landscapes have been shown to have greater densities of both forest bird nest predators and brood parasites (Robinson 1989). Predation and parasitism may inhibit the growth of populations breeding in a fragmented landscape and factor into

the creation of population sinks. Population sinks may not exist every year in fragmented landscapes when other conditions in the landscape change. Periodic cicadas emerge every 13 or 17 years in different regions of the eastern U. S. depending upon which brood of cicadas is being examined. Cicada irruptions provide an abundant source of easily caught prey for many different organisms, including forest birds and the predators of their nests. Periodic cicada emergences occur somewhere in the eastern U. S. almost every year and often cover large geographic regions. These emergences may allow sink populations to temporarily become sources or at least contribute more young to the global population of forest birds. Improved nest survival could result from either reducing the risk of a nest being depredated if nest predators switch to feeding on the more easily captured cicadas, or by improved nutrition for forest birds and their young if forest birds prey on cicadas themselves (Holmes et al. 1986, Arcese and Smith 1988, Schmidt and Whelan 1999, Jones et al. 2003). Forest bird populations may even benefit from both effects simultaneously. If the emergence of periodic cicadas does improve the survival of nests and results in the output of more young than in non-cicada years, cicada cycles may represent an important new variable in modeling forest bird populations over time.

Periodic cicada broods are experiencing population declines themselves, and one brood has already gone extinct (Kritsky 2004). The slow disappearance of cicada populations may point to yet another cause of the decline of forest bird populations, and indicate the potential for continued declines in the future. Knowledge about cicadas can provide conservationists with another way to increase forest bird populations: by preventing the decline of periodic cicada populations. I examined the reproductive ecology of forest birds and its relationship to a periodic cicada irruption.

This thesis is organized into 2 primary chapters. In chapter 2, I describe the breeding ecology of Cerulean Warblers. In chapter 3, I examine the effect of periodic cicadas on forest songbird nesting ecology.

II. CERULEAN WARBLER BREEDING ECOLOGY

INTRODUCTION

Migratory Neotropical songbird populations continue to decline as habitat is lost or degraded on the breeding grounds, along migratory pathways, and on the wintering grounds. The Cerulean Warbler (*Dendroica cerulea*), one of the smallest wood-warblers, has been recognized as one of the most rapidly declining warblers (Robbins et al. 1992), and may become endangered without an international effort to protect their habitat (Hamel 2000a). Cerulean Warblers are insectivorous canopy-foragers that typically inhabit mature forests, and seem to associate with pockets of small, disturbed sites within a mature forest (i.e., canopy gaps and other natural and manmade openings; Oliarnyk and Robertson 1996, Nicholson 2004). Cerulean Warbler nests are small, open cups placed on top of branches in the middle and upper canopy, and often are heavily concealed by foliage immediately above the nest.

Cerulean Warblers are currently a species of special concern in Indiana, and were the subject of a petition for listing as a threatened species under The Endangered Species Act in 2000 (Salveter 2002). Once an abundant warbler in the Ohio River Valley (Hamel 2000a), Cerulean Warbler populations have experienced average estimated population declines of up to 4% per year since 1966 (Sauer et al. 2005). Breeding Bird Survey (BBS) data for Indiana have been used to calculate a relative abundance of 0.29 ceruleans per BBS route, the lowest relative abundance of any state with enough data for statistical analysis (Hamel 2000a). Low relative abundance may result from extensive habitat fragmentation caused by agriculture and urban centers that dominate much of the state. Baseline research has already been carried out describing breeding behavior and

nest success of ceruleans (Oliarnyk and Robertson 1996, Hamel 2000a, Jones and Robertson 2001, Jones et al. 2001, Nicholson 2004, Roth 2004). Conservation of this species may depend upon more detailed descriptions of habitat preferences and investigation into the causes of variation in productivity and survival across the range.

Breeding Habitat

Suspected causes of decline in Cerulean Warbler populations include the loss of breeding habitat in the U.S. and Canada, loss of migratory stopover habitat, and the deforestation of wintering habitat on the eastern slopes of the Andes Mountains in South America (Hamel 2000a). Breeding habitat has been described as mature forests with tall trees (Robbins et al. 1992), and an association with forest gaps has been suggested (Oliarnyk and Robertson 1996, Nicholson 2004).

Habitats used by ceruleans vary widely within the definition of a mature, deciduous forest. Ceruleans have been found in mesic flatwoods, forested ridges and bottoms, walnut groves, and montane forests. Whether this represents a degree of non-specificity in the historical habitat types used by ceruleans, or that all types are linked by some unrecognized parameter (other than large trees) remains unknown. Roth (2004) found Cerulean Warbler territories had taller but fewer trees and greater slope than random locations in southeastern Indiana. Jones and Robertson (2001) also found male ceruleans selected territories in Ontario with tall, well-spaced trees, but they also found greater foliage cover in the midstory. In Tennessee, Nicholson (2004) found ceruleans tended to use more mesic sites, with larger trees, and greater sapling density compared to areas without ceruleans. Aspect and slope appear to be an important habitat parameter in the mountainous regions of Tennessee and West Virginia, but explain much less habitat

variation in regions with less elevation gradient. Researchers must determine which variables are functionally linked to Cerulean Warbler survival and which are merely artifacts of the regional habitat variation incumbent in a given area.

Factors Limiting Productivity

Understanding the relationships governing nest productivity may allow land managers to offset the population decline of Cerulean Warblers attributable to habitat loss by improving productivity (habitat quality) in the current breeding range. Reproductive success rates are variable throughout the breeding range of the Cerulean Warbler. Roth (2004) reported extremely low nest success (16.5%) on Big Oaks National Wildlife Refuge in southern Indiana, whereas Jones et al. (2001) reported nest success as great as 73% in Ontario. Nest success may also vary greatly from season to season in the same study area; Jones et al. (2001) found greatly decreased nest success in Ontario in 1998 (13% nest success), apparently resulting from canopy damage caused by a severe ice storm the previous winter. Few habitat parameters have been linked to predictions of Cerulean Warbler nest survival; Jones et al. (2001) found that greater canopy cover from 6 to 12 m above the ground was correlated with greater nest survival in Ontario.

Some factors that may directly affect nest productivity are predation of nests and food availability, although direct studies of their effects have proven very difficult (Martin 1995). The likelihood of cerulean nest predation may be influenced by a number of habitat characteristics. Severe weather events, such as the 1998 ice storm in Ontario, substantially altered Cerulean Warbler habitat. Reduced canopy cover resulting from tree damage may have allowed nest predators to find more cerulean nests (Jones et al. 2001). Nest predators and brood parasites generally are more abundant in fragmented landscapes

(Wilcove 1985, Robinson 1989). Historically, forest gaps likely were productive for Cerulean Warblers when the landscape was less fragmented. Today however, <50% of the deciduous forests of pre-European settlement of Indiana remain. The development patterns that have removed the forests have created a great deal of edge habitat and forest fragmentation (Jackson 1997). The creation of small gaps (0.02-0.4 ha) has been shown to increase the abundance of Blue Jays (*Cyanocitta cristata*) in Illinois (Robinson and Robinson 1999). Thus, the tendency of ceruleans to select territories associated with canopy gaps may increase the probability of nest predation. Cerulean Warblers may preferentially select for territories near gaps because canopy gaps have greater insect abundance than areas with lower primary productivity (Blake and Hoppes 1986). The abundance of food available for Cerulean Warblers can also be linked to several factors in the environment. Unusual periods of cold weather may decrease the availability of insect prey and cause nestling starvation (Jones et al. 2001, Nicholson 2004). Damage to canopy trees caused by the 1998 Ontario ice storm may have decreased insect abundance and resulted in reduced nest success (Jones et al. 2001).

My goal during this research was to describe the breeding ecology of the Cerulean Warblers on Big Oaks National Wildlife Refuge. I also examined breeding habitat use to determine what habitat characteristics Cerulean Warblers might have selected for. Finally, I examined nest survival in terms of different time-related variables and habitat characteristics to see what may be affecting nest success and whether better nest survival may be managed for.

STUDY AREA

I conducted this study on Big Oaks National Wildlife Refuge (BONWR), which lies in the Ohio River valley, an area that contained abundant Cerulean Warblers during the last century (Hamel 2000a). BONWR is a former military ammunition proving ground (Jefferson Proving Ground) managed by the U.S. Fish and Wildlife Service and owned by the U.S. Army. BONWR is located in southeastern Indiana (Figure 2-1^a). The refuge has been protected from agricultural and human development (which fragments much of the surrounding landscape) since the 1940s when military munitions testing began. The base closed in 1995, yet a great deal of unexploded ordnance remains throughout the enclosure, restricting access in many areas. However, some cerulean habitat lies within areas that have few access restrictions. These forested areas also are commonly used by other breeding forest bird species including the Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), Acadian Flycatcher (*Empidonax vireescens*), and Ovenbird (*Seiurus aurocapillus*).

BONWR encompasses approximately 20,200 ha, some of which provides Cerulean Warbler habitat: mature forest dominated by oaks (*Quercus spp.*), tulip poplar (*Liriodendron tulipifera*), hickories (*Carya spp.*), black walnut (*Juglans nigra*), American sycamore (*Platanus occidentalis*), ashes (*Fraxinus spp.*), and maples (*Acer spp.*). Species such as spicebush (*Lindera benzoin*), common paw-paw (*Asimina triloba*), sassafras (*Sassafras albidum*), and American beech (*Fagus grandifolia*) commonly dominate the understory. The terrain of the refuge is predominantly rolling hills interspersed with

^aAll tables and figures in Appendix

expansive mesic flats and ridges associated with the larger streams.

I focused this study on the northern third of the refuge, where ceruleans are found at moderate densities (Figure 2-2). Study sites in the main study area include 3 general forest types: mesic flatwoods typically dominated by tulip poplar, maple, and beech; mesic slope forests dominated by hickory, oak, and beech; and riparian bottoms dominated by black walnut and American sycamore. The interior of the property is networked by a series of mostly unimproved gravel roads with grass borders that vary in width. In most interior forested areas, the forest canopy covers the roadway gap. The habitat surrounding BONWR is dominated by agriculture surrounding isolated woodlots. A fence surrounds the entire property to restrict unauthorized access and limits the amount of disturbance the area receives from human activity. Logging is not currently occurring on BONWR because of unexploded munitions on the entire property, although selective timber harvests did occur previously while the property was an active U.S. Army installation. One of the five plots used in this study was burned in 2004 as part of the U.S. Fish and Wildlife Service management for the area.

METHODS

I carried out this study during 2004 and 2005 breeding seasons. Five, 40-ha plots were placed in an area likely to contain Cerulean Warblers based on previous research. I marked the plots with flagging every 25 m along transects 100 m apart. I attempted to maximize the number of nests found on study plots; I found some nests incidentally outside of study plots. No maximum time limit was established for nest searching, as Cerulean Warbler nests are unusually difficult to find.

I monitored nests following the field protocol established by Martin et al. (1997). I monitored nests using spotting scopes, binoculars, or telescoping poles with mirrors when possible. I checked nests every 2-4 days, and more frequently when young were expected to fledge. I monitored any nest that appeared inactive on subsequent days to validate a nest failure, unless visible nest destruction was observed. I considered a nest successful if at least 1 host species nestling fledged. Parasitism was recorded by observing the large cowbird young begging in the nests. Nests were not checked for parasitism during incubation. I used infrared time-lapse photography to capture predation events. I placed these cameras on 8 nests in an opportunistic manner in 2005.

I measured vegetation characteristics both at Cerulean Warbler nest sites and random locations where ceruleans had not been observed. I found four inactive nests that were not subject to all vegetative measurements. At each nest, I measured characteristics of the nest placement including nest height, nest aspect in relation to nest tree bole, nest tree species, nest tree height, nest tree diameter at breast height (dbh), amount of foliage cover immediately above nest, species of foliage immediately above nest, distance from the nest to tree bole, distance from the nest to canopy edge of the nest tree, and the slope and aspect of the ground below the nest. I recorded the location of all nests and random points using Garmin Etrex Vista GPS units achieving at least 10-m accuracy. I determined random locations using a random number generator for both compass bearing and distance. I used each nest as the starting point for reaching a random point measured in the same year of the nest discovery, located 100 to 600 m from the nest. A minimum distance of 100 m was used to ensure points were randomly selected outside of the

cerulean's territory. Any random point that fell within an area I knew to be used by breeding Cerulean Warblers was relocated using another randomized set of directions.

The vegetation measurement protocol was modified from that used by Jones and Robertson (2001). Each nest was the center of a 5-m radius plot. At a distance of 0.4 m from the edge of the central plot, I placed the edge of another equally sized plot in each of the 4 cardinal directions. For analysis purposes, center or nest plots are called the nest-site, and the 4 surrounding plots were termed the nest-patch (Jones and Robertson 2001). On each plot I measured the following: the number of trees (≥ 3 cm dbh) and the species of each, the number of woody stems (1-3 cm dbh), the height of the tallest tree and its species, canopy cover measured facing in each of the 4 cardinal directions at the center of each plot using a spherical densiometer and then averaged together, and foliage cover in 4 height intervals. I estimated foliage cover visually in a 1-m radius cylinder at the center of each plot and extending to the top of the canopy. I estimated cover as the percent cover in zones less than 6 m high, 6 to 12 m high, 12 to 18 m high, and from 18 m high to the top of the canopy.

I also measured vertical vegetation stratification using a method adapted from Hubbell and Foster (1986). I placed a 15.2 m telescoping pole at the center of the center plot at both random and nest sites. From 22.8 m away in each of the 4 cardinal directions, I measured the amount of pole obscured by vegetation in zones at less than 6 m high, 6 to 12 m high, 12 to 18 m high, and from 18 m to the top of the canopy. I visually estimated intervals beyond the extent of the telescoping pole. That method differed from foliage cover estimated in the area of a 1-m radius cylinder, as all intervals

above the lowest interval (less than 6 m) included lower vegetation in each estimate because of the necessity of viewing the telescoping pole at an angle.

Data Analysis

I calculated daily nest survivorship and nest success using the Mayfield method (1975) that corrects for the likelihood that researchers are more apt to find a nest that is surviving. I standardized the length of the nest cycle as 22 days, with 12 days allotted for incubation (Evans and Fischer 1997). I compared daily survival of nests between study years using program Contrast and $\alpha = 0.05$ (Hines and Sauer 1989). I compared between year vegetative and nest character parameters using 2-tailed T-tests assuming unequal variance and $\alpha = 0.05$. The aspect of the nest in relation to the bole of the nest tree was analyzed using Rayleigh's Test (Z) of Uniformity for circular data to determine whether nests were placed more often in a specific direction (Zar 1999).

I analyzed nest survival for relatedness to habitat and temporal characteristics using the Logistic Exposure method of Shaffer (2004), which uses logistic regression to statistically test models and examines the results with Akaike Information Criterion (AIC) model selection (Anderson et al. 2000). The Logistic Exposure method of analysis treats the period between monitoring visits to a nest as a survival interval. This method rewards nests and their associated characteristics (nest placement, habitat, temporal effects) for surviving longer, and so also corrects for the biases noted by Mayfield (1975), that are often corrected in calculations of nest success but rarely in modeling of survival (Shaffer 2004). Mayfield (1975) created the first nest survival analysis scheme that corrected for the fact that researchers find nests that are surviving more than those that do not, and provided a way to account for varying nest survival probability over time. I

applied the correction factor, AICc, to all models based upon sample size as suggested by Anderson et al. (2000), despite some recent ambiguity in its' effectiveness for all data (Richards 2005). I selected the best subset of models based upon ΔAICc scores ≤ 2 . I evaluated the best subset of models using Akaike weights, which are based upon the Kullback-Leibler distance that quantifies the difference between the true outcomes of a study versus those predicted by each model (Anderson et al. 2000). Akaike weights are the proportion of the number of times that a model will be selected as the best model if the study were repeated (Anderson et al. 2000, Richards 2005). Model-averaged parameter estimates were used to estimate the effect of a parameter on the dependent variable. The averaged parameter estimate value is a mean of the parameters effect on the dependent variable across all models tested (Anderson et al. 2000). When the 95% confidence intervals of the model-averaged estimate bounded zero, I concluded that the parameter did not appear to have an effect on the dependent variable.

I created survival models a priori and ran the models in 3 separate groupings; temporal models, nest-site models, and nest-patch models (Table 2-1). I based model composition on both previous research and biologically plausible associations made between survival and habitat. The model list was not conservative in scope, based on the lack of knowledge about significant influences on nest success in Cerulean Warbler literature. The dependent variable was survival in all models. Survival is a binary variable where a value of 1 meant the nest survived the observation interval, and a value of zero meant the nest did not survive the observation interval.

I developed models to distinguish between sites where Cerulean Warblers nested in versus those they did not using logistic regression. I then chose the models best

describing the data using Model Averaging and AIC model selection (Anderson et al. 2000). I ran these models in 2 separate groupings; nest-site comparison models and nest-patch models for used versus non-used sites (Table 2-2). The dependent variable was use, a binary variable in which a value of 1 indicated use by breeding Cerulean Warblers and a value of 0 indicated no use. Nest-site models incorporated characteristics of both nest placement and vegetation measurements made within the 5-m radius nest plot. I based nest-patch models on measurements from the surrounding 4 plots in the cardinal directions from the nest plot. I made these measurements near the nest, but not all measurements were within each cerulean's territory when nest sites were located on territory boundaries. The goal of this analysis was to determine whether ceruleans made different choices at the site of the nest versus the immediately surrounding area, and whether the nest-site or nest-patch differed from randomly selected areas not used by ceruleans. The percent canopy cover was log transformed in all analyses to achieve a normal distribution, but I report the original means here.

RESULTS

Nest Placement Characteristics

The mean height of Cerulean Warbler nest trees was 27.5 ± 2.1 m (2 SE) (2004 – 2005 combined, Table 2-3). Mean nest tree height was similar in 2004 (28.6 ± 2.8 m) and in 2005 (26.1 ± 3.0 m; $t = 1.25$, $P = 0.11$). The range of nest tree heights was 13.2 to 51.2 m. Mean nest height for the entire sample was 17.8 ± 1.2 m (2 SE); both years differed (marginally) with nest heights of 18.7 ± 1.9 m and 16.7 ± 1.5 m in 2004 and 2005, respectively ($t = 1.70$, $P = 0.05$, Table 2-3). The range of nests heights fell from a low of 6 m to the highest at 31.3 m. The mean diameter of nest trees at breast

height (dbh) was 42.3 ± 5.0 cm (2 SE). Nest tree dbh was similar in 2004 and 2005 (44.25 ± 7.14 cm and 40.02 ± 7.12 cm, respectively; $t = 0.84$, $P = 0.20$).

Nest-site selection varied by the aspect of the nest in relation to the nest tree bole (Rayleigh's $Z = 2.96$, $P = 0.05$). The mean direction of nest placement was $180.4 \pm 46.4^\circ$ (2 SE) (Figure 2-1). The 57 Cerulean Warbler nests characterized during the study were built in 13 species of trees. The majority of Cerulean Warbler nests were found in black walnuts and white oaks (26.3 % and 24.6%, respectively, of all nest trees). Other common nest tree species included American sycamore (14%) and both American (*Ulmus americanus*) (8%) and red elm (*Ulmus rubra*) (7%) (Table 2-4). Most nests found in 2004 were built in white oak (32%), American sycamore (16%), and black walnut (13%). Black walnut was the most common nest tree species in 2005 (42.3%), followed by white oak (15.4%), and red elm (15.4%).

Differences existed between the dbh of oak, black walnut, and American sycamore nest trees ($F = 8.60$, $df = 38$, $P = 0.001$). Oak nest trees had greater dbh (60.8 ± 11.2 cm) than either black walnuts (36.2 ± 5.6 cm) or American sycamores (38.6 ± 12.4 cm) ($P < 0.05$). The dbh of black walnuts and American sycamores did not differ ($P > 0.05$). The height of nest trees also differed ($F = 6.37$, $df = 37$, $P = 0.004$). Oaks were taller (34.8 ± 3.6 m) than black walnut nest trees (25.0 ± 2.8 m; $P < 0.05$). American sycamore nest tree height (28.9 ± 6.6 m) did not differ from either black walnuts or oaks ($P > 0.05$). There were no differences in the height of nests placed in oaks, black walnuts, or American sycamores ($F = 2.71$, $df = 37$, $P = 0.081$).

Mean distance of the nest from the bole of the tree was 4.4 ± 0.3 m (Table 2-3). The mean distance from the nest to the edge of the nest tree canopy was 3.2 ± 0.5 m

(Table 2-3). Mean distance from the nest to the edge of the canopy did not differ between years ($t = 1.48$, $P = 0.15$). The mean slope of the land under the nest tree was 5.4 ± 2.0 degrees and ranged from flat (0°) to moderately steep at 32° . The mean slope was consistent between both years of the study ($5.4 \pm 2.4^\circ$ in 2004 and $5.4 \pm 3.6^\circ$ in 2005, $t = 0.02$, $P = 0.98$).

The majority of nests were concealed immediately overhead by vegetation from the host nest tree species (63.5 %). The most common cover species for a Cerulean Warbler nest was Virginia creeper (*Parthenocissus quinquefolia*), which provided concealment for 34.9 % of all nests sampled. Half of all nests that had Virginia creeper for concealment were found in black walnuts, but creeper also provided concealment in 7 other species of nest tree. The only other vegetation used for concealment was wild grape (*Vitis spp.*), but it was only used to conceal a single nest in an American sycamore. Seven nests (12.7 %) were concealed immediately overhead by a combination of nest tree foliage and vines (Virginia creeper or grape). The mean percent canopy cover immediately over the nest was 78.1 ± 7.4 %. Canopy cover over the nest did not differ between years (80.2 ± 9.0 % in 2004, 75.4 ± 12.4 % in 2005, $t = 0.54$, $P = 0.62$). The percent of canopy cover from 2 m above ground to the canopy top around the nest was 91.2 ± 1.6 %. Canopy cover differed between years around the nest (94.3 ± 1.2 % in 2004, 87.7 ± 2.4 % in 2005, $t = 4.91$, $P < 0.001$).

Vertical vegetation (pole method) averaged 40.5 ± 5.8 % cover between the substrate and 6 m above. From 6 to 12 m above ground, mean cover was 47.0 ± 5.4 %, 54.1 ± 5.4 % from 12 to 18 m above ground, and 55.2 ± 3.2 % from 18 m to the maximum height of the canopy (Table 2-3). Ocular column estimation of vegetation

cover averaged 40.7 ± 9.2 % from the substrate to a height of 6 m. From 6 to 12 m, mean cover was 35.2 ± 8.4 %, 48.4 ± 9.6 % from 12 to 18 m high, and 45.0 ± 9.2 % from 18 m high to the upper limit of the canopy (Table 2-3).

Used Versus Non-used Sites

A single model was selected as the best of 19 tested models to discriminate between random sites and Cerulean Warbler nest sites. The best model had a 71% likelihood of being the best model, and predicted Cerulean Warbler use as a function of canopy cover, the number of trees, and the number of woody stems at the nest site (Table 2-5). The number of trees was the most important factor in predicting use, followed by the number of woody stems (Table 2-5). Parameter estimates for canopy cover included zero using 95% confidence intervals, indicating that canopy cover should be dropped from the model. The probability a site would be chosen as a nest site by a Cerulean Warbler increased as the number of trees decreased and the number of woody stems increased. Mean differences in the number of trees at nest-sites compared to random sites were more apparent than differences in the number of woody stems (Table 2-6).

A single model was also selected from 17 tested models to discriminate between random sites and Cerulean Warbler nest patches. The best model had a 74.4% likelihood of being the best model, and also included canopy cover, the number of trees, and the number of woody stems as predictors of use by breeding Cerulean Warblers (Table 2-7). Confidence intervals for parameter estimates of the effect of canopy cover also included zero in this model, leaving the number of trees and woody stems as the important variables that characterized Cerulean Warbler habitat (Table 2-8). The parameter estimates for the number of trees and woody stems at the nest-patch scale predicted use

by breeding Cerulean Warblers in the same direction as at the nest-site scale (Table 2-8). Nest sites had fewer woody stems than the nest patch ($P < 0.000$; Table 2-6). The number of trees did not differ at the 2 scales ($P = 0.64$; Table 2-6).

Nest Survival

During the 2-year study, 15 of 53 (28.3%) Cerulean Warbler nests fledged at least one cerulean young. Eleven of 28 cerulean nests fledged in 2004, and 4 of 25 in 2005. Mayfield nest success in 2004 was 33.4 %, and daily survival was 95.1 ± 0.02 %. Nest success in 2005 was 17.2 %, with a daily survival of 92.3 ± 0.04 %. Overall Mayfield nest success was 22.0% and a daily nest survivorship of 93.3 ± 0.02 %. Daily survival of nests did not differ between study years ($\chi^2 = 1.85$, $P = 0.174$). Over half (52%) of all nests that survived to incubation stage failed during incubation (Table 2-9). Nearly half (42.3%) of nests with nestlings failed before fledging (Table 2-9).

Three nests failed because of nest parasitism by Brown-headed Cowbirds in 2005, but none were known to have failed in 2004 from nest parasitism. Another nest in 2005 was suspected to have been parasitized because a cowbird eggshell was found below the nest, but the nest was predated before hatching. Two of the 3 parasitized nests fledged a single cowbird young. No host young were observed alive in parasitized nests. Based on this evidence, it is likely that eggs were either pecked by adult cowbirds or that host young were starved or pushed from nests by the dominant cowbird nestling. One Cerulean Warbler nest likely failed because of strong storms in 2005, and severe weather was suspected in 2 other failures. A Sharp-shinned Hawk destroyed a nest containing eggs in 2005, but did not consume any of the contents. A female in 2004 incubated eggs

that never hatched after more than twice the normal incubation period had elapsed (>25 days).

In 2004, 2 cerulean nests apparently fledged 2 young, and another fledged only a single cerulean. Four nests had >1 young, whereas another 4 had >2 young. The minimum mean number of young fledged per successful nest was 2.27 ± 0.19 . Of the 4 nests that fledged in 2005, 1 nest had >1 young and 3 nests had 3 young. Definitive numbers of fledglings were often difficult to determine because fledglings were not easily located in dense undergrowth. The minimum mean number of young fledged per successful nest in 2005 was 2.75 ± 0.25 .

Time-lapse photography only resulted in a single recorded predation event by a Sharp-shinned Hawk in 2005. The female cerulean left the nest approximately 40 seconds before the hawk was visible. The hawk landed near the nest, and eventually pulled it out of the tree spilling the eggs and nest from the tree. Of the seven other cameras recording nests, 2 produced only cowbird young, 3 produced host young, and 2 lost sight of the nest because of strong storms.

Temporal modeling resulted in 2 of 9 models being the best subset of models for nest survival ($\Delta AIC_c \leq 2$, Table 2-10). The best temporal model described interval survival in terms of the age of the nest at the start of each interval and had a 69.0% likelihood of being the best temporal model. The second best temporal survival model incorporated both the nest age and the date, and had the remaining 31% of the AIC_c weight (likelihood of being the best model). However, the variables in both models, nest age and date, had confidence intervals for their parameter estimates that included zero (Table 2-8).

Analysis of survival at the nest-site scale resulted in selection of a best subset of 5 of the 16 tested models. All models had low support (6.9-17.9% likelihood). The best model included survival as a function of canopy cover and the distance from the nest to the edge of the nest tree canopy (Table 2-11). The second best supported model had an AIC_c weight of 13.7%, and evaluated whether survival was constant. Besides constant survival, the top four models contained 6 unique variables, but all of the model-averaged parameter estimates for these variables included zero (Table 2-8).

Analysis of survival at the scale of the nest patch resulted in 2 of 11 models being selected. The best supported model included survival as a function of the number of trees and canopy cover, with a 43.7% likelihood of being the best model (Table 2-12). The second best supported model in the set included the same variables with the addition of the number of woody stems, and had a 16.3% likelihood of being the best model. The confidence intervals of the parameter estimates for the number of woody stems, the number of trees, and canopy coverage also included zero for survival at the nest-patch scale (Table 2-8).

DISCUSSION

Nest Characteristics

The height of Cerulean Warbler nests on BONWR ($\bar{x} = 17.8$ m) was within the wide range of heights reported in the literature (Hamel 2000a, 4-36 m). The nest data also followed the trend shown by Hamel (2000a) that mean nest height is positively correlated with the mean height of nest trees in a region. The nest heights in this study were very consistent with those reported by Roth (2004, $\bar{x} = 18.4$ m) in the same study area. Nests were most often placed on the south side of the nest tree (Figure 2-3). If

foliage is thicker on the south side of a tree because of increased sunlight exposure, nests may be more shaded and less visible to predators. There also may be more vine species growing on the south side of trees, which would also provide additional cover. However, I made no measurements of nest trees to determine whether these are plausible explanations. Many of the other nest characteristics were also similar to those reported by Roth (2004), including nest aspect, distance from the nest to bole, nest tree dbh, nest tree species, and proportion of nests covered by Virginia creeper (Table 2-13). These results suggest consistent habitat selection from year to year by breeding ceruleans in the study area.

The nest tree species used at BONWR were consistent with other Cerulean Warbler studies. Black walnuts were the most frequent nest tree species in this study, mainly because of the past human use of the study area. Several walnut groves naturally occur within the study area. Lack of understory in these groves often resulted in improved visibility of female ceruleans while nest building, which may have contributed to black walnuts being the most frequently recorded nest tree species. However, I found nests in most territories present on the study plots regardless of nest tree type. Walnut groves differed markedly from the other nest sites used by Cerulean Warblers on BONWR because of the lack of understory and little vertical vegetation under the upper canopy. Selection of these areas for breeding may have contradicted the belief that ceruleans strictly associate with diverse vertical canopy structure. Ceruleans may be selecting black walnut groves because of the extra nest concealment provided by the abundant Virginia creeper found at these sites. However, daily survival probability of

nests in black walnut trees ($95.9 \pm 2.6\%$) was not greater than that of nests built in other species of trees ($93.4 \pm 2.4\%$; $\chi^2 = 2.00$, $P = 0.16$).

Habitat Use

The 2 best supported models of nest-site and nest-patch selection by Cerulean Warblers were similar. The likelihood of use of a site by a breeding pair of Cerulean Warblers increased as the number of woody stems increased and the number of trees decreased. These findings are indicative of mature forest conditions. Mature forests have fewer trees, as trees that cannot compete die out as a forest ages. More woody stems may not normally be indicative of a mature forest, if the woody stems are young tree saplings. However, a mature forest may have other shrub-like species in the understory (i.e. common paw-paw, spicebush, etc.), and I did not distinguish understory type.

Roth (2004) found Cerulean Warbler territories on BONWR to be associated with fewer trees, but also with greater slope and taller trees. However, Roth (2004) measured vegetation at the center of 53% of mapped territories because no nest was found. Some of those sites may have been territories of unmated males within less preferred habitat, or the vegetation plots may not have been located near a nest. Use of random locations in my study was complicated by the likelihood that not all Cerulean Warbler habitat on the refuge may be occupied by ceruleans in any single breeding season, thus some of the random locations may have represented unoccupied cerulean habitat.

The greater number of woody stems present in areas used by breeding pairs may not indicate regeneration of typical forest overstory tree species. Canopy cover was not

correlated to tree density in this study, so it is unlikely that increases in the number of woody stems was related to decreased tree density because of increased penetration of the forest floor by sunlight. Common paw-paw and spicebush are common understory species and were classed as saplings. In future studies, it may be important to discriminate between tree saplings and other woody understory species (i.e., shrubs) when characterizing habitat. I expect that the number of tree saplings would be low along with the number of trees in areas used by ceruleans, whereas the number of other understory species may be greater. Nicholson (2004) included both trees and shrubs in his definition of saplings, and found results similar to my study. Cerulean Warbler occurrence decreased with increasing sapling density in West Virginia, where shrubs were differentiated from tree saplings (Wood et al. 2006).

Modeling results showed consistent patterns of habitat selection at nest-site and nest-patch scales, although the number of woody stems found in the nest patch was greater than at the nest site. The increased number of woody stems in the nest patch may be selected to provide cover for recently fledged ceruleans. Newly fledged ceruleans were commonly found on or near the ground, and additional cover from predators would be beneficial during those first few days of vulnerability. Secondly, when leaving a nest, female ceruleans often drop out of the nest and dive straight at the ground, sometimes only leveling their flight 2 m from the ground. Females may select nest sites with fewer saplings than the surrounding habitat to provide an open area under the nest for the “bungee-dropping” flight behavior (Hamel 2000b). Selection for nest sites with open understories 5-20 m under the nest has been reported in other studies (Hamel 2000a). This behavior may be an adaptation to confuse nest predator attempts to locate a nest.

Slope and aspect do not seem to play an important role in the nest-site selection of Cerulean Warblers on BONWR, as has been found in other research (Nicholson 2004, Weakland and Wood 2005, Wood et al. 2006). Most studies that attempted to use these parameters to predict cerulean occurrence were conducted in mountainous regions. Dettmers and Bart (1999) did appear to successfully model cerulean habitat including slope and aspect in the Ohio Hills region, but the slopes appeared to be more pronounced in terms of height and occurrence there than slopes on my study area. Slope and aspect does affect tree species composition because of moisture and soil conditions in Indiana forests, but the magnitude of the effect is much less pronounced than that found in mountainous terrain. Roth (2004) found slope to be greater in cerulean territories, but because of differing methodologies (territories vs. nest sites), results were not strictly comparable.

Productivity

Based on the nest productivity data (22.0% nest success), Big Oaks National Wildlife Refuge may be sink habitat for Cerulean Warblers. Source/sink analysis supports this finding, if my assumptions about Cerulean Warbler populations are true (see Ch.3 Figure 3-4). Roth (2004) reported average nest success of only 16.5 % after 2 years of study on BONWR and reached a similar conclusion. Cerulean Warblers have been reported to be much more successful in other regions (Oliarnyk and Robertson 1996, Nicholson 2004). Poor nest success at BONWR may reflect the isolation of the refuge as an island of habitat in a landscape dominated by agriculture in southeastern Indiana. The refuge's existence as a fragment may allow greater penetration of the interior forests by Brown-headed Cowbirds, and greater numbers of nest predators than larger, more

continuous forested blocks (Figure 2-4). The detrimental effect on nest survival may be magnified by the network of road corridors on the property that could facilitate dispersal of both brood parasites and predators throughout the breeding areas used by ceruleans.

Year was not an important predictor of daily nest survival of Cerulean Warblers. In 2004, a 17-year brood of cicadas erupted, providing abundant food for both breeding passerines and nest predators. Although the overall nest survival of many forest bird species did not improve during 2004, nests placed above the ground had a greater probability of surviving during the peak of the outbreak than during the rest of the 2004 breeding season (see Chapter 3). The improvement in overall survival of cerulean nests in 2004 was not significant ($P = 0.12$), but there may have been some effect on nest survivorship. In 2004, 11 of 28 nests fledged; in 3 previous years of research it took more than twice as many nests to have 11 successes (Roth 2004). Canopy cover in the nest patch was more sparse in 2005 than in 2004. Reduction in canopy cover in 2005 may have resulted from loss of tree limbs and defoliation caused by periodic cicada egg laying in 2004. Jones et al. (2001) reported a significant drop in Cerulean Warbler nest success in Ontario following a similar die-off of tree branches and foliage caused by an unusual ice-storm. Whether reduced canopy cover was a factor in poor cerulean productivity in 2005 is uncertain because other breeding seasons have resulted in similarly poor productivity (Roth 2004).

BONWR may remain a breeding area for ceruleans as long as the global populations remain viable, but the area may not be a source population. BONWR's continuation as a breeding area may depend on attracting immigrants from elsewhere. BONWR is located near the core of the current Cerulean Warbler breeding range, and

may easily be colonized by members of other populations (Figure 2-5). More adjoining land would need to be acquired and the road networks removed and allowed to revert to forest for larger forest patches to be created. It is unknown how large forest blocks need to be to avoid apparent impacts associated with fragmentation. Many forested patches within BONWR are less than 400 ha when roads are considered patch boundaries.

Sink populations are believed to be a natural part of any functioning gene pool. In the case of the Cerulean Warbler, many sinks may be the result of human activity and not be representative of cerulean populations prior to European settlement of North America. The BONWR population of Cerulean Warblers could still be an important part of the global population. The refuge may put relatively few individuals back into the overall population, but the birds that do breed successfully here may be better adapted for the fragmented landscape that may continue to grow across the breeding range in the future. This could become an important source of behavioral variation if the global population continues to decline. Behavioral variation could exist in either nesting behavior that reduces predation and parasitism or in terms of migration routes. Berthold et al. (1992) found evidence of rapid genetic altering (<30 years) of migration routes in birds that led to the colonization of new wintering grounds. Preserving current genetic diversity would likely facilitate events like colonization, which may become increasingly important in a fragmented landscape.

Daily nest survival was not related to any of the habitat parameters I measured. Despite finding a sample of 53 nests (4 additional nests were found inactive), many nests failed soon after discovery and contributed a limited number of nest monitoring intervals to the analysis. Thus the power of the tests likely was low. Another possible explanation

for these results, however, is that nest predation may be a largely random event. Nest predation is believed to be the most frequent cause of failure for Cerulean Warbler nests on BONWR. When targeting nests, a predator may be more likely to key in on parental behavior than using a habitat-based search image to maximize prey acquisition. Keying in on parental behavior would create a random predation effect on nests, as the predator would not control which adults will reveal the nest location first. Predation will happen by chance, provided that the predator does not hunt in a single, specific habitat type. The surge of avian nests in the spring may even cause normally habitat-specific predators to expand their range to take full advantage of the temporal abundance of prey. Avian predators, in particular, may be less confined to hunting within a specific set of habitat parameters because of their ease of mobility.

Nest predation likely is random when nests are not the focus of a predator, such as during a periodic cicada outbreak. Nests may often be found incidentally while feeding on other items, a largely random occurrence provided that predators are not also faithful to a particular type of habitat. When considering that nests may be predated by a suite of different predators, predicting which nests will succeed may be difficult. For example, raccoons feed heavily on crayfish along streams in riparian areas in the spring and summer. Nests along these riparian bottoms could be expected to experience greater predation pressure from raccoons. In this case, the distance of the nest to the nearest stream would be an important predictor of nest survival. When other predators that exist in the environment are considered, such as fox (*Sciurus niger*) and eastern gray squirrels (*Sciurus carolinensis*), distance to stream is likely to lose any predictive ability. During early stages of cerulean breeding, squirrels feed heavily on the buds of tulip poplar trees

that are found throughout potential cerulean breeding habitat. Tewksbury et al. (2006) found that nest predators found in natural, buffer, and agricultural areas affect a wide range of nesting species across different habitat types. Other research has also indicated the unpredictability of nest predation (Martin 1995). A single area, such as BONWR, that supports nest predators from several of these communities will exhibit a very complex pattern of predation (Tewksbury et al. 2006). Where nest predation risk is great, the pattern of predation is likely to be lost in the overall generality of predation across habitat types. Mankin and Warner (1992) found that nest predation varied little across habitat types in a fragmented study area where squirrels and Blue Jays were thought to be common nest predators.

Potential nest predators on BONWR include Blue Jays, woodpecker species, owls, hawks, snakes, raccoons, opossums, fox squirrels, and eastern gray squirrels. Sharp-shinned Hawk and American Crow predation of cerulean nests has been documented on BONWR (Roth 2004). Nest predators, taking advantage of the spring and summer surge in feeding opportunities, would also have little need for a specific type of habitat to hunt successfully. Nests do not require ambush behavior to be subdued, and so there would be little need of higher stem densities to hide the predator and provide an advantage when targeting mobile prey.

If nest predation is a purely random event, then it is unlikely that any nest predator avoidance behavior exists that may be valuable to the global population. Predator avoidance may be manifested in improved nest concealment behavior, but ceruleans may already be using the best available nest cover without a significant improvement in survival. I did not measure behavioral differences between breeding

pairs on the refuge in terms of singing rate at the nest, female vocalization at the nest, number of trips to the nest, etc. Anecdotally, it did appear the range of behaviors by breeding cerulean females did vary widely, but the degree of genetic control on this behavior is unknown. Some females were very vocal at the nest at all stages of breeding whereas others were silent at all times observed. I also noticed that females that failed were often much more secretive when renesting. Increased parental activity at the nest during the nestling stage has been linked to increased risk of predation (Martin et al. 2000). Because of the difficulty in mist-netting females, I did not determine if breeding behavior or nest success was a function of female age and experience. “Noisy” females may be much more likely to attract predators than quieter females that may be older and more experienced.

Based on my estimates, nest parasitism did not have a major impact on the survival of Cerulean Warbler nests (5.6% of nests parasitized). The measured parasitism rate likely was an underestimate, however, as I did not check nests for cowbird eggs during incubation. Therefore, the influence of nest parasitism on survival rates should still be regarded as unknown for this population. The degree of nest parasitism can also be underestimated if the host species is capable of recognizing and abandoning nests with eggs from a parasite. However, Cerulean Warblers may not have been associated with Brown-headed Cowbirds until recent history, and may not be capable of recognizing cowbird eggs or young. The most likely explanation for the few observations of parasitism is that more cerulean nests are being parasitized than I measured, but they are also being heavily predated, and do not reach the nestling stage when parasitism becomes obvious to observers. Parasitism may have little effect on avian reproduction in areas

where nest predation rates are great enough so that parasitized nests are predated before fledging (Goguen and Mathews 2000). Brown-headed Cowbirds may parasitize nests that are more visible and obvious to both themselves and nest predators; the actual rate of predation of parasitized nests may even be greater than non-parasitized nests (Gates and Gysel 1978). Research by Gates and Gysel (1978) suggested that cowbirds may find it difficult to observe nest-building activity in areas of dense foliage. When nests are successful, but also parasitized, the number of surviving host young is often reduced. However, none of the successful nests in this study were parasitized so I was unable to assess the level of brood reduction associated with parasitism.

No portion of the BONWR study area provided adequate forested interior to protect interior forest species from parasitism. Cowbirds can travel distances in excess of 7 km from feeding areas to lay eggs in host nests (Rothstein et al. 1984). The innermost forested areas of BONWR are at a maximum of 4.9 km from Brown-headed Cowbird habitat outside of the refuge. Therefore, cowbirds are likely to have access to virtually any cerulean nest on BONWR.

I did not compare survival probabilities of nests based on landscape characteristics such as patch size or amount of edge per area forest, as my study did not encompass a large geographic region. Those variables may not be significant at the scale of BONWR because it may be of insufficient size to have measurable variation in survival across different habitat conditions (i.e., predation and parasitism may saturate the area). At coarser scales those landscape variables may become more important predictors of survival as human disturbance varies more drastically across multi-state regions. Increases in human activity across large regions has been linked to decreased diversity in

the avian community (Flather 1996). Before European settlement, nest site selection may have been the most important determinant of survival (e.g., breeding in territories with greater abundance of insect prey). This scale of habitat selection may not be the primary determinant of nest success today because of the recent selection pressures created at the landscape scale through human activity. Selection of areas with greater forest patch size and reduced edge may be the key to fledging young, but this may be a function of natal fidelity for most breeding pairs and not selection at a broad regional scale. Another Cerulean Warbler study did find landscape characteristics to be important determinants of use, but did not include analysis of survival (Wood et al. 2006).

III. CICADA EMERGENCE EFFECTS ON BREEDING BIRDS

INTRODUCTION

Natural Food Manipulation Effects

One of the primary influences on the size and viability of any wildlife population is reproductive success. Many forest bird species exist in disjunct populations that experience different degrees of breeding success depending upon local site characteristics that often vary temporally (Martin 1995). Conservation efforts for global populations are most effective when accounting for as many of these characteristics of different regions as possible (Martin 1995).

Influences on Nest Success

Nest success for forest birds is influenced by many factors including nest predation, nest location, weather, food abundance and availability, and brood parasitism (Martin 1995). Variations in food availability are a primary influence on avian population size (Lack 1966). Feeding experiments have shown that artificial supplementation of high-quality nutrition to breeding birds can increase clutch size, nestling weight, number of renests, and overall number of fledged birds (Arcese and Smith 1988). Annual variation in food abundance affects the productivity and population fluctuations of forest birds (Holmes et al. 1986, Jones et al. 2003, Stodola 2005).

Periodic Cicada Emergences

During the 2004 breeding season, I had the opportunity to monitor the effects of a natural increase in food abundance and availability on forest bird productivity at Big Oaks National Wildlife Refuge, Indiana. The large periodic cicada population, called Brood X, emerged from underground to breed and deposit eggs under the bark of living

trees. During the 17-year underground stage, cicadas feed on sap through the root systems of living trees (Dybas and Lloyd 1974). Brood X is one of about 12 periodic cicada broods in the eastern U. S. that emerge from the soil every 17 years to breed in numbers reaching into the billions. This population explosion acts as a mechanism to satiate potential predators so that a large number of the cicadas will survive and breed successfully (Karban 1982). Brood X consists of 3 different cicada species; *Magicicada septendecula*, *M. cassini*, and *M. septendecim*. The different species are distinguishable by size (*M. septendecim* \approx 2.8cm long, *M. cassini* and *M. septendecula* \approx 2.0cm), a few morphological characters, and by vocalizations of the males. Periodic cicadas are easy prey items because they are slow flying, do not bite or sting, are non-toxic, and generally are poor at escaping from predators (Karban 1982).

A cicada emergence may influence nest success through several different pathways. First, an abundance of food in the environment could have a direct effect of providing abundant nutrition for both breeding adults and nestlings, and improve survivorship (Holmes et al. 1986, Arcese and Smith 1988, Jones et al. 2003). The potential positive effects of an abundant cicada food source (i.e., larger clutches, greater size of nestlings, and increased juvenile survival) are likely amplified by the event's temporal concurrence with the peak of the avian breeding season (Perrins and McCleery 1989, Perrins 1991). Nutrition of nestlings could be a limiting factor of success, especially during years when cold weather causes a decline in arthropod abundance and an increase in thermo-regulatory requirements. The previous 17-year periodic cicada emergence in Indiana was shown to improve juvenile survivorship in short-tailed shrews (*Blarina brevicauda*; Krohne et al. 1991). Well-nourished adults may have larger

clutches, and be able to renest more often (Arcese and Smith 1988). Koenig and Liebhold (2005) found that 63% of 24 avian species that they studied showed significant population changes that coincided with periodic cicada emergences, although the direction and duration of the effect varied among species and was difficult to explain.

Nest Predation Effects

Cicada emergence may also decrease nest predation. Many nest predators (e.g., Blue Jays, American Crows) consume cicadas, and are not likely to expend additional energy searching for nests when cicadas are easily obtainable and exceed their need for nutrition. Predation of a prey species is related to the density and quality of alternate prey items (Leopold 1933). Holling (1959) demonstrated the functional predator response to increasing prey densities for mammalian predators and insects, in which predators handle more prey as prey densities increase until their ability to handle additional prey is exceeded (satiation). This paradigm of predator-prey relationships has since been validated for the relationship between avian predators and periodical cicada prey (Williams et al. 1993). In a captive bird experiment, several common forest birds and avian predators consumed 20-54 cicadas per day (Karban 1982). Holling (1959) found that the maximum amount of prey that caged mammalian predators could consume corresponded almost directly with the number of prey the free-living individuals could consume.

Nest predation may be the most limiting factor on avian nest success (Schmidt and Whelan 1999), and this indirect effect of the cicada emergence may have the greatest effect on nest survivorship. Nest predation may be as influential as the procurement of food resources in affecting bird communities and their partitioning of habitat (Martin

1988). Predation rates on artificial nests were lower during a cicada outbreak than the period afterwards (Schmidt and Whelan 1999). Williams et al. (1993) found that avian predators appeared satiated with periodic cicadas for several weeks during an emergence.

Nest predation may even usurp food limitations as the driving force in the evolution of the variation in avian life history traits (Martin 1995). Redpath et al. (2001) demonstrated that supplemental feeding of an avian predator, Hen Harriers (*Circus cyaneus*), greatly reduced the number of Red Grouse (*Lagopus scoticus*) chicks fed to harrier nestlings. Redpath et al. (2001) did not examine nest predation, but demonstrated that abundant, easily captured prey can distract an avian predator from its typical prey. Nest predation may also decrease because a greater proportion of a breeding bird's time budget may be available for nest defense during periods of unusual food abundance (Arcese and Smith 1988).

Cicadas were distributed across the entire study area, but they concentrated around edges and interior forest gaps because warmer soil temperatures caused earlier emergence in those areas (Rodenhouse et al. 1997). If these areas of greater cicada concentration attracted greater densities of nest predators, then nests in those localized areas may experience reduced success because of increased risk of a predator incidentally finding a nest. However, on a local scale, Karban (1982) found that predators do not appear to respond numerically to areas of greater cicada densities because all areas tend to have sufficient populations to satiate predators.

Brood X could impact different groups within the forest bird community in different ways. Because some nest predators may spend more time either on the ground or in the canopy, ground nests and arboreal nests may be predated upon by different

communities of nest predators on BONWR. After emergence, cicadas are only near the ground for a matter of minutes or hours before moving to higher locations within the surrounding vegetation to breed. If large numbers of cicadas were only available to predators of ground nests for a few days during the peak emergence, then ground-nesting forest birds may not experience greater survivorship than during a normal breeding season.

Brood Parasitism Effects

Nest success may also decrease if brood parasitism increases because of cicada emergence. Female Brown-headed Cowbirds could parasitize more nests in a season if additional nutrition gained from cicadas allowed the production of more eggs per female cowbird. However, Arcese and Smith (1988) found nest parasitism was reduced by 27% in Song Sparrows in the presence of abundant forage, and attributed this reduction to the increased time available for nest defense by host species when food was unusually abundant. Therefore an increase in parasitism during a periodic cicada emergence may be unlikely.

Predation is not the only cause of cicada mortality. All emerged periodic cicadas die during the breeding season, and predators can only consume a limited portion of the population. The remainder of the population dies from either natural causes after breeding, from severe weather, or from a sexually transmitted fungal infection that appears to be adapted to the cycle of cicada emergences (Kritsky 2004). Fungal infection has been found responsible for a small proportion of mortalities in emergences, whereas natural deaths and storm-related mortalities accounted for the majority of mortalities

(Williams et al. 1993). Williams et al. (1993) estimated that predators consumed only about 15% of the total cicada population.

If nest survival does improve as a result of the presence of periodic cicadas, then emergences could represent an important new variable to be considered for population modeling. If periodic cicada emergences are beneficial to forest bird populations, then there also may be reason for increased concern for forest birds as periodic cicada populations are also declining. I conducted this study to determine whether a periodic cicada emergence would affect the survival of forest bird nests. In doing so, I hoped to learn about how food abundance affects avian productivity.

STUDY AREA

This study was conducted on Big Oaks National Wildlife Refuge, which lies in the Ohio River valley. The refuge lies within the large geographic range of the 17-year periodic cicada Brood X. BONWR is a former military ammunition proving ground (Jefferson Proving Ground) managed by the U.S. Fish and Wildlife Service and owned by the U.S. Army. BONWR is located in southeastern Indiana (Figure 2-1). The refuge has been protected from both agricultural and human development (which fragments much of the surrounding landscape) since the 1940's when military munitions testing began. The base closed in 1995, yet a great deal of unexploded ordnance remains throughout the enclosure, completely restricting access to approximately 50% of the area. Forested areas are commonly used by breeding forest bird species including the Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), Acadian Flycatcher (*Empidonax vireescens*), and Ovenbird (*Seiurus aurocapillus*).

BONWR encompasses approximately 20,200 ha, some of which is mature forest dominated by oaks (*Quercus spp.*), tulip poplar (*Liriodendron tulipifera*), hickories (*Carya spp.*), black walnut (*Juglans nigra*), American sycamore (*Platanus occidentalis*), ashes (*Fraxinus spp.*), and maples (*Acer spp.*). Species such as spicebush (*Lindera benzoin*), common paw-paw (*Asimina triloba*), sassafras (*Sassafras albidum*), and American beech (*Fagus grandidolia*) commonly dominate the understory. The refuge is predominantly a rolling landscape interspersed with expansive mesic flats and ridges associated with the larger streams.

This study was focused on the northern third of the refuge (Figure 2-2). Study sites in the main study area include 3 general forest types: mesic flatwoods typically dominated by tulip poplar, maple, and beech; mesic slope forests dominated by hickory, oak, and beech; and riparian bottoms dominated by black walnut and American sycamore. The interior of the property is networked by a series of mainly unimproved gravel roads with grass borders that vary in width. In most interior forested areas, the forest canopy covers the roadway gap. The habitat surrounding BONWR is dominated by agriculture surrounding isolated woodlots. A fence surrounds the entire property to restrict unauthorized access and limits the amount of disturbance the area receives from human activity. Logging is not currently occurring on BONWR because of unexploded munitions on the entire property, although selective timber harvests did occur previously while the property was an active U.S. Army installation. One of the five plots used in this study was burned in 2004 as part of the U.S. Fish and Wildlife Service management for the area.

METHODS

Nest Monitoring

I nest searched on the northern third of BONWR in 2004 and 2005. Effort was focused on five 40-ha study plots (Figure 2-2). Plots were marked with flagging every 25 m along transect lines 100 m apart. I focused nest searching on study plots, but some nests were found incidentally outside of study plots. No maximum time limit was established for nest searching, as Cerulean Warbler nests are difficult to find. The nests of all other avian species were actively searched for while surveying each plot.

I followed the field protocol established by Martin et al. (1997) for monitoring nests. I monitored nests using spotting scopes, binoculars, or telescoping poles with mirrors when possible. I checked nests every 2-4 days, and more frequently when nests were expected to fledge. I monitored any nest that appeared inactive on subsequent days to validate a nest failure, unless visible nest destruction existed. I considered a nest successful if at least 1 nestling of the host species fledged.

Nest Data Analysis

I calculated daily survivorship and nest success using the Mayfield method (1975), which corrects for the fact that researchers are more likely to find a nest that is surviving. I calculated daily survivorship and nest success for nests built <1 m off of the ground, nests built ≥ 1 m above ground, and all nests found during the study. I analyzed Cerulean Warblers, Acadian Flycatchers, and Wood Thrush separately because of sufficient sample sizes. I modeled daily survival probability using program MARK with the data organized into time periods and by year (White and Burnham 1999). I used Akaike Information Criterion (AIC) model selection methodology to evaluate program

MARK results (Anderson et al. 2000). The peak cicada period in 2004 was 23 May to 10 June. The non-peak period for 2004 was 1 May to 23 May and 11 June to 30 July. I analyzed the 2005 data based on similar time periods, despite there being no cicada emergence that year. Thus, 2005 served as a control year for comparison to the emergence of 2004. Observation days were split for nests that were observed in more than 1 time period.

I analyzed source/sink status of forest bird populations using a Leslie matrix population analysis program developed by Giocomo (2005). I set adult survival rates of Acadian Flycatchers at 48% and Wood Thrush at 45.5% for the analysis, which were reported for the southeast region (including BONWR) by the Institute for Bird Populations (DeSante 2000). I set juvenile survival at 50% of adult survival for all species examined, assuming decreased survival of young birds (Gill 1994). I set adult survival of Cerulean Warblers at 60% to present what may be a slightly optimistic case. Other published adult survival rates for warblers have ranged from 40 to 70% (Martin 1995), and the only published estimate of cerulean survival is $54 \pm 6.0\%$ (Jones et al. 2004). I also assumed a range of renesting attempts possible (3, 4, or 5) given the duration of each species breeding season. Acadian Flycatchers, Wood Thrush, and Cerulean Warblers may all renest after a nest failure, but the number of re-nesting attempts has not been well documented. I based the number of fledged young per successful nest on data from monitored nests. However, I may have underestimated the number of young per successful Cerulean Warbler nest, as it was difficult to locate all fledglings at several nests. I assumed Cerulean Warblers were a single-brooded species, whereas I assumed Acadian Flycatchers and Wood Thrush were potentially double-

brooded. I conducted a sensitivity analysis of the number of renesting attempts, adult survival, and juvenile survival to account for uncertainty in published parameters.

I examined the forest matrix present within a 10-km radius of my study area using the methodology of Robinson et al. (1995), including an analysis of percent area forested, percent core forest present (forest >250 m from an edge), and the mean forested patch size. I also used data for comparison from Robinson et al. (1995) and adapted their method of graphical representation of the data.

I analyzed clutch sizes to determine whether egg-laying females would produce larger clutches as a result of abundant food when cicadas were at their greatest densities. For this analysis, I assumed clutches laid between 11-29 June to have been the result of female feeding during the actual peak cicada period (23 May – 10 June). I based this assumption on food-supplementation studies of Nazca Boobies (*Sula granti*) and Blue Tits (*Parus caeruleus*), which suggested that early egg formation begins approximately 18 days before an egg is laid, the period that coincided with the dates of their experimental food manipulation tests to manipulate clutches (Ramsay and Houston 1997, Clifford and Anderson 2001).

Periodic Cicada Monitoring Protocols

Bird species that prey on cicadas are known to typically discard rather than consume the wings of periodic cicadas (Williams et al. 1993). Avian predation rates on periodic cicadas were measured using surface stations (1 m²) described by Williams et al. (1993). I cleared surface stations of all debris down to bare mineral soil and demarcated the boundaries with white twine held by a tent stake at each of the four corners of the square station. I placed sixteen stations systematically along points in each of the 5 study

plots ($n = 80$). I checked surface stations 3 days a week during the cicada outbreak (19 May – 15 July 2004). I counted every two wings I found as a single predated cicada. If an odd number of wings were present in a sample, I counted the single unpaired wing as a consumed cicada. I also counted the number of cicadas that died naturally (no sign of predation or disease) or from fungal infection (presence of white masses).

I used emergence traps to measure the temporal variation in the availability of periodic cicada adults to predators in each study plot. Nymphal stage cicadas emerge from the soil at night and subsequently eclose (shedding of exoskeleton) to become adults that cannot easily escape mesh traps staked to the ground (Williams et al. 1993). I modeled emergence trap design after Williams et al. (1993), in which each conical trap sampled 0.5 m^2 of substrate. My traps were made from flexible PVC pipe bent into a circle. I then fastened mesh fabric around each ring with staples and cable ties to form a cone-shaped trap. I staked traps to the ground with 3 or more tent stakes. I placed twelve traps on each plot ($n = 60$) in areas where cicadas were likely to emerge (i.e., edges and secondary growth). I monitored and emptied emergence traps every 3 days during the main emergence event. I determined an estimate for the total cicada population size that emerged from each plot in late July. At 75 systematically selected points in each plot ($n = 375$), I cleared a 1-m^2 area of leaf litter and debris and counted the number of cicada emergence holes.

Periodic Cicada Data Analysis

I calculated all periodic cicada demographics and predation effects following the formulas used by Williams et al. (1993):

$$\text{Daily Emergence Rate (ER}_t\text{)} = \text{Newly emerged during collection period } t$$

divided by total number that emerged

$$ER_t = [\text{New adults}_t / \sum \text{New adults}_t],$$

Daily emergence (DE_t) = Daily emergence rate times total number that emerged

$$DE_t = ER_t \times N_{\text{emerge}},$$

Daily mortality rate of cicadas (MR_t) = deaths during collection time t
divided by total number of deaths

$$MR_t = [\text{Deaths}_t / \sum \text{Deaths}_t],$$

Daily mortality (DM_t) = daily mortality rate times the total number of deaths

****where the total number of deaths equals the total number emerged**

$$DM_t = MR_t \times N_{\text{mortality}} \text{ (Note: } \sum DM_t = N_{\text{emerged}} \text{)},$$

Daily population size of adult cicadas (DA_t) = cumulative daily emergence minus cumulative daily mortality

$$DA_t = [\sum DE_t] - [\sum DM_t],$$

Standing crop (SC_t , number of cicadas available to predators) = daily population added to daily mortality

$$SC_t = (DA_t + DM_t),$$

$$\text{Daily predation efficiency} = (DM_t / SC_t)$$

Predation efficiency = (daily mortality / standing crop) times 100%

Forest Songbird Survey Protocol and Density Analysis

I made territory maps by walking the transect lines of each plot and recording the location and movements of every bird that I saw or heard singing using the mapping methodology described by Bibby and Burgess (2000). I performed all territory mapping before 10 a.m. E.S.T daily when weather conditions permitted. I made 6 maps of 4 study plots in each year of the study; a minimum of 5 maps are required to delineate territories in forested habitat with acceptable accuracy (Robbins 1970). I began mapping in late May and ended in early July each year. I amended Cerulean Warbler territory data using nest locations and known territories when possible.

I analyzed territory maps of the plots following the protocol established by Robbins (1970), who suggested using a minimum of 2 registrations in a logical proximity to establish the existence of a territory when using 6 territory maps. I delineated territories conservatively often using more than the suggested 2 registrations. I did not attempt to delineate territories of Blue Jays, American Crows, Yellow-billed Cuckoos (*Coccyzus americanus*), or Brown-headed Cowbirds because of large territory sizes, overlapping territoriality, and/or low detectability. I calculated occurrences for these species based on the mean number of encounters during spot mapping an observer had with each species in each year of the study. I compared the likelihood of observing these species while mapping territories statistically using 2-tailed T-tests assuming unequal variances and α of 0.05.

RESULTS

Periodic Cicada Emergence Characteristics

I observed the first periodic cicadas emerging on 13 May 2004. The greatest number of cicadas emerged during 22-24 May. No cicadas were captured in emergence traps after 21 June. Emergence traps captured a total of 244 cicadas of 3 different species during the Brood X emergence (Table 3-1). Overall, the ratio of captured males and females was nearly 1:1. However, twice as many *M. septendecula* females emerged than males. Counts of emergence holes in the soil under emergence traps indicated that the traps had the potential to capture 405 cicadas, indicating that 161 cicadas escaped or were eaten in traps. Damage to several traps indicated most of the missing cicadas were likely consumed after being removed by mammals. Hole counts revealed a mean of 5.1 emergence holes per 1 m² of forest floor (Range: 0 to 45 holes/m²). I estimated the population of cicadas that emerged on the 5 study plots (total of 200 ha) to be 10,196,036 ± 1,294,258 cicadas (2 S.E.). Cicada distribution was not equal on all study plots, but all study plots had significant cicada populations of at least 1.5 million cicadas (Range = 1.5 – 3.3 million cicadas/40-ha plot).

Surface station measurements indicated that cicada mortality was primarily caused by avian predation. However, surface stations were not likely to record mortality resulting from mammalian predation because mammalian predators were more likely to consume the entire cicada. A total of 488 periodic cicada mortalities were recorded on surface stations (\bar{x} = 6.1 cicada deaths/m²). A minority of those deaths did not result from avian predation (18 natural deaths, 3 fungal infections). Cicadas were consumed by avian predators from the beginning of sampling (19 May) through 6 July 2004. The

cicada population seemed to satiate avian predators from 23 May through 10 June (Figure 3-1). Predators were considered satiated when the proportion of the cicada population they consumed reached its lowest point and lasted until the proportion consumed began to increase again (Figure 3-1).

In 2005, I did not systematically monitor cicada populations, but kept track of vocalizations heard incidental to other monitoring activities. I observed a few instances in 2005 where periodic cicadas that lost breeding synchrony with the main population were heard vocalizing singly or in very small groups.

Avian Response-Nest Survival

During the 2004 periodic cicada emergence a total of 200 nests were monitored of 17 avian species (Table 3-2). I monitored 104 nests during 2005. Modeling of time period effects on daily nest survival related to periodic cicada abundance (Table 3-3) gave different results depending on the nesting group being examined. The grouping of all nests together resulted in selection of 5 of 6 models as the best model subset (Table 3-4). The best supported model indicated that daily nest survival during the peak cicada period in 2004 differed from all other periods, while all other time periods had equal daily survival probabilities. This model indicated a periodic cicada effect on nest survival during the peak of emergence, but constant survival during all other time periods. The best-supported model explained 30% of the daily survival variation, and was 36% more probable to be the best model than the model with the next greatest weight (Table 3-4). Constant survival across all time periods was the least supported model, and was not included in the best model subset.

Modeling of above ground nests resulted in the selection of 3 of 6 models as the best model subset. The model with the most support explained 33% of the daily survival variation and was the same model with the most support in analysis of the all nest grouping (Table 3-4). The next best-supported model design examined whether daily survival varied between the peak and non-peak of the cicada emergence, but did not vary in the control year, whereas the control year differed from 2004. This model explained 32% of the variation in daily survival, and was only 4% less likely to be the best model than the model with the best support (Table 3-4). This model also indicated a possible association of cicadas with daily survival, but indicated that it affected all of 2004 and was not constant over time. The constant survival model was the least supported model (1% of variation explained), and was not included in the best model subset with a $\Delta AIC_c > 2$.

Daily survival of ground nests was best explained by a subset of 4 models. The best-supported model was constant survival between all periods examined, and accounted for 34% of observed variation (Table 3-4). Constant survival was nearly twice as likely as the next best cicada effect model to explain the survival data.

Modeling of Acadian Flycatcher nests resulted in selection of all 6 models as the best subset of models. The best-supported model explained 22% of survival variation, and indicated that survival during the peak of the cicada outbreak in 2004 differed from all other periods in cicada and the control year (Table 3-5). This model was 44% more likely to be the best model than constant survival, which accounted for 12.5% of survival variation (Table 3-5).

Wood Thrush daily survival was best explained by a subset of 3 of 6 models. The best model explained 33% of variation, and tested whether temporal survival varied regardless of cicada emergences (Table 3-5). The second best model included constant survival and accounted for 22% of Wood Thrush survival variance, but was 36% less likely to be the best model (Table 3-5).

All 6 models tested to explain variation in Cerulean Warbler survival were selected as the best subset. The model receiving the most support explained 25% of the variation, and indicated that survival varied between years but not within years (Table 3-5). Constant survival was the next most supported model and was only 15% less likely to be the best model than the best-supported model (Table 3-5).

Overall nest success (Mayfield) of Acadian Flycatchers was 7.8% greater in the cicada year (22.5%) than in 2005 (14.7%). Wood Thrush nest success was 9.7% greater in the cicada year (36.5%) compared with 2005 (26.8%). Cerulean Warbler nest success was 18.6% greater in 2004 (26.0%) than in 2005 (7.4%) and 10% greater than in the 2002-2003 study by Roth (2004).

Source/sink analysis of Wood Thrush, Acadian Flycatcher, and Cerulean Warbler populations indicated that BONWR may have been a population sink for all 3 species during the study (Figures 3-2,3-3,3-4). However, sensitivity analysis indicated that Wood Thrush may have been a source population in 2004, dependent upon assumed rates of renesting, adult survival, and juvenile survival.

Analysis of the 10-km radius region surrounding my study area indicated that 58.9% of the region was forested (Figure 3-5). The forested regions contained 5,228.5 ha

of core forest (core forest is > 250m from an edge, Figure 3-5). The average size of a forest patch was 34.9 ha (Figure 3-5).

Clutch size differed for both Acadian Flycatcher and Wood Thrush nests in 2004 (Table 3-6). Acadian Flycatcher clutches that were related to the peak cicada period were larger than those laid before and after the peak period ($t = -3.58$, $P = 0.001$). Wood Thrush nests demonstrated the opposite trend with larger clutches laid before and after the peak cicada period ($t = 3.29$, $P = 0.002$). In 2005, there was no difference in Acadian Flycatcher clutch size ($t = 0.19$, $P = 0.850$), whereas Wood Thrush clutches demonstrated the same trends as in 2004 ($t = 3.48$, $P = 0.039$).

Brood parasitism rates were consistent between years. Wood Thrush nests were most frequently parasitized in both study years: 19.5% (9 of 46) in 2004, and 19.0% (4 of 21) in 2005. Acadian Flycatcher nests were parasitized at a rate of 5.7% in 2004 and 3.3% in 2005. No Cerulean Warbler nests were observed to be parasitized in 2004, but 12.0% (3 of 25) were parasitized in 2005.

Avian Response-Density Effects

The number of territories present on our study sites did not change dramatically for most species between years (Table 3-7). Annual changes on individual study plots were often more obvious, but population trends on the individual plots did not follow the same trends. Ovenbirds showed the greatest yearly change with an additional 45 territories recorded in 2005. Cerulean Warblers seemed to decline significantly on our study plots from 2004 to 2005, but spot mapping data suffered from low detectability of Cerulean Warblers later in the season. Some ceruleans may also shift territories away

from study plots in some years, resulting in lower populations on study plots but not necessarily on the refuge.

Blue Jays ($t = -3.11$, $P = 0.003$) and Brown-headed Cowbirds ($t = -2.72$, $P = 0.010$) increased on our study plots in 2005 (Table 3-8). On average, I encountered 41% more cowbirds and 36% more Blue Jays for every visit to a study plot in 2005 as compared with 2004. The trend was also apparent in the individual plots visited in both years. Nearly twice the number of American Crows were recorded in 2005 compared with 2004, but the chance of encountering them on any one visit to a plot did not differ between years (Table 3-8, $t = -1.71$, $P = 0.097$). Observers recorded almost 1 more Yellow-billed Cuckoo per survey during 2004 compared with 2005, but the probability of recording them did not differ between years (Table 3-8, $t = 1.30$, $P = 0.200$).

DISCUSSION

Estimates of periodic cicada densities vary widely between study areas and different broods in different years. The estimated density of 5.1 cicadas/m² is comparable to 6.6 cicadas/m² found in Brood XIX in Arkansas (Williams et al. 1993), but much less than the 27.2 cicadas/m² recorded for Brood IV in Kansas (Whiles et al. 2001). The 3 species of periodic cicadas captured were the 3 species that have been historically associated with the 17-year Brood X emergence.

Mortality caused by the parasitic fungus of periodic cicadas accounted for a very small proportion of all mortalities I recorded, which is similar to the results of Williams et al. (1993). However, the proportion of natural deaths was much smaller in this study, whereas the proportion of mortality attributable to avian predation was much greater than found by Williams et al. (1993). This difference may have resulted from severe June

thunderstorms that caused the death of 40% of the brood studied by Williams et al. (1993). My analysis of avian predation of periodic cicadas indicated that the ability of avian predators to consume cicadas was exceeded as predicted by Holling (1959) and as previously measured by Williams et al. (1993; Figure 3-1). The rapid increase in cicada densities made it impossible to determine the precise density of cicadas at which avian predators could no longer handle more prey.

Forest songbird reproduction was associated with the emergence of Brood X during 2004. This large-scale event provided millions of easily captured meals for birds breeding on our study sites and typical predators of their nests. The impact of the cicada emergence was greatest for nests built above the ground. All well-supported models for this group indicated that 2004 nest survival was greater than in 2005. Above ground nests were more likely to survive during the peak of the cicada emergence than in any of the other 3 time periods (Table 3-4). Improved nest survival during the peak cicada emergence in 2004 was also indicated by parameter estimates that showed at least a 2% increase in daily survival during that period compared with any other periods (Table 3-9). The difference in overall nest success for a 2% decrease in daily survival (e.g., 96 to 94%) for a species that nests for 28 days is about 14%, a biologically significant effect.

Ground nests did not exhibit this same trend and constant survival was the best model of ground nest survival. Ground-nesting birds may benefit less from periodic cicadas, as cicadas move up vegetation within hours after emerging. Eventually most cicadas were off of the ground and may have left ground-based foragers without an abundant alternative to predating nests. Analysis of all nest data combined was explained by a wider breadth of models, but the model indicating a cicada effect was best able to

account for daily survival variance. The results for the all nest group are less clear because of the inclusion of the ground nests that did not appear to receive the same benefit from cicadas that above-ground nests did.

The effect of the periodic cicada emergence was more difficult to document at the individual species level, possibly because of sample size limitations. Acadian Flycatcher and Cerulean Warbler data were insufficient to remove any of the models from consideration. Wood Thrush nest analysis resulted in a reduced subset of best models, but the inclusion of constant survival as a likely predictor made interpretation difficult. Regardless, the cicada emergence appeared to have an effect on the overall productivity of Cerulean Warblers as 11 of 28 nests fledged in 2004. In 3 non-cicada years combined (2002, 2003, and 2005), it took over twice as many cerulean nests ($n = 65$) to produce the same number of successful nests ($n = 11$).

A periodic cicada emergence occurs somewhere in the eastern U. S. almost every year (Kritsky 2004). This may allow above-ground nesting forest birds to produce more young than in non-cicada years, and slow population declines. Periodic cicada emergences often encompass large geographic regions, and so the number of young produced as a result of an emergence may be of significance to entire populations of affected forest bird species.

Source/sink analysis indicated all 3 species studied were population sinks on BONWR during at least one year of my study if my assumptions were true for those populations (Figures 3-2,3-3,3-4). The models I used were sensitive to all input variables, meaning that if any of my assumptions (number of re-nests possible, adult survival, or juvenile survival) were far from the true values of the refuge's populations,

the results could have been different. For example, only a 5% change in either adult or juvenile survival could mean that Wood Thrush became a source population in the cicada year.

Despite some of the positive trends in daily survival that seem to result from the periodic cicada emergence, overall nest success was extremely low for Cerulean Warblers, Acadian Flycatchers, and Wood Thrush. These poorly-reproducing populations may exist because of the fragmented nature of the area surrounding BONWR that is possibly increasing nest predation and brood parasitism. The 10-km radius area around the study site had a moderate amount of forest cover and interior forest cover compared to the rest of the Midwest, but the mean patch size was very small (34.9 ha, Figure 3-5). This result indicated that the region has a few larger areas of forest, but is dominated by small patches (<35 ha in size). Despite the frequent occurrence of small forested areas, Acadian Flycatcher and Wood Thrush nests in my study sites were parasitized, on average, less often than in some other areas of the Midwest with comparable forest cover (Robinson et al. 1995, Figure 3-6). This suggests that nest predation may have the most influence on nest success, as the daily survival probabilities of Acadian Flycatcher and Wood Thrush nests on BONWR were still lower than expected relative to the rest of the Midwest (Robinson et al. 1995, Figure 3-7).

Despite the probability that BONWR Cerulean, Wood Thrush, and Acadian Flycatchers populations were sinks, these populations may still be vital in the maintenance of global populations. The forests of the eastern United States exist in many fragmented regions often surrounding isolated large areas of forested habitat. Forest birds may exist within a metapopulation framework in which populations in some areas

occasionally become extirpated, but this may be balanced by colonization of new areas (Levins 1969). The few young produced in areas such as BONWR may be vital, because they have the potential to colonize new source areas that may not be used otherwise. Many characteristics of migration including the direction, distance, and timing are all genetically controlled and may evolve relatively rapidly because of a great deal of phenotypic and genetic variation in their expression (Berthold 1993). Berthold (1992) found evidence of rapid genetic altering (< 30 years) of migration routes in birds that led to the colonization of new wintering grounds. It may be important for the future conservation of forest bird populations to preserve the various migration route patterns so that available habitat will be more readily colonized in the future.

There may be a relationship between increased food availability as a result of the cicada emergence and increased clutch size for Acadian Flycatchers (Table 3-6). Wood Thrush clutch size did not seem to be affected (Table 3-6). It is somewhat surprising that this species does not follow the same trends seen in Acadian Flycatcher clutches because both species consume cicadas, which may indicate the existence of complicated interactions or biological effects that were not considered.

Territory mapping suggested an increase in the number of breeding Ovenbirds in 2005. Ovenbirds may have experienced improved overall productivity in 2004, but the limited Ovenbird nest data suggested productivity was very poor ($n = 17$, nest success = 7.2%). Modeling results also gave no indication that ground-nesting birds benefited from the periodic cicada emergence. No other forest bird of interest appeared to increase in breeding numbers in the year following the cicada emergence.

Yellow-billed Cuckoos are known to track periodic cicada emergences (Koenig and Liebhold 2005), but I could not demonstrate that this occurred in this study. However, 9 nests were found in 2004 compared to none in 2005, and we recorded vocalizing cuckoos 57 times in 2004 compared with 37 times in 2005, consistent with this pattern of behavior.

The periodic cicadas heard in 2005 likely did not reach sufficient numbers to affect nest survivorship. Some periodic cicadas are known to break with each brood's temporal breeding cycle (Kurban 1982). Given time, cicadas with errant biological clocks may lead to the formation of new emergence broods with their own unique reproductive timing. Many of these aberrant emergences may fail because predators can consume emergences of up to 10,000 cicadas before any cicadas are able to reproduce (Alexander and Moore 1962, cited in Kurban 1982). Periodic cicada emergences appear to act as a mechanism that improves the probability of avian nest survival when the number of emerged cicadas is sufficient to satiate potential nest predators. The effect this may have on global populations of birds is still unknown.

The lack of overall improvement in productivity of some species is supported by territory mapping that showed few species increased in density on our plots. However, increased recruitment in 2005 may not be observed on our 40-ha study plots if the new individuals settled in habitat outside our study plots. Juvenile dispersal distances are greater in areas where habitat exists in fragmented patches (Paradis et al. 1998). I also do not know the long-term population trends on the study plots. The lack of significant change in territory density may be a positive indicator, particularly if avian populations

had previously been declining. Overall, more research is needed to understand the effects emergences have on each individual species across space and time.

Understanding the implications of periodic cicada emergences are confounded by predator response to the increased food abundance. Increased Blue Jay, American Crow, and Brown-headed Cowbird occurrence the year following the emergence could result in several years of suppressed reproduction for forest bird species. These same patterns in predator populations were also found by Koenig and Liebhold (2005) when analyzing Breeding Bird Survey (BBS) data before, during, and after cicada emergences. In highly fragmented landscapes any benefits of an emergence may be offset in subsequent years because of increased nest predator and parasite populations, leading to decreased nest success and brood size.

IV. MANAGEMENT RECOMMENDATIONS

Cerulean Warbler breeding habitat on BONWR was characterized by an increased number of woody stems, and a decrease in tree density compared with random sites. Low tree density may be a reflection of a more mature forest on BONWR, which may require protection to continue attracting breeding ceruleans. However, managing for woody stem density may be a more complex management issue. Other studies have suggested that a well-developed mid-story is an important characteristic of cerulean habitat (Jones and Roberston 2001, Weakland and Wood 2005). However, even without management, a mid-story commonly develops in many of the forest types on the refuge as canopy trees die and spicebush and common paw-paw develop in shaded areas.

Management of Cerulean Warblers on BONWR is challenging. Generally, Cerulean Warblers depend on large mature forests to breed successfully, and the existence of BONWR within a fragmented landscape is one likely explanation for the poor reproductive output found on the refuge (Robbins et al. 1992). An important factor limiting productivity on BONWR likely is nest failures indirectly caused by forest fragmentation. Cerulean Warblers were found to occur less frequently within fragmented forests and within 340 m of forest edges in West Virginia (Weakland and Wood 2005, Wood et al. 2006). Many of the edge habitats found on and near BONWR are distinct, where forest meets pasture, row crops, housing, roads, or grasslands. Those edges provide easier access to forest interior by nest predators and brood parasites.

The best prescription for Cerulean Warblers on BONWR may be to allow increased maturation of the forest, particularly in areas that have been disturbed more

recently. That could be combined with attempts to consolidate existing patches of forest that border the refuge by allowing the land to revert to mature forest. The roads on BONWR were laid out in a grid-like fashion, creating corridors for brood parasites and nest predators to penetrate into core forest areas. Many forested areas bounded by roads were <400 ha in size. Some roadways on the refuge could be strategically closed (while still allowing necessary access) to potentially improve the survival probability of nests in the forest interior. I did not find enough nests near roads to determine habitat differences or changes in nest survival probability.

These proposed actions could increase the availability of successful breeding sites on BONWR and decrease populations of nest parasites and predators, facilitating the creation of a source population for Cerulean Warblers. Acadian Flycatchers and Wood Thrush likely are suffering from population pressures similar to Cerulean Warblers, and should benefit from the same type of management plan presented for Cerulean Warblers.

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APPENDIX

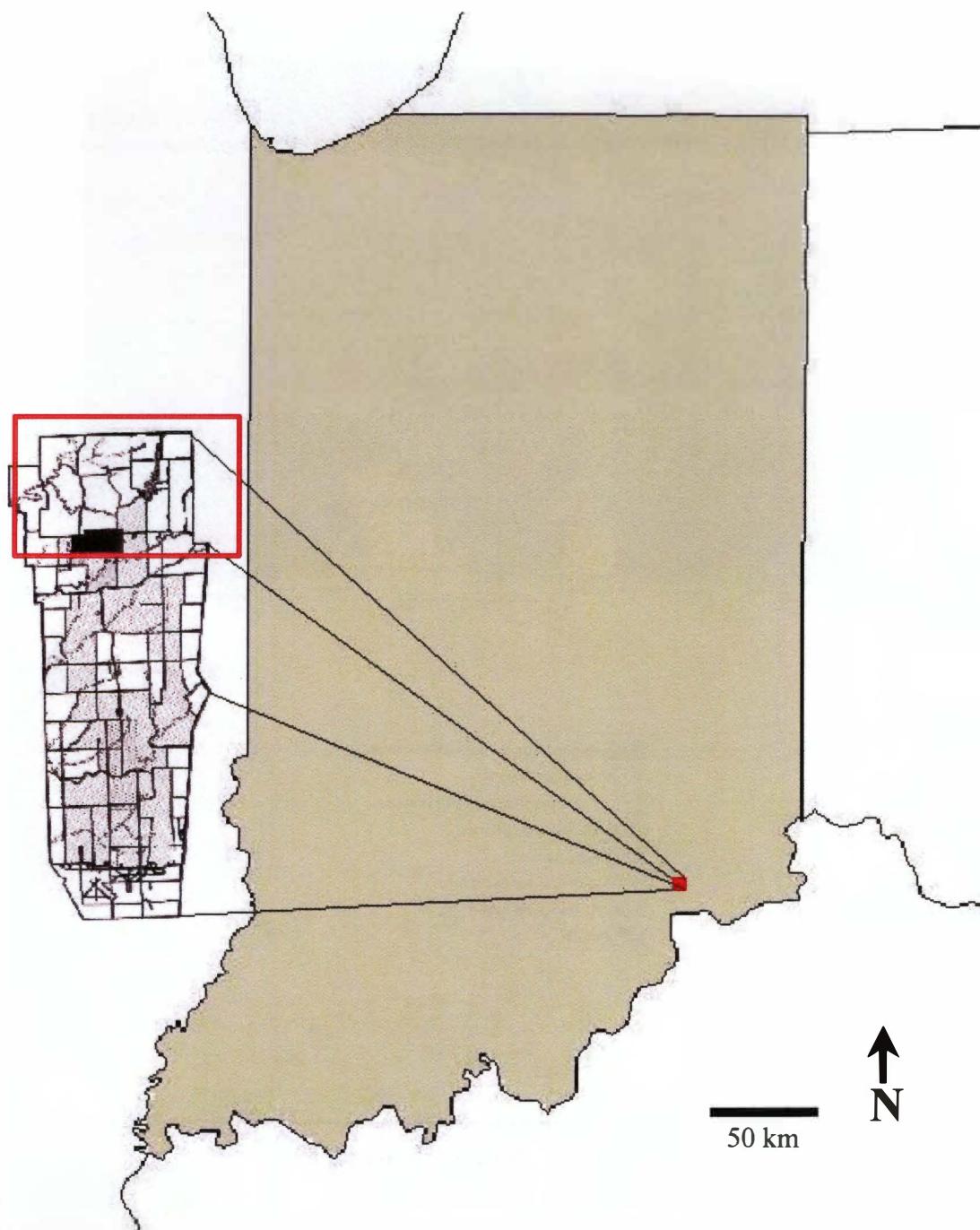


Figure 2-1. Location of Big Oaks National Wildlife Refuge in southeastern Indiana. The black portion of the refuge inset is a practice range operated by the Indiana Air National Guard. The red rectangle delineates the general study area location on the refuge. [Adapted from USFWS, unpublished data]

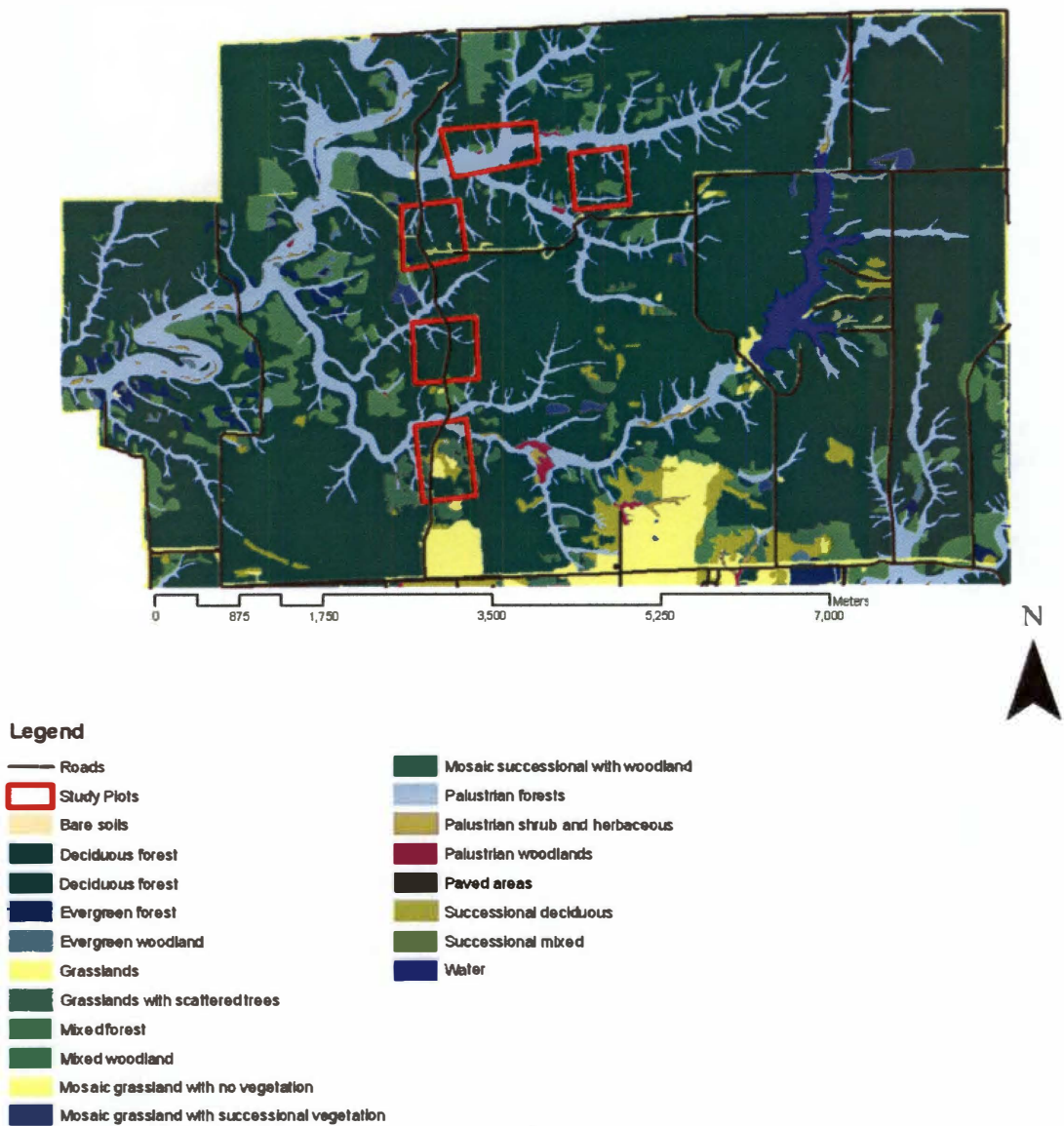


Figure 2-2. Landcover types and 40-ha study plots on the northern third of Big Oaks National Wildlife Refuge (above K road) in southeastern Indiana.

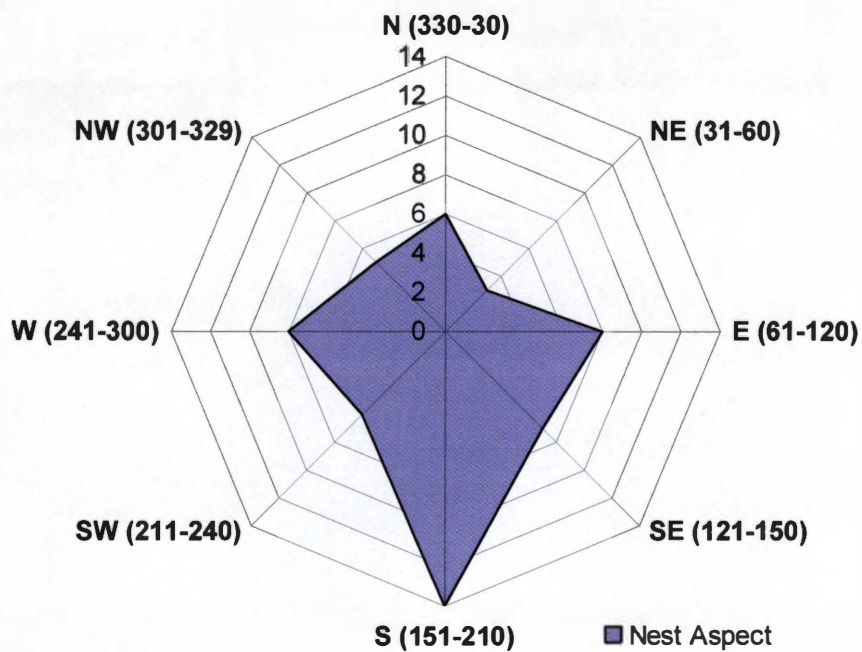


Figure 2-3. Number of Cerulean Warbler nests found at different aspects in relation to the nest tree bole on Big Oaks National Wildlife Refuge, IN, during the 2004 and 2005 breeding seasons.

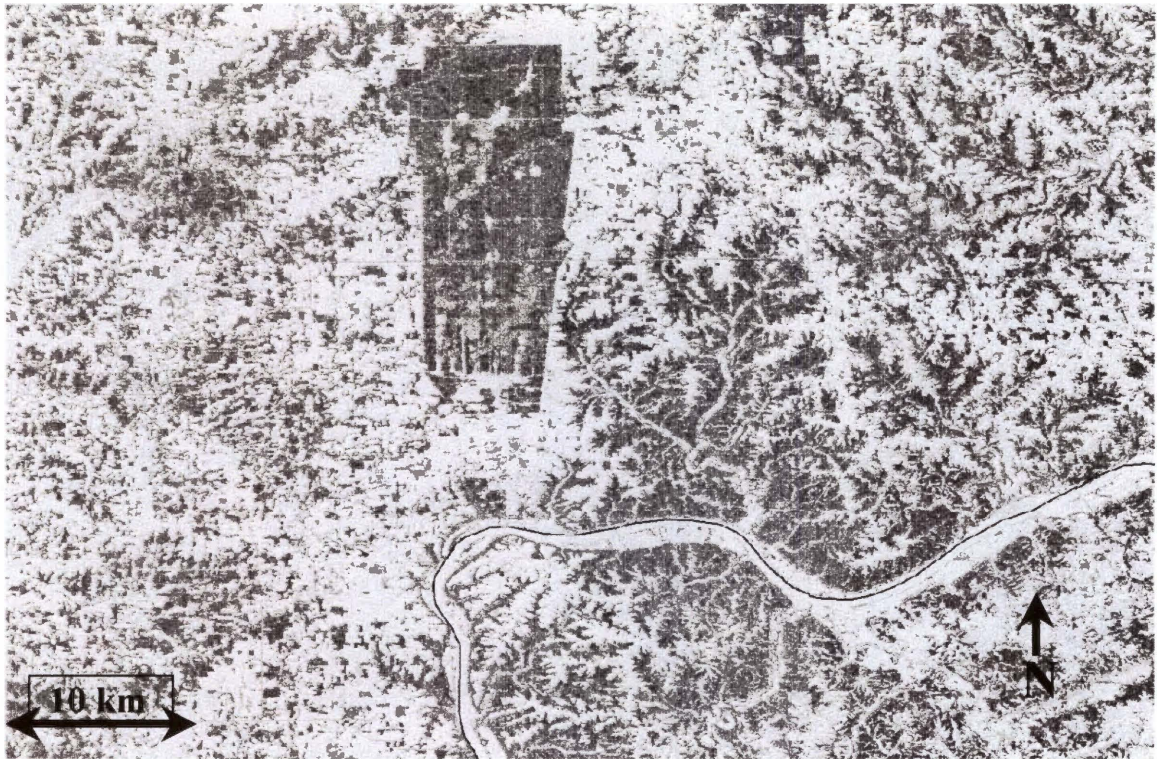
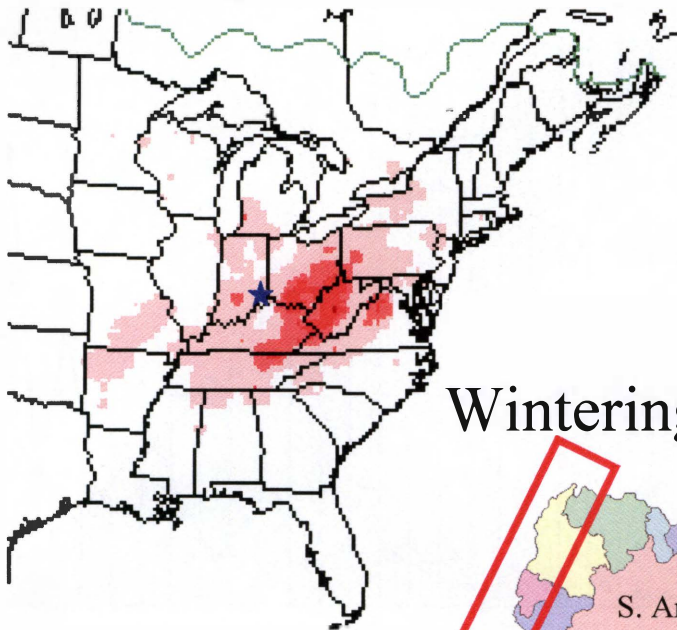


Figure 2-4. Forest canopy cover (dark) in southeastern Indiana. White areas are primarily agricultural and urban. Big Oaks National Wildlife Refuge is the rectangular large block of forest (top center of image).

Breeding range



Wintering range



Figure 2-5. Location of study area (blue star) in relation to the core breeding range of Cerulean Warblers, and the known general wintering range in South America. [Adapted from USGS maps].

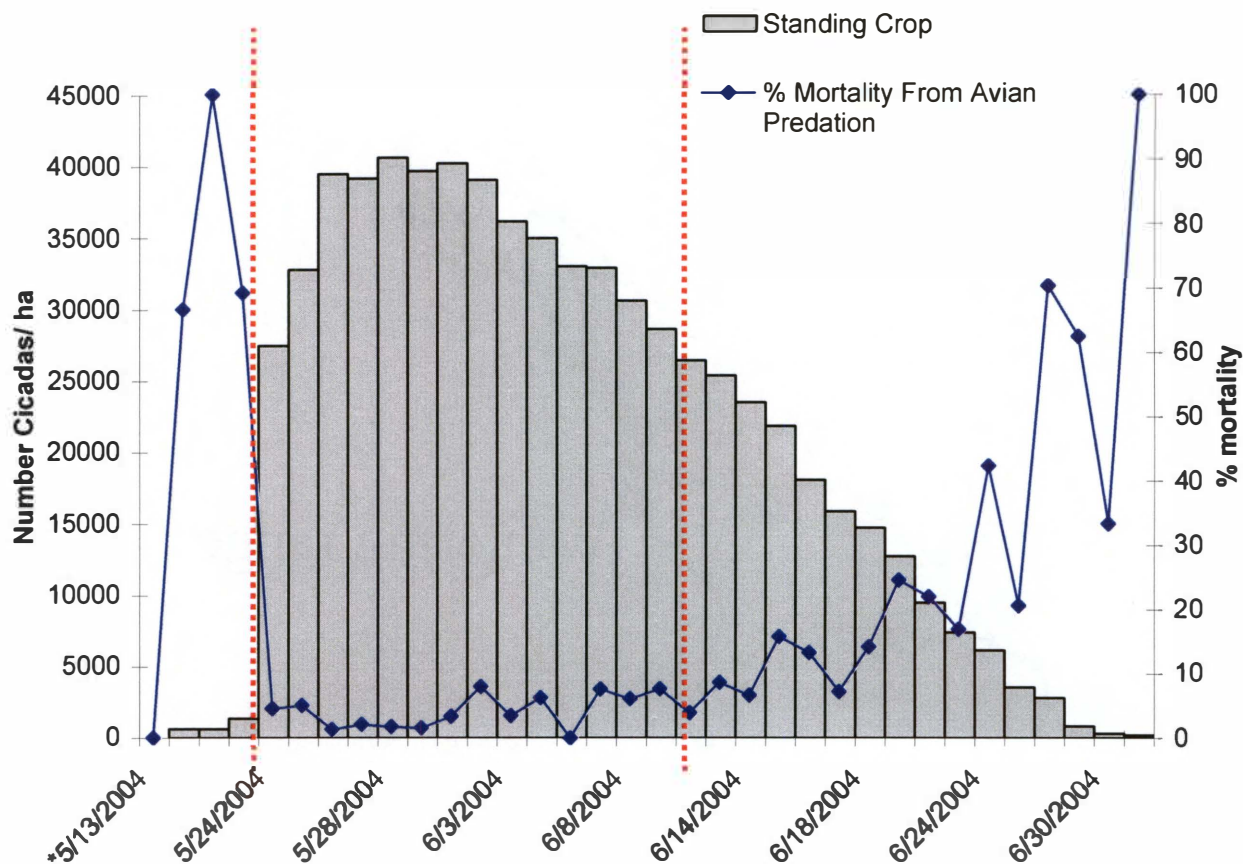


Figure 3-1. Standing crop of cicadas (living population) in comparison to the ability of predators to consume them on Big Oaks National Wildlife Refuge, IN, 2004. The period of avian predator satiation by cicadas (peak cicada period) is between the dashed lines (23 May–10 June). The first emerging cicadas were observed on May 13th, but no data were collected on that date.

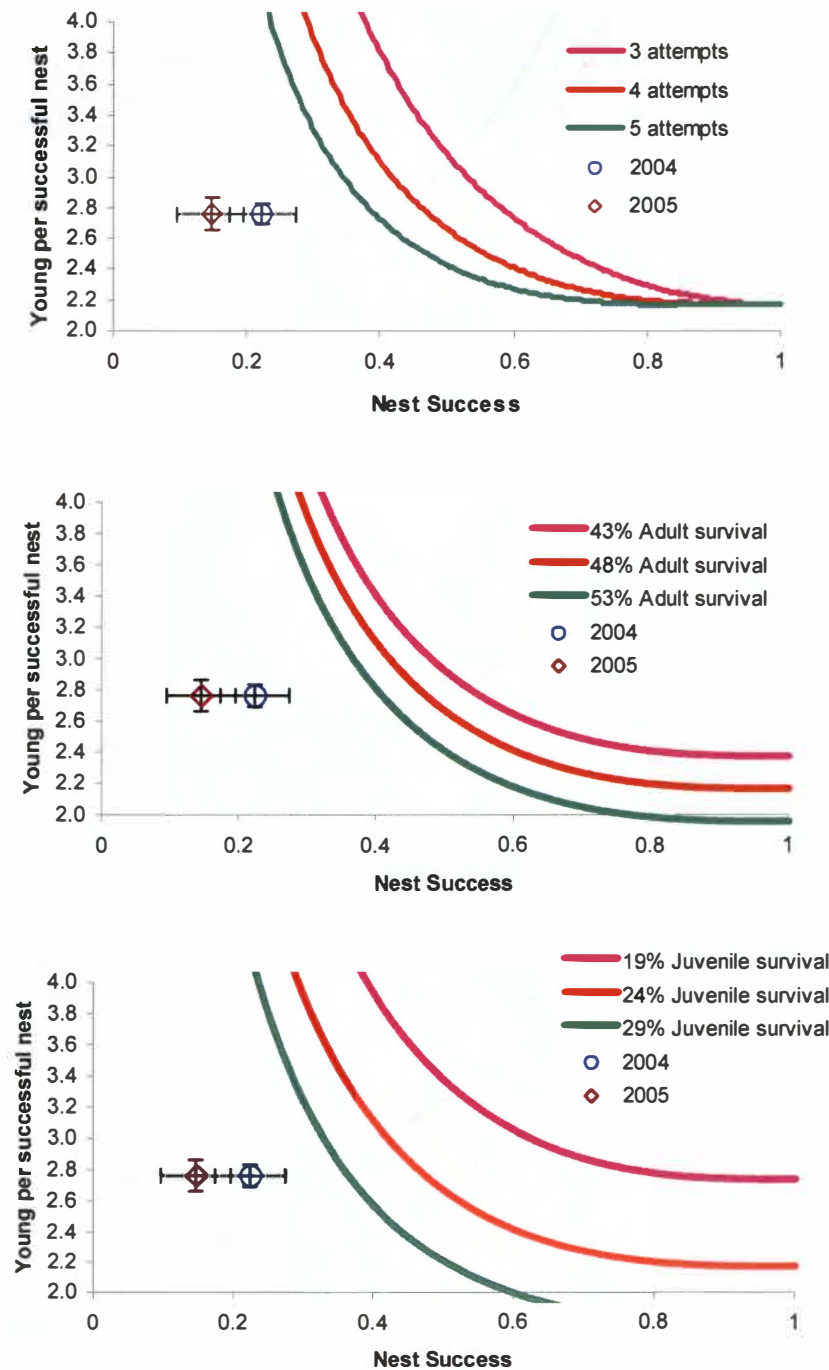


Figure 3-2. Relationship of nest success (± 1 S.E.) and the number of young produced per successful nest (± 1 S.E.) in 2004 and 2005 to the viability of the Acadian Flycatcher population on Big Oaks National Wildlife Refuge, IN. The 3 lines represent stable populations ($\lambda = 1$) for various numbers of renesting attempts per breeding pair per season (2, 3, or 4 attempts). Points below the lines represent sink populations, points above are sources. Acadian Flycatchers were modeled as a double-brooded species.

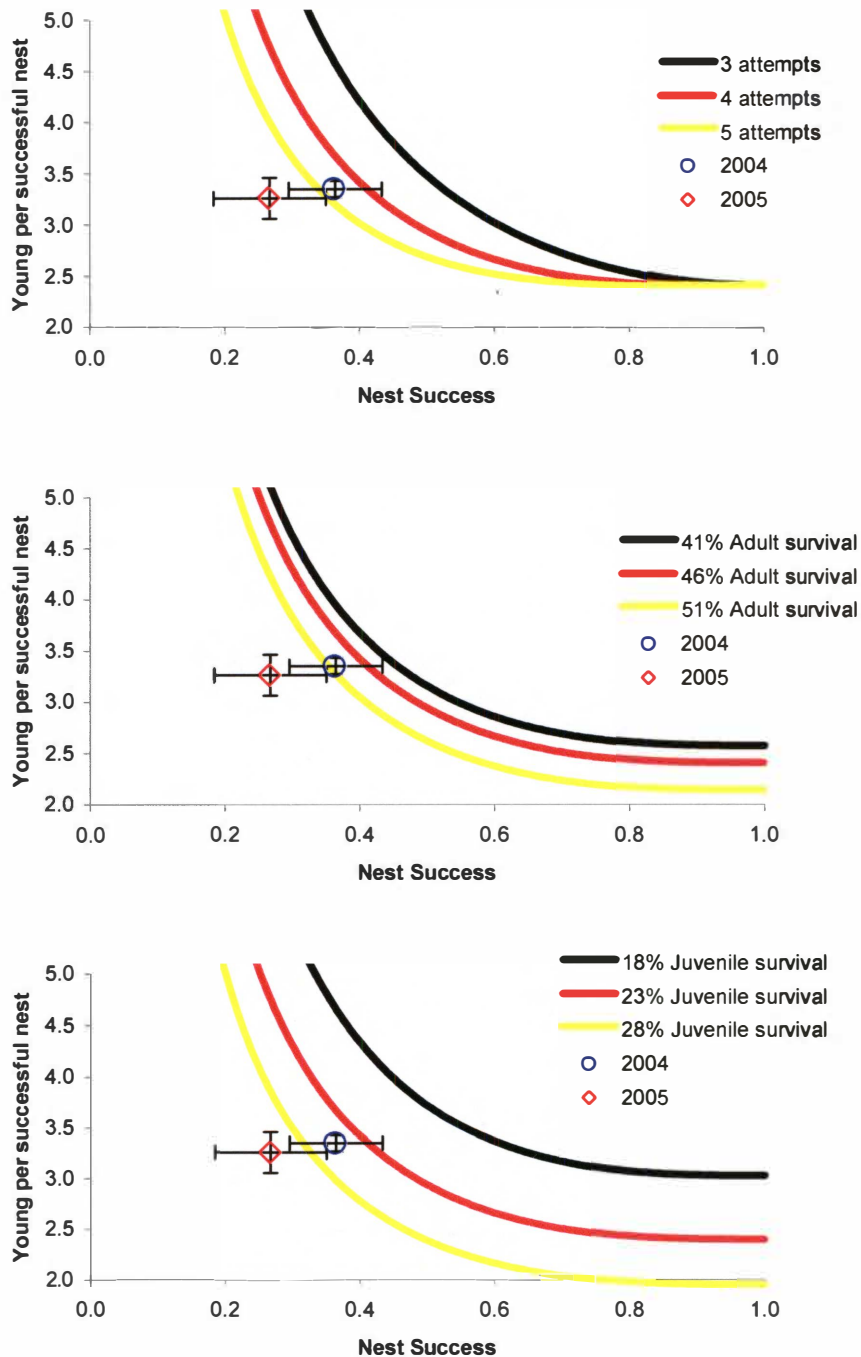


Figure 3-3. Relationship of nest success (± 1 S.E.) and the number of young produced per successful nest (± 1 S.E.) in 2004 and 2005 to the viability of the Wood Thrush population on Big Oaks National Wildlife Refuge, IN. The 3 lines represent stable populations ($\lambda = 1$) for various numbers of renesting attempts per breeding pair per season (2, 3, or 4 attempts). Points below the lines represent sink populations, points above are sources. Wood Thrush were modeled as a double-brooded species.

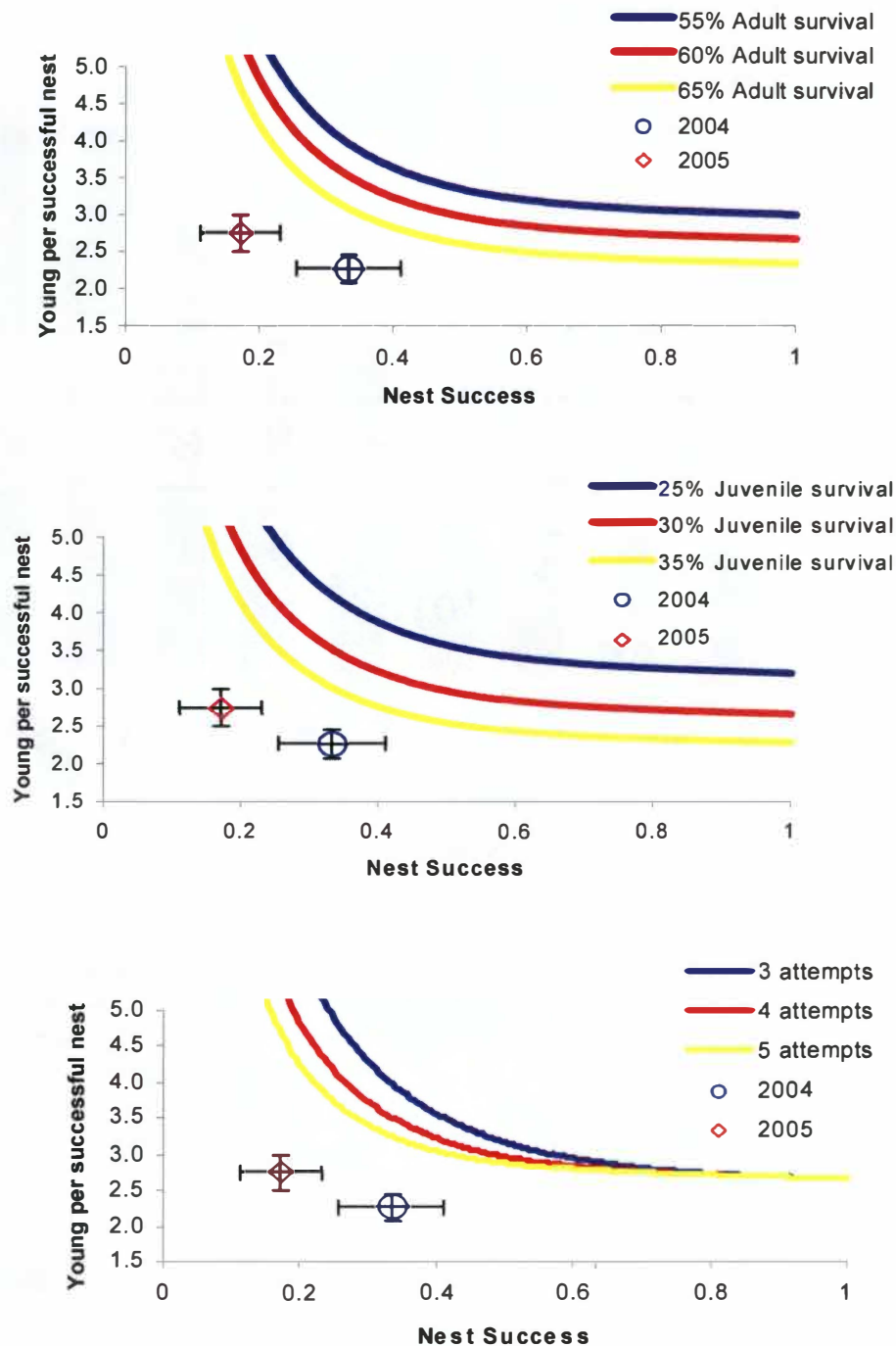


Figure 3-4. Relationship of nest success (± 1 S.E.) and the number of young produced per successful nest (± 1 S.E.) in 2004 and 2005 to the viability of the Cerulean Warbler population on Big Oaks National Wildlife Refuge, IN. The 3 lines in each graph represent stable populations ($\lambda = 1$) for various numbers of renesting attempts per breeding pair per season (2, 3, or 4 attempts). Points below the lines represent sink populations, points above are sources.

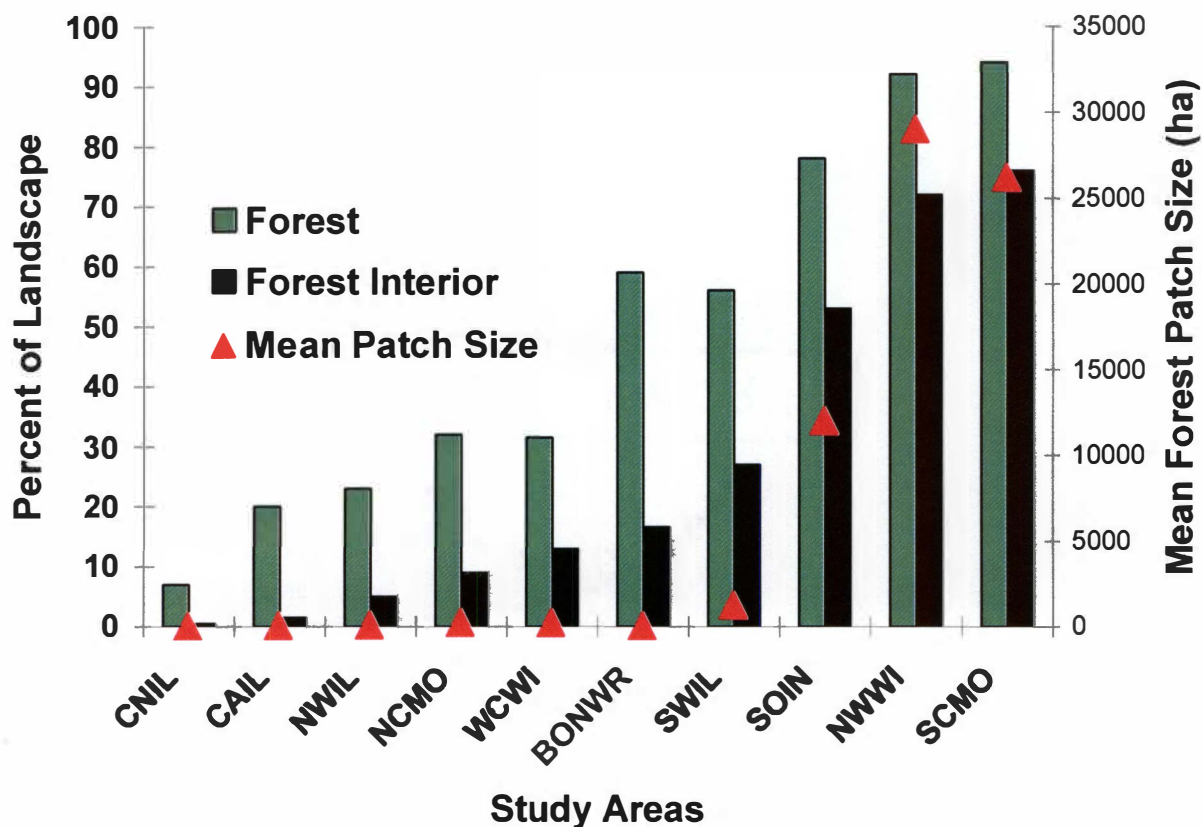


Figure 3-5. The mean percent forest cover, mean percent forest interior (forest > 250m from an edge), and mean forest patch size within a 10-km radius of the center of avian study sites in the Midwest. Data (excepting BONWR) taken from Robinson et al. (1995). Abbreviations: CNIL, central Illinois; CAIL, Cache River Illinois; NWIL, north-western Illinois; NCMO, north-central Missouri; WCWI, west-central Wisconsin; SWIL, south-western Illinois; BONWR, Big Oaks National Wildlife Refuge, Indiana; SOIN, southern Indiana; NWWI, north-western Wisconsin; SCMO, south-central Missouri.

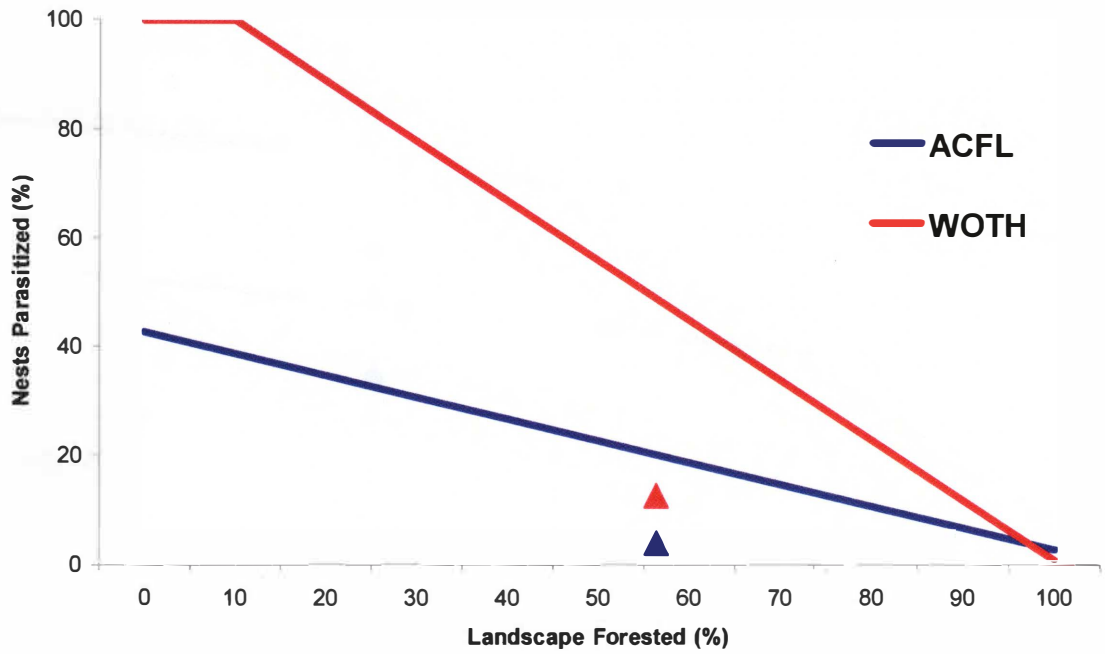


Figure 3-6. Relationship of the amount of forested landscape and nest parasitism rates for Acadian Flycatchers (ACFL) and Wood Thrush (WOTH) in the Midwest, U. S. (Robinson et al. 1995). Triangles represent parasitism rates on Big Oaks National Wildlife Refuge.

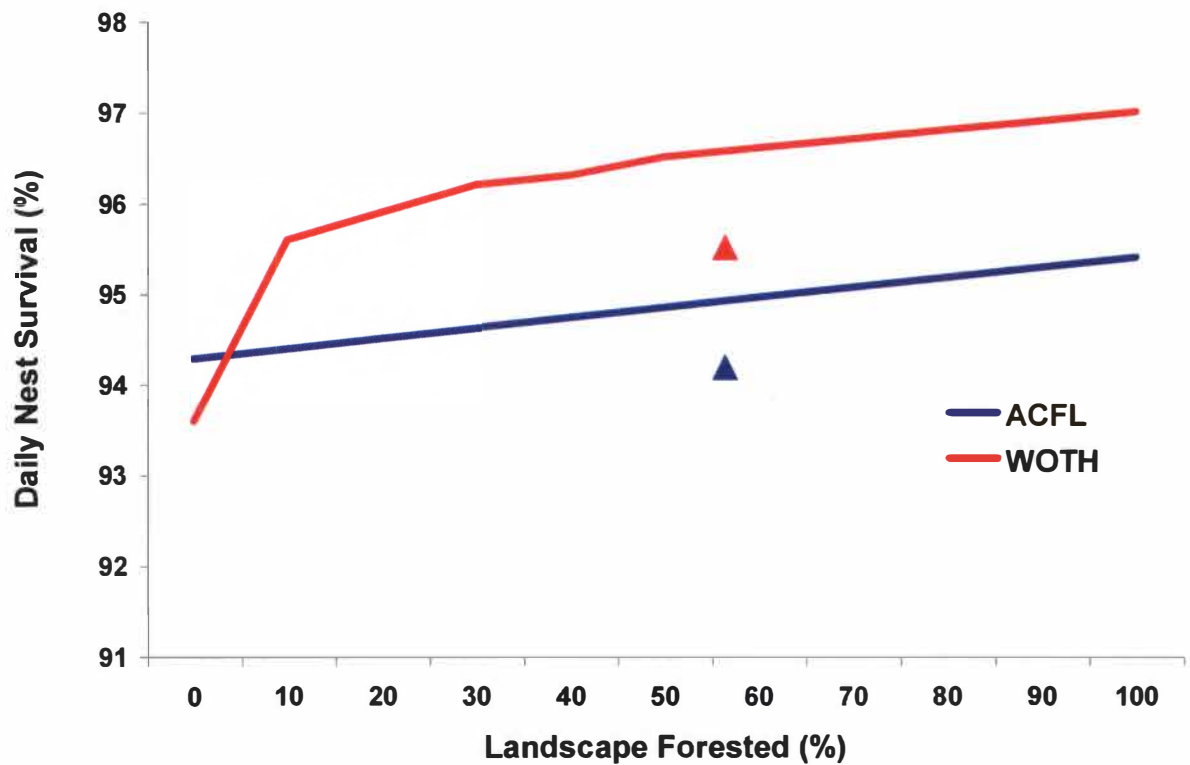


Figure 3-7. Relationship of the amount of forested landscape and the probability of daily nest survival for Acadian Flycatchers (ACFL) and Wood Thrush (WOTH) in the Midwest, U. S. (Robinson et al. 1995). Triangles represent the probability of daily nest survival on Big Oaks National Wildlife Refuge.

Table 2-1. Temporal, nest site, and nest patch models evaluated to determine their relationship to Cerulean Warbler nest success on Big Oaks National Wildlife Refuge, IN. Model variable definitions are; Sdate = date (at start of each observation interval), Sage = age of nest, and Stage = laying, incubation, or nestlings, NestHt = height of nest, CC = canopy coverage, NestAspect = aspect of nest in relation to nest tree bole, NestTree = oak, black walnut, or other, NestTreeHt = height of nest tree, NestBole = distance from bole to nest, NestCanopy = distance from nest to outer nest tree foliage, Nwoody stems = number of woody stems, Nsnags = number of dead trees, Ntrees = number of trees FCN = canopy coverage estimated in 4 height intervals of less than 6 m, 6 to 12 m, 12 to 18 m, and greater than 18 m, PCN = vertical vegetation measured at territory level with a stratification pole at same intervals as FCN, Location = whether within 50 m of road, stream, or neither, PlotTreeRichness = Tree species diversity, and Slope = slope of ground.

Temporal Models	Nest -site Models	Nest patch Models
Sdate	NestHt	NtreesPlot
Sage	CCNest	NtreesPlot + Slope
Sage ²	FCN12-18	Location + Slope
Sage ³	FCN>18	Location + PlotTreeRichness
Stage	CCNest + NestHt	Nwoody stems Plot + NsnagsPlot
Year	CCNest + NestAspect	NtreesPlot + Nwoody stems Plot
Year + Stage	CCNest + NestCanopy	CCNestPlot + NtreesPlot
Sdate + Stage	NestTree + NestAspect	NtreesPlot + N woody stemsPlot + CCNestPlot
Sdate + Sage	NestHt + NestBole	PCN<6 + PCN6-12 + PCN12-18 + PCN>18
Sdate*Sdate	NestHt + NestTreeHt	Slope + PCNall4Intervals
Constant Survival	NestHt + NestAspect	Constant Survival
	CCNest + NtreesNest + NwoodystemsNest	
	NestHt + NestCanopy + NestAspect + NestTree	
	FCN<6 + FCN6-12 + FCN12-18 + FCN>18	
	CCNest + FCNall4Intervals	
	Constant Survival	

Table 2-2. Models tested to describe habitat used by breeding Cerulean Warblers on Big Oaks National Wildlife Refuge, IN, for both nest sites and the surrounding nest patch. Nest-site variable definitions are: MaxTreeHt = height of tallest tree, Nwoody stems = number woody stems, Ntrees = number of trees, DistStream = whether nest within 50 m of stream, CC = canopy coverage, FCN = canopy coverage estimated in 4 height intervals of less than 6 m, 6 to 12 m, 12 to 18 m, and greater than 18 m, Slope = slope of ground. Nest-patch variables are defined as: PCN = vertical vegetation measured at the nest patch scale with a stratification pole at same intervals as FCN, FCP = FCN at nest-patch scale, all other variables are defined similarly with addition of being measured at the nest-patch scale.

Nest Site Models	Nest Patch Models
MaxTreeHt	NtreePlot
Nwoodystems	PlotCC
Ntrees	Plotdbh
DistStream	FCP12-18
CC	FCP>18
FCN12-18	PCN12-18
FCN>18	PCN>18
CC + Nwoody stems	NtreePlot + NplotWoodyStems
CC + Ntrees	PlotCC + NplotWoodyStems
CC + Ntrees + Nwoody stems	PlotCC + NtreePlot
Nwoody stems + N trees	PlotCC + NtreePlot + NplotWoodyStems
DistStream + Slope	PlotCC + FCP<6 + FCP6-12
CC + FCN6-12 + FCN12-18	PlotCC + FCP6-12 + FCP12-18
DistStream + FCNall4Intervals	PlotCC + FCP12-18 + FCP>18
Nwoody stems + FCN12-18 + FCN>18	PlotCC + PCN6-12 + PCN12-18
MaxTreeHt + FCNall4Intervals	PlotCC + PCN12-18 + PCN>18
MaxTreeHt + FCN6-12 + FCN12-18	FCP<6 + FCP6-12 + FCP12-18 + FCP>18
MaxTreeHt + Nwoody stems	
FCN<6 + FCN6-12 + FCN12-18 + FCN>18	

Table 2-3. Habitat characteristics of 57 Cerulean Warbler nests and nest sites (5m radius plot around the nest) found on Big Oaks National Wildlife Refuge, IN, in 2004 and 2005. The number of observations (n), the mean (\bar{x}), 1 standard error (S.E.) and range are reported. Four nests were found inactive, and measured late in the breeding season.

Measurement	n	\bar{x}	S.E.	Range
Nest aspect from bole	57	179 ⁰	12.0	7 ⁰ - 358 ⁰
Nest height (m)	57	17.8	0.6	6.0 – 31.3
Nest tree height (m)	57	27.5	1.0	13.2 – 15.2
Nest tree dbh (cm)	57	42.3	2.5	14.0 – 97.3
Distance nest to bole (m)	56	4.4	0.3	0.6 – 11.8
Cover over nest (%)	55	78.1	3.7	20 – 100
Canopy Coverage (%)	51	91.3	0.8	77.3 – 98.5
Slope	55	5.4 ⁰	1.0	0 ⁰ - 32 ⁰
Number trees/ 0.1-ha	57	7,000	600	0 – 24
Number woody Stems / 0.1-ha	57	12,000	1,500	0 – 43
Distance to stream (m)	57	259.8	34.8	0 – 1101

Table 2-3 Continued.

Measurement	n	\bar{x}	S.E.	Range
Vertical canopy cover (%) (pole method)				
<6 m	52	40.5	2.9	6.3 – 96.3
6-12 m	52	47.0	2.7	11.3 – 78.8
12-18 m	52	54.1	2.7	10 – 82.5
>18 m	52	55.2	1.6	21.4 – 77.6
Vertical canopy cover (%) (ocular method)				
<6 m	52	40.7	4.6	0 – 95
6-12 m	52	35.2	4.2	0 – 95
12-18 m	52	48.4	4.8	0 – 100
>18 m	52	45.0	4.6	0 – 95

Table 2-4. The number of Cerulean Warbler nests found in different tree species and the number that survived to fledge young on Big Oaks National Wildlife Refuge, IN, during 2004 and 2005. Two nests were found after the breeding season. These nests were found in a sugar maple and a shagbark hickory in 2004.

	<u>2004</u>	<u>2005</u>	
Nest Tree Species	(#successful)		Totals
Black Walnut	4 (2)	10 (4)	14 (6)
White Oak	9 (1)	4 (0)	13 (1)
American Sycamore	5 (3)	3 (0)	8 (3)
American Elm	3 (0)	2 (0)	5 (0)
Red Elm	---	4 (0)	4 (0)
Tulip Poplar	3 (2)	---	3 (2)
Sugar Maple	1 (1)	---	1(1)
Pignut Hickory	1 (0)	---	1 (0)
Sweetgum	1 (1)	---	1 (1)
Chinkapin Oak	1 (1)	---	1 (1)
Black Locust	---	1 (0)	1 (0)
Sassafras	---	1 (0)	1 (0)

Table 2-5. Top ten models (sorted by Akaike weights) of Cerulean Warbler habitat use on Big Oaks National Wildlife Refuge at the nest-site scale. The maximized log likelihood function ($-2 \ln [L]$), deviance, number parameters (K), Akaike Information Criterion Values (AIC), the difference from the minimum Akaike Information Criterion Values (ΔAIC), and the Akaike weights (w_i) are reported.

Model	Predictors	$-2 \ln [L]$	K	AIC	ΔAIC	w_i
1	CC	-138.00	4	146.00	0.00	0.71
	Ntrees					
	NWoodyStems					
2	Ntrees	-143.41	3	149.41	3.41	0.13
	NWoodyStems					
3	Ntrees	-146.93	2	150.92	4.92	0.06
4	MaxTreeHt	-144.20	4	152.20	6.19	0.03
	FCN6-12					
	FCN12-18					
5	MaxTreeHt	-149.15	2	153.15	7.14	0.02
6	FCN12-18	-150.55	2	154.55	8.54	0.01
7	MaxTreeHt	-142.81	6	154.81	8.81	0.01
	All 4 FCN Intervals					
8	DistStream	-143.34	6	155.34	9.34	0.01
	All 4 FCN Intervals					
9	DistStream	-152.11	2	156.11	10.10	0.00
10	CC	-148.83	4	156.83	10.83	0.00
	FCN6-12					
	FCN12-18					

Table 2-6. Mean values (± 2 S.E.) for habitat variables that discriminate between used and non-used sites of breeding Cerulean Warblers on Big Oaks National Wildlife Refuge, in 2004 and 2005.

Measurement location	Number of Trees	Number of Woody stems	Canopy Coverage
Nest site (central plot)	7.0 ± 1.2	12.0 ± 3.0	91.3 ± 1.5
Random site (central plot)	10.1 ± 1.6	11.1 ± 3.9	90.1 ± 2.9
Nest Patch	6.6 ± 0.8	26.8 ± 5.8	90.3 ± 2.1
Random Nest Patch	9.3 ± 1.3	11.4 ± 3.9	91.0 ± 1.9

Table 2-7. Top ten models (sorted by AIC values) of Cerulean Warbler habitat use on Big Oaks National Wildlife Refuge at the nest-patch scale. The maximized log likelihood function ($-2 \ln [L]$), deviance, number parameters (K), Akaike Information Criterion Values (AIC), the difference from the minimum Akaike Information Criterion Values (ΔAIC), and the Akaike weights (w_i) are reported.

Model	Predictors	$-2 \ln [L]$	K	AIC	ΔAIC	w_i
1	PlotCC	-104.90	4	112.90	0.00	0.74
	NtreesPlot					
	Nwoody stems Plot					
2	NtreesPlot	-109.47	3	115.47	2.57	0.21
	Nwoody stems Plot					
3	PlotCC	-110.36	4	118.36	5.46	0.05
	PCN12-18					
	PCN>18					
4	PCN>18	-121.85	2	125.85	12.94	0.00
5	PlotCC	-131.95	3	137.95	25.04	0.00
	Nwoody stems Plot					
6	NtreesPlot	-143.59	2	147.59	34.69	0.00
7	PlotCC	-142.06	3	148.06	35.16	0.00
	NtreesPlot					
8	PCN12-18	-153.14	2	157.14	44.24	0.00
9	PlotCC	-155.01	2	159.01	46.11	0.00
10	PlotCC	-151.06	4	159.06	46.15	0.00
	PCN6-12					
	PCN12-18					

Table 2-8. The most important variables in models of Cerulean Warbler nest survival and habitat use as determined by model-averaged parameter estimates. Variables are arranged in descending degree of effect within each model group.

Variables	Parameter Estimate \pm 2 S.E.
<u>Habitat Use Models</u>	
Nest site Variables	
Intercept	-2.7398 \pm 4.784
Number of trees	-0.1843 \pm 0.105
Canopy cover	0.0420 \pm 0.055
Number of woody stems	0.0397 \pm 0.037
Nest patch Variables	
Intercept	-3.1096 \pm 7.304
Number of trees	-0.0963 \pm 0.048
Canopy cover	0.0479 \pm 0.080
Number of woody stems	0.0262 \pm 0.012
<u>Nest Survival Models</u>	
Temporal Variables	
Intercept	3.2229 \pm 0.784
Nest age ^a	-0.0168 \pm 0.054
Date ^b	-0.0028 \pm 0.013
Nest-site Variables	
Intercept	2.3559 \pm 1.258
Distance nest to canopy edge	0.0088 \pm 0.058
Canopy cover	0.0039 \pm 0.011
Number of trees	-0.0035 \pm 0.014
Number of woody stems	0.0009 \pm 0.004
Nest aspect	0.0001 \pm 0.000
Nest Patch Variables	
Intercept	2.1770 \pm 4.614
Number of trees	-0.0285 \pm 0.030
Canopy cover	0.0164 \pm 0.054
Number of woody stems	0.0002 \pm 0.002

^aThe age of a nest at the start of an observation interval; each nest has as many ages as the number of times it was observed

^bThe date at the start of an observation interval for a nest

Table 2-9. The number of Cerulean Warbler nests that failed during different stages of the nesting cycle on Big Oaks National Wildlife Refuge in southeastern Indiana. The number of nests that survived each stage is noted parenthetically.

Study Year	Incubation	Nestling
2004	12 (16)	5 (11)
2005	15 (9)	5 (4)
Totals	27 (25)	11 (15)

Table 2-10. Nine models of Cerulean Warbler nest survival based on temporal characteristics of nests found in Big Oaks National Wildlife Refuge, IN. The maximized log likelihood function ($-2 \ln [L]$), deviance, number parameters (K), Akaike Information Criterion Values (AIC_c), the difference from the minimum Akaike Information Criterion Values (ΔAIC_c), and the Akaike weights (w_i) are reported.

Model	Predictors	$-2 \ln [L]$	Deviance	K	AIC_c	ΔAIC_c	w_i
1	StartAge	-97.37	194.74	2	198.76	0.00	0.69
2	StartDate StartAge	-97.18	194.35	3	200.39	1.63	0.31
3	Year	-109.62	219.23	2	223.25	24.49	0.00
4	Year Stage	-107.65	215.30	4	223.36	24.60	0.00
5	Stage	-109.01	218.03	3	224.07	25.30	0.00
6	ConstantSurvival	-111.38	222.76	1	224.76	26.00	0.00
7	Stage StartDate	-108.95	217.90	4	225.97	27.21	0.00
8	StartDate	-111.17	222.35	2	226.37	27.60	0.00
9	StartDate ²	-111.32	222.64	2	226.66	27.89	0.00

Table 2-11. Ten greatest Akaike weighted (w_i) models of Cerulean Warbler nest survival based on nest-site characteristics in Big Oaks National Wildlife Refuge, IN. The maximized log likelihood function ($-2 \ln [L]$), deviance, number parameters (K), Akaike Information Criterion Values (AIC_c), and the change in Akaike Information Criterion Values (ΔAIC_c) are reported.

Model	Predictors	$-2 \ln [L]$	Deviance	K	AIC_c	ΔAIC_c	w_i
1	CCNest NestCanopy	-109.09	218.19	3	224.19	0.000	0.179
2	Constant	-111.38	222.76	1	224.76	0.538	0.137
3	Survival	-110.52	221.04	2	225.06	0.830	0.118
4	CCNest	-110.89	221.79	2	225.80	1.579	0.081
5	FCN>18 NestHt	-110.04	220.08	3	226.11	1.889	0.070
6	NestBole CCNest Ntrees	-109.11	218.23	4	226.29	2.068	0.064
7	NwoodyStems	-111.29	222.58	2	226.60	2.376	0.055
8	NestHt	-111.36	222.72	2	226.74	2.518	0.051
9	FCN12-18 CCNest	-110.36	220.72	3	226.76	2.533	0.051
10	NestHt CCNest NestAspect	-110.43	220.86	3	226.90	2.670	0.047

Table 2-12. Ten models of Cerulean Warbler nest survival based on nest patch characteristics in Big Oaks National Wildlife Refuge, IN. The maximized log likelihood function ($-2 \ln [L]$), deviance, number parameters (K), Akaike Information Criterion Values (AIC_c), the change in Akaike Information Criterion Values (ΔAIC_c), and the Akaike weights (w_i) are reported.

Model	Predictors	$-2 \ln [L]$	Deviance	K	AIC_c	ΔAIC_c	w_i
1	NtreesPlot CCNestPlot	-107.01	214.01	3	220.05	0.00	0.437
2	NtreesPlot Nwoody stems Plot CCNestPlot	-106.98	213.96	4	222.02	1.97	0.163
3	NtreesPlot	-109.09	218.18	2	222.20	2.15	0.149
4	NtreesPlot Slope	-108.29	216.58	3	222.62	2.57	0.121
5	NtreesPlot Nwoody stems Plot	-108.99	217.98	3	224.02	3.96	0.060
6	Constant Survival	-111.38	222.76	1	224.76	4.71	0.041
7	Location Plot Tree Richness	-110.10	220.19	4	228.26	8.21	0.007
8	Location Slope	-110.10	220.19	4	228.26	8.21	0.007
9	Nwoody stems Plot Nsnags Plot	-111.23	222.47	3	228.51	8.45	0.006
10	All PCN intervals	-109.72	219.44	5	229.54	9.48	0.004

Table 2-13. Comparison of Cerulean Warbler nest characteristics between a 2002-2003 study (Roth 2004), and this study 2004-2005 on Big Oaks National Wildlife Refuge, IN.

Study (Years)	N (nests)	\bar{x} Nest aspect from bole	\bar{x} Distance nest to bole (m)	\bar{x} Nest tree dbh (cm)	Nest tree species use	% Nests covered by V. Creeper
Roth (`02-`03)	43	161°	4.75	50.4	28% B. Walnut 26% Wht. Oak	33%
Varble (`04-`05)	55	179°	4.4	42.3	26% B. Walnut 25% Wht. Oak	35%

Table 3-1. The number of male and female cicadas of each of the three species of periodic cicada caught in emergence traps during the 2004 emergence of Brood X on Big Oaks National Wildlife Refuge in southeastern Indiana.

	<i>Magicicada cassini</i>	<i>Magicicada septendecim</i>	<i>Magicicada septendecula</i>
Female	25	46	57
Male	22	66	21

* 7 cicadas were not identifiable

Table 3-2. The species, number found, and number failed of bird nests located and monitored on Big Oaks National Wildlife Refuge in southeastern Indiana during 2004 and 2005.

	Number Nests Found (No. Failed)	
	2004	2005
Cerulean Warbler	28(17)	25(21)
Acadian Flycatcher	52(33)	30(25)
Wood Thrush	47(23)	21(13)
Red-eyed Vireo	12(10)	9(5)
Ovenbird	17(14)	3(3)
Kentucky Warbler	10(8)	5(2)
Hooded Warbler	2(1)	2(1)
Indigo Bunting	12(6)	3(2)
Yellow-billed Cuckoo	9(4)	---
Scarlet Tanager	3(3)	---
Northern Cardinal	7(5)	5(5)
Louisiana Waterthrush	1(0)	---
Worm-eating Warbler	---	1(0)
Ground Nests	40(28)	13(8)
Above Ground Nests	160(96)	91(69)
All Nests	200(124)	104(77)

Table 3-3. Daily survival models tested to determine whether the peak period of the 2004 cicada emergence on Big Oaks National Wildlife Refuge in southeastern Indiana increased daily survival probabilities of forest bird nests. Parameter notation is the study year followed by either the peak period (P) of cicada emergence (May 23rd-June 10th), or the non-peak period (NP) before and after the peak interval. Periodic cicadas emerged in 2004; 2005 is a control year.

Model	Description
2004 P = 2004 NP = 2005 P = 2005 NP	Constant survival
(2004 P) ≠ (2004 NP = 2005 P = 2005 NP)	Daily survival during the peak cicada period is different than any other period, all other periods do not differ
(2004 P = 2004 NP) ≠ (2005 P = 2005 NP)	Daily survival differed between years but not within a year
(2004 P = 2005 P) ≠ (2004 NP = 2005 NP)	Daily survival varies annually regardless of cicada emergences
(2004 P) ≠ (2004 NP) ≠ (2005 P = 2005 NP)	Daily survival varied between the peak and non-peak of the cicada emergence, but did not vary in the control year, the control year differed from 2004
(2004 P) ≠ (2005 P) ≠ (2004 NP = 2005 NP)	Daily survival differed between the peak period in a cicada year and the control year, which both differed from the non-peak period, the non-peak periods did not differ across years

Table 3-4. Daily survival rate modeling of forest bird nests with respect to time intervals related to the peak (P) (May 23rd-June 10th) and non-peak (NP) (before and after peak) periods of cicada emergence in a year with a significant periodic cicada emergence (2004) and a control year without periodic cicadas (2005) on Big Oaks National Wildlife Refuge in southeastern Indiana. Model results are presented for the models with ΔAIC_c values less than 2.0 for these nest groups; all nests monitored, nests above the ground, and ground nests. The deviance, number of parameters (K), Akaike Information Criterion Values (AIC_c), the difference from the minimum Akaike Information Criterion Values (ΔAIC_c), and the Akaike weights (w_i) are reported.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
All Nests					
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	1038.77	2	1042.77	0.00	0.299
(2004 P = 2005 P) \neq (2004 NP = 2005 NP)	1039.66	2	1043.66	0.89	0.191
(2004 P) \neq (2004 NP) \neq (2005 P = 2005 NP)	1037.66	3	1043.67	0.90	0.191
(2004 P) \neq (2005 P) \neq (2004 NP = 2005 NP)	1038.25	3	1044.25	1.48	0.142
(2004 P = 2004 NP) \neq (2005 P = 2005 NP)	1040.64	2	1044.61	1.84	0.119
Above Ground Nests					
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	860.13	2	864.14	0.00	0.332
(2004 P) \neq (2004 NP) \neq (2005 P = 2005 NP)	858.20	3	864.21	0.07	0.321
(2004 P) \neq (2005 P) \neq (2004 NP = 2005 NP)	859.59	3	865.60	1.46	0.160
Ground Nests					
2004 P = 2004 NP = 2005 P = 2005 NP	175.52	1	177.73	0.00	0.345
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	174.77	2	178.80	1.27	0.183
(2004 P = 2004 NP) \neq (2005 P = 2005 NP)	174.83	2	178.86	1.33	0.177
(2004 P = 2005 P) \neq (2004 NP = 2005 NP)	175.15	2	179.18	1.65	0.151

Table 3-5. Daily survival rate modeling of forest bird nests with respect to time intervals related to the peak (P) (May 23rd-June 10th) and non-peak (NP) (before and after peak) periods of cicada emergence in a year with a significant periodic cicada emergence (2004) and a control year without periodic cicadas (2005) on Big Oaks National Wildlife Refuge in southeastern Indiana. Model results are presented for the models with ΔAIC_c values less than 2.0 for these species; Acadian Flycatchers, Wood Thrush, and Cerulean Warblers. The deviance, number of parameters (K), Akaike Information Criterion Values (AIC_c), the difference from the minimum Akaike Information Criterion Values (ΔAIC_c), and the Akaike weights (w_i) are reported.

Model	Deviance	K	AIC_c	ΔAIC_c	w_i
Acadian Flycatcher					
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	310.92	2	314.93	0.00	0.223
(2004 P = 2004 NP) \neq (2005 P = 2005 NP)	311.17	2	315.18	0.25	0.197
(2004 P = 2005 P) \neq (2004 NP = 2005 NP)	311.17	2	315.18	0.25	0.197
(2004 P) \neq (2004 NP) \neq (2005 P = 2005 NP)	309.54	3	315.57	0.64	0.162
2004 P = 2004 NP = 2005 P = 2005 NP	314.09	1	316.09	1.16	0.125
(2004 P) \neq (2005 P) \neq (2004 NP = 2005 NP)	310.58	3	316.61	1.68	0.096
Wood Thrush					
(2004 P = 2005 P) \neq (2004 NP = 2005 NP)	194.56	2	198.58	0.00	0.334
2004 P = 2004 NP = 2005 P = 2005 NP	197.44	1	199.45	0.87	0.216
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	196.20	2	200.22	1.64	0.147
Cerulean Warbler					
(2004 P = 2004 NP) \neq (2005 P = 2005 NP)	214.67	2	218.69	0.00	0.254
2004 P = 2004 NP = 2005 P = 2005 NP	217.00	1	219.01	0.32	0.216
(2004 P) \neq (2005 P) \neq (2004 NP = 2005 NP)	213.17	3	219.21	0.52	0.196
(2004 P) \neq (2004 NP = 2005 P = 2005 NP)	215.94	2	219.96	1.27	0.135
(2004 P = 2005 P) \neq (2004 NP = 2005 NP)	216.47	2	220.49	1.80	0.103
(2004 P) \neq (2004 NP) \neq (2005 P = 2005 NP)	214.59	3	220.63	1.94	0.096

Table 3-6. Mean clutch sizes (± 2 S.E.) for Acadian Flycatchers and Wood Thrush on Big Oaks National Wildlife Refuge in 2004 and 2005 during different periods of food availability (peak and non-peak cicada periods). Note: Eggs laid from 11-29 June were developing within females foraging during the peak cicada period and so this period of laying after the peak period is considered to be the indicator of a cicada effect.

Species	Peak (n ^a)	2004		Overall	2005		Overall
		Non-Peak (n)			Non-Peak (n)		
Acadian Flycatcher	3.00 ± 0.00 (9)	2.68 ± 0.18 (28)	2.76 ± 0.14	2.67 ± 0.42 (6)	2.71 ± 0.26 (14)	2.70 ± 0.2	
Wood Thrush	3.09 ± 0.18 (11)	3.58 ± 0.24 (24)	3.43 ± 0.18	2.33 ± 0.66 (3)	3.67 ± 0.36 (12)	3.40 ± 0.4	

^anumber of clutches

Table 3-7. Number of territories mapped for Ovenbirds (OVEN), Acadian Flycatchers (ACFL), Wood Thrush (WOTH), Red-eyed Vireos (REVI), and Cerulean Warblers (CERW) on Big Oaks National Wildlife Refuge in southeastern Indiana in 2004 and 2005.

Species	Year	Plot 1	Plot 2	Plot 3	Plot 5	Total
OVEN	2004	32	45	39	35	151
	2005	17	58	61	60	196
ACFL	2004	35	37	53	53	178
	2005	33	44	63	42	182
WOTH	2004	46	13	54	39	152
	2005	29	28	65	28	150
REVI	2004	41	49	62	60	212
	2005	25	53	62	59	199
CERW	2004	10	7	4	18	39
	2005	12	4	1	5	22

Table 3-8. The occurrence of Blue Jays (BLJA), American Crows (AMCR), Brown-headed Cowbirds (BHCO), and Yellow-billed Cuckoos (YBCU) measured as the mean number of birds (± 2 S.E.) recorded when any of 4 study plots was surveyed during 2004 and 2005 on Big Oaks National Wildlife Refuge in southeastern Indiana. Occurrences are statistically compared between years using t-tests with unequal variance and $\alpha = 0.05$.

Mean number of birds recorded per plot survey			
Species	Year	± 2 S.E.	P-value
BLJA*	2004	8.21 ± 1.74	0.003
	2005	12.92 ± 2.48	
AMCR	2004	2.33 ± 0.80	0.097
	2005	4.25 ± 2.08	
BHCO*	2004	4.71 ± 1.21	0.010
	2005	8.04 ± 2.13	
YBCU	2004	2.46 ± 1.05	0.200
	2005	1.58 ± 0.84	

* a single asterisk denotes significantly greater occurrence in 2005

Table 3-9. Daily survival (± 2 S.E.) for species and guild groupings of forest birds during the peak and non-peak cicada periods in both a periodic cicada emergence year (2004) and a control year (2005) on Big Oaks National Wildlife Refuge in southeastern IN.

Nest Grouping [Year] (# nests, # exposure days)	Peak Daily Survival	Non-peak Daily Survival	Overall Daily Survival
Above Ground Nests [2004] (158, 1911)	0.969 \pm 0.014	0.942 \pm 0.013	0.951 \pm 0.010
Above Ground Nests [2005] (90, 1121)	0.948 \pm 0.021	0.936 \pm 0.019	0.941 \pm 0.014
Ground Nests [2004] (42, 331)	0.907 \pm 0.053	0.905 \pm 0.040	0.906 \pm 0.032
Ground Nests [2005] (14, 159)	0.960 \pm 0.045	0.940 \pm 0.051	0.950 \pm 0.035
All Nests [2004] (200, 2267)	0.959 \pm 0.014	0.936 \pm 0.013	0.944 \pm 0.010
All Nests [2005] (104, 1280)	0.949 \pm 0.019	0.936 \pm 0.018	0.942 \pm 0.013
Acadian Flycatcher Nests [2004] (52, 636)	0.976 \pm 0.023	0.947 \pm 0.019	0.948 \pm 0.018
Acadian Flycatcher Nests [2005] (30, 378)	0.964 \pm 0.035	0.930 \pm 0.029	0.934 \pm 0.026
Wood Thrush Nests [2004] (47, 582)	0.981 \pm 0.021	0.950 \pm 0.022	0.961 \pm 0.016
Wood Thrush Nests [2005] (21, 253.5)	0.986 \pm 0.019	0.923 \pm 0.046	0.949 \pm 0.028
Cerulean Warbler Nests [2004] (28, 350)	0.966 \pm 0.028	0.937 \pm 0.037	0.951 \pm 0.020
Cerulean Warbler Nests [2005] (25, 221)	0.882 \pm 0.059	0.952 \pm 0.041	0.923 \pm 0.036

VITA

Dustin W. Varble was born in Madison, Indiana on 4 July 1981. He graduated from Southwestern High School in 1999. He then received a B.A. in Biology from Hanover College in 2003 and produced an undergraduate thesis on the habitat associations and community characteristics of carrion beetles in southeastern Indiana. Dustin spent the next 12 months working on a Cerulean Warbler study as an intern, and working as a firefighter for the U. S. Fish and Wildlife Service. He began his graduate research at the University of Tennessee, Knoxville, in May 2004. His research interests include population viability assessment, geographical habitat analysis, and avian intelligence.