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Multiple responses by Cerulean Warblers to experimental forest disturbance in the Appalachian Mountains

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To the Graduate Council:

I am submitting herewith a dissertation written by Than James Boves entitled "Multiple responses by Cerulean Warblers to experimental forest disturbance in the Appalachian Mountains." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

David A. Buehler, Major Professor

We have read this dissertation and recommend its acceptance:

Patrick D. Keyser, David S. Buckley, Todd M. Freeberg

Accepted for the Council:
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Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Multiple responses by Cerulean Warblers to experimental forest disturbance in the Appalachian Mountains

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Than James Boves
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ABSTRACT

The Cerulean Warbler (*Setophaga cerulea*) is a mature forest obligate and one of the fastest declining songbird species in the United States. This decline may be related to a lack of disturbance within contemporary forests; however, the consequences of disturbance on the species have not been rigorously evaluated. Thus, we assessed multiple responses by Cerulean Warblers to a range of experimental forest disturbances across the core of their breeding range in the Appalachian Mountains. We quantified individual and population responses to these manipulations, and assessed the potential consequences of disturbance on the sexual signaling system. Male ceruleans were strongly attracted to intermediate and heavy disturbances at the stand scale. Despite attraction to disturbed habitats, nest success declined in these conditions, particularly in the highly productive Cumberland Mountains of northern Tennessee. Taken together, these opposing responses suggest that anthropogenically-disturbed forests may act as local ecological traps, but the impact of these local traps on the global population is dependent on several unestimated parameters. At a finer scale, selection for habitat features varied spatially. Males consistently selected for territories near canopy gaps and on productive slopes, but they displayed inconsistent territory selection in regards to tree diameter, basal area, overstory canopy cover, and canopy height. Females were more consistent in their selection of features within territories, selecting nest patches with large, well-spaced trees near disturbances. Floristically, female ceruleans consistently selected for sugar maples (*Acer saccharum*), white oaks (*Quercus alba*), and cucumber magnolias (*Magnolia acuminata*) as nest trees and they selected against red maples (*A. rubrum*) and red oaks (*Q. rubra*). Disturbances had little effect on male age structure, but males that occupied disturbed forest habitat were in better condition than those in undisturbed habitat. Parental behavior differed among disturbances, with birds in more highly disturbed habitats provisioning their young at greater rates, but bringing smaller food loads, potentially helping to explain the decrease in nest survival in disturbances. Finally, we found that male ceruleans displayed various plumage ornaments that signaled individual quality. However, the relationship between breast band width and body mass was contingent on habitat, and only existed in intermediate disturbances.

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INTRODUCTION

Urbanization, agricultural conversion, and natural resource extraction have been responsible for forest loss and degradation worldwide (Marzluff et al. 2001, Achard et al. 2002, Wickham et al. 2007) and, concomitantly, have proven to be significant factors underlying losses of biodiversity and declines in many animal populations (Sodhi et al. 2009). At the global scale, these human activities have had broad negative impacts on organisms, however at regional and local scales, forest cover has recently increased in some areas, including the eastern United States (Smith et al. 2002). Consequently, many organisms in this region have been adversely affected by a lack of disturbance, often via the suppression and alteration of natural disturbance regimes (Lorimer and Frelich 1994, Brawn et al. 2001, Artman et al. 2005). Ecologists have recently come to appreciate the fundamental importance of disturbance in maintaining many forest ecosystems. Management strategies that 'emulate natural disturbance regimes' (ENDR) are now often advocated to restore ecosystems where natural disturbances have been excluded or diminished (Perera et al. 2004). ENDR and other similar strategies utilize anthropogenic activities such as timber harvesting and prescribed fire to restore natural patterns of disturbance to forests that were historically shaped by periodic disruptions (Seymour et al. 2002, Long 2009).

Appalachian Mountain forest ecosystems in the eastern United States provide an example of natural disturbance regimes that have been altered by humans. Prior to European colonization, old-growth forests in the eastern U.S. were regularly disturbed by natural events of varying intensity such as wind-throw, tree senescence (which occurred more often in old forests), and fire (Lorimer 1980, Nowacki and Abrams 2008). During the late 1800s and early 1900s, forests in the eastern U.S. were almost completely cleared for agriculture and large-scale timber extraction (Williams 1989). Since then, much of the region has regenerated as second-growth forest and natural disturbance regimes have been largely suppressed (Williams 1989, Lorimer and Frelich 1994). The regrowth of Appalachian, and other eastern U.S. forests, over the past century has been correlated with increasing populations of many mature forest avian species, such as Northern Parula (*Setophaga americana*) and Blackburnian Warblers (*S. fusca*). However, this process of reforestation has been negatively related with population trends of other mature forest bird species that would appear to benefit from an increase in putative breeding habitat (Ziolkowski et al. 2010). One notable late successional forest species of the eastern United States that has experienced steep population declines in the past 45 years is the Cerulean Warbler (*S. cerulea*). The Cerulean Warbler is a Nearctic-Neotropical migratory species that breeds solely in the canopies of mature deciduous forests in eastern North America, with >70% of the population breeding in the Appalachians (Hamel 2000, Hamel and Rosenberg 2007). Ceruleans are one of the fastest declining avian species in North America; populations declined 3.2%/yr from 1966 to 2003 and more recently (2003–2008) at -4.6%/yr (Ziolkowski et al. 2010). Ceruleans are listed as a species of conservation concern by the U. S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008) and considered ‘vulnerable to extinction’ by Birdlife International (BirdLife International 2010).

Contemporary second-growth forests may lack the structural heterogeneity or floristic characteristics required by some species currently regarded as late successional obligates, such as Cerulean Warblers (Hamel 2000, Bakermans and Rodewald 2009). Because of modern suppression policies, fire has become virtually non-existent as a natural source of disturbance in the eastern U.S., and because <1% of forests are currently in old-growth condition (Parker 1989), treefall gaps created by other manners occur less frequently as well (Bormann and Likens 1979, Lorimer and Frelich 1994). This reduction of fire and other natural disturbances in eastern U.S.

forests has been linked to declines in disturbance-adapted tree species, such as White Oak (*Quercus alba*, Abrams 2003), reduction in canopy heterogeneity (Lorimer and Frelich 1994), proliferation of invasive species (MacDougall and Turkington 2005), and a reduction in tree diversity at the local level (Strong et al. 1997). This lack of disturbance may negatively affect avian species such as Cerulean Warblers, which recent evidence suggests are often associated with forested canopy gaps, heterogeneous canopy structure, and tree species such as White Oak (Oliarnyk and Robertson 1996, Hamel 2000, Rodewald 2004, Wood et al. 2006, Bakermans and Rodewald 2009). Because of this, ENDR has been suggested as a method of mitigating degraded forest conditions and restoring habitat for Cerulean Warblers and other mature forest avian species (Brawn et al. 2001, Wood et al. 2005, Bakermans and Rodewald 2009).

Many studies have documented numerical responses of populations (i.e., abundance or density) to various types of disturbance, including responses to anthropogenic disturbance via forest management (e.g., Petranka et al. 1993, Holmes and Pitt 2007, Vanderwel et al. 2007). Our understanding of the mechanisms that are responsible for these numerical responses is much more limited (Marzluff et al. 2000, Shochat et al. 2006). Populations and individual animals can respond to disturbance in many ways. Responses can be instigated by bottom-up factors, such as alteration of food availability (Dias and Macedo 2011), top-down factors, such as changes in predation (Lampila et al. 2005), or perhaps most likely, interactions between both sets of factors (Zanette et al. 2006). Individual responses to disturbance can include changes in habitat selection, physiology (e.g., body condition), parental behavior, and dispersal (Haas 1998, Liker et al. 2008, Rodewald and Shustack 2008). Population responses include changes in reproductive success, adult survival, and age structure (Gram et al. 2003, Lampila et al. 2005, Evans et al. 2009). In addition, habitat disturbance may alter the selective environment and impact the signaling system and information content of plumage ornaments (Roulin et al. 2008, Rodewald et al. 2011).

Despite increasing evidence which suggests Cerulean Warblers are associated with interior forest disturbances, simple selection, or even preference, for habitats does not necessarily indicate the quality of that habitat (Van Horne 1983, Battin 2004). Mismatches between habitat selection and individual fitness have been identified in many taxa, particularly those inhabiting contemporary human-modified landscapes where ecological processes have been altered recently and rapidly (Dwernychuk and Boag 1972, Boal and Mannan 1999, Pelicice and Agostinho 2008). Habitats where maladaptive preferences exist have been termed ”ecological traps” (Schlaepfer et al. 2002). Robertson and Hutto (2006) outlined three criteria which must be met for a habitat to be considered an ecological trap: (1) individuals must display preference for one habitat over another (a severe trap) or prefer both habitats equally (an equal-preference trap), (2) individual fitness (or a reasonable surrogate of fitness) in the two habitats must be different, and (3) fitness in the preferred habitat must be lower. Therefore, before considering ENDR an appropriate strategy for restoring habitat for declining forest species, individual and demographic responses should be quantified to ensure that our actions do not create such a trap. Functionally, the relationships among the various individual and population responses that we measured can be conceptually illustrated by Figure 1.

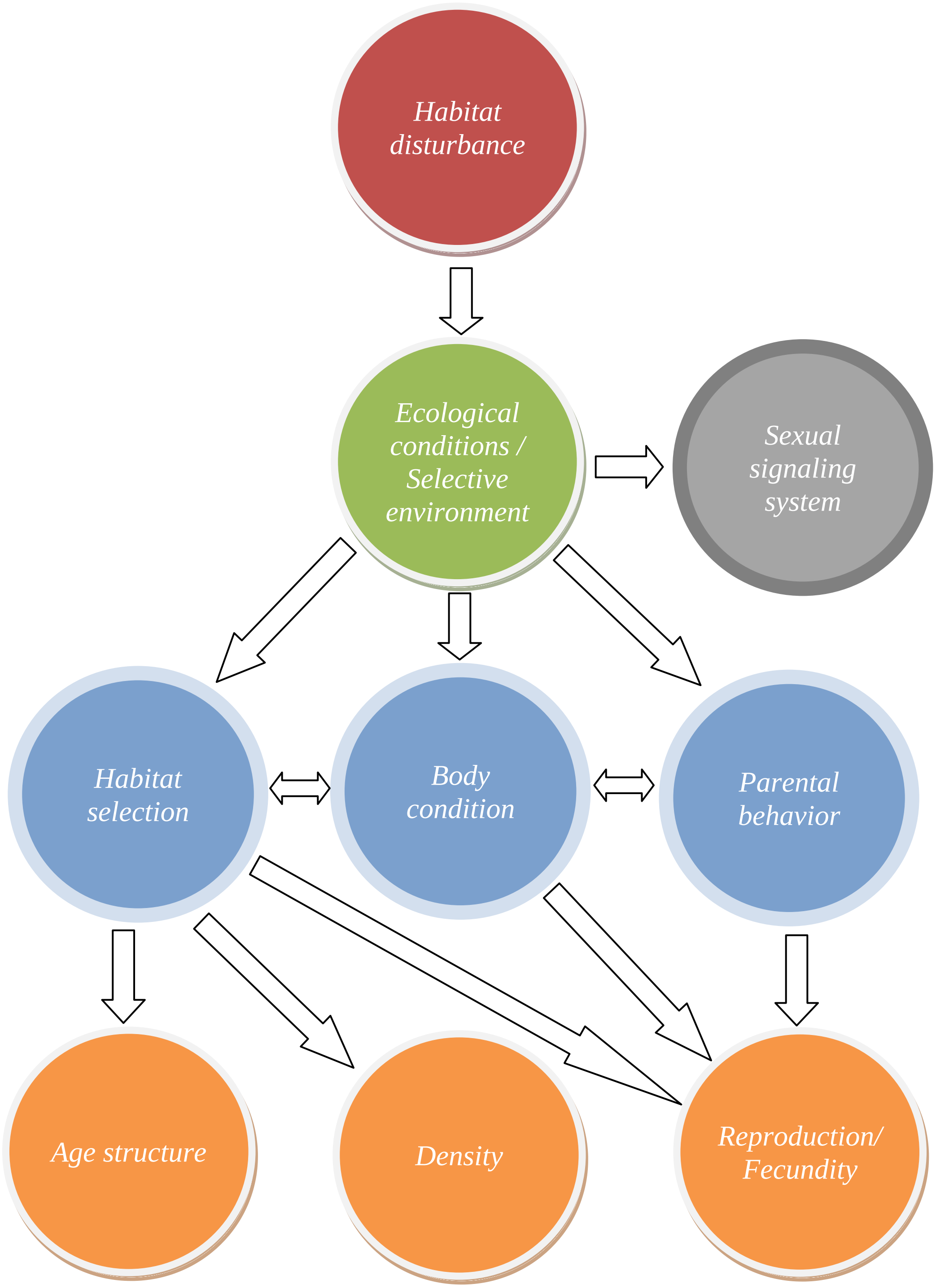

Figure 1. Conceptual flowchart illustrating the relationships between habitat disturbance and various measured responses. Individual responses are in blue, population responses are in orange, consequences to signaling system in gray.

In this study, we explored the consequences of experimental forest disturbance on a potentially disturbance-adapted forest species, the Cerulean Warbler. To do so, we worked with state and federal agencies and forest industry partners to implement disturbances of various intensities using partial timber harvests and then documented responses. The disturbances spanned the range of canopy disruptions most likely to occur naturally in mature forests across the core of the Cerulean Warbler's breeding range in the Appalachian Mountains. In Chapter 1, we assessed the short-term responses by ceruleans to these various disturbances at the stand level in terms of density, reproductive success, age structure, and body condition. In Chapter 2, we evaluated the spatial variability of multi-scale habitat selection in regards to specific habitat features, including vegetation structure, topographic, and floristic components. We also considered how these selected habitat features influenced patterns of nest survival. In Chapter 3, we evaluated the potential of male Cerulean Warblers' plumage to convey multiple messages and how this information may be mediated by habitat disturbance. Finally, in Chapter 4, we assessed how parental behavior was influenced by habitat features related to disturbance as well as by other proximate factors.

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CHAPTER 1: BRINGING DISTURBANCE BACK TO THE FOREST: AN EXPERIMENTAL TEST OF THE IMPACTS OF EMULATING NATURAL DISTURBANCES ON A MATURE FOREST OBLIGATE

Abstract. Forest cover in the eastern United States has increased over the past century, yet some late successional forest obligates continue to experience steep population declines. These declines appear to be, at least partially, a consequence of species' adaptations to conditions which differ from those found in contemporary second-growth forests now dominating eastern landscapes. Many ecologists have recently come to appreciate the fundamental importance of disturbance in maintaining forest ecosystems and often advocate strategies such as 'emulating natural disturbance regimes' (ENDR) to mitigate negative impacts of disturbance suppression and alteration on disturbance-adapted species. To evaluate the impacts of ENDR on potentially disturbance-adapted mature forest species, we assessed the response of a model late successional forest species, the Cerulean Warbler (*Setophaga cerulea*), to 3 levels of experimental disturbance at 7 replicated sites across the core of their breeding range in the heavily forested Appalachian Mountains. This study represents the largest spatially replicated experiment of its kind in the region. When compared with controls, territory densities of ceruleans increased significantly after intermediate and heavy canopy disturbances. Males occupying disturbed treatments also maintained greater body condition than males on controls and buffers. Despite the attractiveness, nest success was lower on all disturbed treatments than on controls at southern sites and lower on light treatments than on controls at northern sites. These results suggest that Cerulean Warblers are adapted to disturbances in the interior of heavily forested landscapes, but some emulated disturbances may produce habitats which, in contemporary landscapes, function as ecological traps. We also observed spatial variability in reproductive output among our sites; only habitats in our southern sites likely acted as sources (when assuming published estimates of annual survival). These results suggest that future management for Cerulean Warblers should be regionally-specific and will require a balance between emulating natural disturbances at the

appropriate scale where existing forest structure is unsuitable and limiting disturbance in forests which currently support high densities of warblers.

INTRODUCTION

Urbanization, agricultural conversion, and natural resource extraction have been responsible for forest loss and degradation worldwide (Marzluff et al. 2001, Achard et al. 2002, Wickham et al. 2007) and, concomitantly, have proven to be significant factors underlying losses of biodiversity and declines in many animal populations (Sodhi et al. 2009). At the global scale, these human activities have had broad negative impacts on organisms, however at regional and local scales, forest cover has increased in some areas, including in the eastern United States (Smith et al. 2002). Consequently, some organisms in this region have been adversely affected by a lack of disturbance, often via the suppression and alteration of natural disturbance regimes (Lorimer and Frelich 1994, Brawn et al. 2001, Artman et al. 2005). Ecologists have recently come to appreciate the fundamental importance of disturbance in maintaining many forest ecosystems, and management strategies that emulate natural disturbance regimes (or ENDR) are now often advocated (Perera et al. 2004). ENDR and other similar strategies utilize anthropogenic activities such as timber harvesting and prescribed fire to restore natural patterns of disturbance to forests that were historically shaped by periodic disruptions (Seymour et al. 2002, Long 2009).

Appalachian Mountain forest ecosystems in the eastern United States provide an example of natural disturbance regimes that have been altered by humans. Prior to European colonization, old-growth forests in the eastern U.S. were regularly disturbed by natural events of varying intensity such as wind-throw, tree senescence (which occurred more often in these old forests), and fire (Lorimer 1980, Nowacki and Abrams 2008). During the late 1800s and early 1900s, forests in the eastern U.S. were almost completely cleared for agriculture and large-scale timber extraction (Williams 1989). Since then, much of the region has regenerated as second-growth forest and natural disturbance regimes have been largely suppressed (Williams 1989, Lorimer and Frelich 1994). The regrowth of Appalachian, and other eastern U.S. forests, over the past century has been correlated with increasing populations of many mature forest avian species, such as Northern Parula (*Setophaga americana*) and Blackburnian Warblers (*S. fusca*). However, this process of reforestation has been negatively related to population trends of other mature forest bird species that would appear to benefit from an increase in breeding habitat (Ziolkowski et al. 2010). One notable late successional forest species of the eastern United States that has experienced steep population declines in the past 45 years is the Cerulean Warbler (*S. cerulea*). The Cerulean Warbler is a Nearctic-Neotropical migratory species that breeds solely in the canopies of mature deciduous forests in eastern North America, with 70% of the population breeding in the southern and central Appalachians (Hamel 2000, Hamel and Rosenberg 2007). Ceruleans are one of the fastest declining avian species in North America; populations declined 3.2%/yr from 1966 to 2003 and more recently (2003–2008) at -4.6%/yr (Ziolkowski et al. 2010). Ceruleans are listed as a species of conservation concern by the U. S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008) and considered ‘vulnerable to extinction’ by Birdlife International (BirdLife International 2010).

Contemporary second-growth forests may lack the structural heterogeneity or floristic characteristics required by some species regarded as late successional obligates, such as Cerulean Warblers (Hamel 2000, Bakermans and Rodewald 2009). Because of modern suppression policies, fire has become virtually non-existent as a natural source of disturbance in the eastern U.S., and because <1% of forests are currently in old-growth condition (Parker 1989), treefall gaps are smaller and occur less frequently (Bormann and Likens 1979, Lorimer and Frelich 1994). This reduction of fire and other natural disturbances in eastern U.S. forests has been linked to declines in disturbance-adapted tree species, such as White Oak (*Quercus alba*; Abrams 2003), reduction in canopy heterogeneity (Lorimer and Frelich 1994), proliferation of invasive species (MacDougall and Turkington 2005), and a reduction in tree diversity at the local level (Strong et al. 1997). A growing body of evidence also suggests that this lack of disturbance negatively affects avian species such as Cerulean Warblers, which appear to be associated with forested canopy gaps, heterogeneous canopy structure, and tree species such as White Oak (Oliarnyk and Robertson 1996, Hamel 2000, Rodewald 2004, Wood et al. 2006, Bakermans and Rodewald 2009). Because of this, ENDR has been suggested as a method of mitigating degraded forest conditions and restoring habitat for Cerulean Warblers and other mature forest avian species (Brawn et al. 2001, Wood et al. 2005, Bakermans and Rodewald 2009).

Many studies have documented numerical responses of populations (i.e., abundance or density) to various types of disturbance, including responses to anthropogenic disturbance via forest management (e.g., Petranka et al. 1993, Holmes and Pitt 2007, Vanderwel et al. 2007). Our understanding of the mechanisms that are responsible for these numerical responses is much more limited (Marzluff et al. 2000, Shochat et al. 2006). Populations and individual animals can respond to disturbance in many ways. Responses can be instigated by bottom-up factors, such as alteration of food availability (Dias and Macedo 2011), top-down factors, such as changes in predation (Lampila et al. 2005), or perhaps most likely, interactions between both sets of factors (Zanette et al. 2006). Individual responses to disturbance can include changes in habitat selection, physiology (e.g., body condition), breeding behavior, and dispersal (Haas 1998, Liker et al. 2008, Rodewald and Shustack 2008). Population responses include changes in reproductive success, adult survival, and age structure (Gram et al. 2003, Lampila et al. 2005, Evans et al. 2009).

Despite increasing evidence which suggests Cerulean Warblers are associated with interior forest disturbances, simple selection, or even preference, for a habitat does not necessarily indicate the quality of that habitat (Van Horne 1983, Battin 2004). Mismatches between habitat selection and individual fitness have been identified in many taxa, particularly those inhabiting contemporary human-modified landscapes where ecological processes have been altered recently and rapidly (Dwernychuk and Boag 1972, Boal and Mannan 1999, Pelicice and Agostinho 2008). Habitats where maladaptive preferences exist have been termed ”ecological traps” (Schlaepfer et al. 2002). Robertson and Hutto (2006) outlined three criteria which must be met for a habitat to be considered an ecological trap: (1) individuals must display preference for one habitat over another (a severe trap) or prefer both habitats equally (an equal-preference trap), (2) individual fitness (or a reasonable surrogate of fitness) in the two habitats must be different, and (3) fitness in the preferred habitat must be lower. Therefore, before considering ENDR an appropriate strategy for restoring habitat for declining forest species, detailed habitat selection and demographic studies are needed to ensure that our actions do not create such a trap.

In this study, we explored the consequences of emulating natural disturbances for potentially disturbance-adapted forest species, using the Cerulean Warbler as a model. To do so, we experimentally disturbed forest stands at various intensities, spanning the range of disruptions occurring naturally in mature forests, across the core of the Cerulean Warbler’s breeding range in the Appalachians. We then assessed the short-term (4 years) responses by ceruleans to these manipulations in terms of density, reproductive success, age structure, and body condition. In addition, we evaluated the impacts of emulating disturbance on source-sink dynamics and conservation of Cerulean Warblers. Spatially extensive, replicated manipulations have been advocated by many, but are still rare in ecological studies (Marzluff et al. 2000, Donovan et al. 2002). This study is, to our knowledge, the largest such experiment ever undertaken in the eastern U.S. and has important implications for our understanding of disturbance ecology and conservation of mature forest species, in particular the vulnerable Cerulean Warbler.

METHODS

Study sites

We selected seven study sites in the Appalachian Mountains, all within the Central Hardwoods' mixed-mesophytic forest region (Fralish 2003), which also corresponds to the core of the Cerulean Warbler range (Figure 1.1). These sites were: Royal Blue Wildlife Management Area, TN (RB), Sundquist Forest, TN (SQ), Raccoon Ecological Management Area, OH (REMA), Daniel Boone National Forest, KY (DB), Lewis Wetzel Wildlife Management Area, WV (LW), Wyoming County, WV (WYO), and Monongahela National Forest, WV (MON). For analysis purposes, we considered RB and SQ as the southern region and the other 5 as the northern region. We selected sites based on the presence of cerulean warbler breeding populations and the potential to implement disturbance prescriptions via partial timber harvest. All sites were embedded within a matrix of mature forest; mean percent forest cover within 10 km of the site center was 83 ± 2.8% (range = 74 – 95, 2001 NLCD). Mean elevation was 550 ± 80 m (range = 250 – 850 m). Plant composition differed slightly among sites, but common overstory tree species included Tulip Poplar (*Liriodendron tulipifera*), Sugar Maple (*Acer saccharum*), Northern Red Oak (*Quercus rubra*), various hickories (*Carya* spp.), and White and Chestnut Oak (*Q. alba, Q. montana*). Common avian conspecifics included American Redstart (*S. ruticilla*), Black-throated Green Warbler (*S. virens*), Blackburnian Warbler (*S. fusca*), Red-eyed Vireo (*Vireo olivaceous*), and Scarlet Tanager (*Piranga olivacea*). Likely nest predators included Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), *Accipiter* spp., Eastern Chipmunk (*Tamias striatus*), Flying Squirrel (*Glaucomys* spp.), Gray Squirrel (*Sciurus carolinensis*), and Black Rat Snake (*Elaphe obsoleta*). Brown-headed Cowbirds (*Molothrus ater*), which are documented brood parasites of ceruleans outside of the Appalachians, were present but uncommon at all sites.

Disturbance treatments

We randomly assigned disturbance treatments to four 20-ha stands at each site: light, intermediate, and heavy canopy disturbance, as well as an undisturbed control plot. Each treatment included a 10-ha disturbed area (except on controls), and two 5-ha buffers of undisturbed forest on either end of the disturbance to allow for examination of edge effects. Disturbances were designed to emulate natural processes that spanned the range of potential mature forest disruptions and to provide enough separation among disturbance levels to facilitate our ability to identify process-induced responses. Light treatments (least intense disturbance) mimicked stands disrupted by multiple tree-fall gaps; we reduced basal area (BA) and overstory canopy cover on these treatments by approximately 20% (residual BA = 21.1 ± 1.2 m^2/ha; residual CC = 60.9 ± 5.5%). Intermediate treatments mimicked more severe natural disturbances such as fire, blow-downs, or larger tree fall gaps; here we reduced BA and CC by approximately 40% (residual BA = 14.1 ± 1.2 m^2/ha; residual CC = 45.5 ± 6.4%). Heavy treatments (most intense disturbance) emulated even more severe natural disturbances such as large blow-downs, ice-storms, landslides, or more intense fire; we reduced BA and CC by 75% (residual BA = 6.5 ± 1.1 m^2/ha; residual CC = 18.2 ± 4.3%). We left control plots undisturbed throughout the life of the study (BA = 27.7 ± 0.7 m^2/ha; CC = 73.2 ± 5.2%). On all treatments, disturbances were applied uniformly across the 10-ha stand. Overstory species composition was largely unchanged by the disturbances and residual stands on the intermediate and heavy treatments were comprised of dominant and co-dominant trees. Treatment plots were separated by >300 m of undisturbed forest to maintain independence among plots. Plots were located on north or east-facing slopes to maximize cerulean presence (Buehler et al. 2006, Wood et al. 2006) and to control for potential interactions between aspect and response. All treatments were implemented via timber harvest in the fall of 2006 or spring of 2007.

Territory density response

We used a before-after-control-impact design (BACI) to evaluate cerulean warbler density response to disturbances. We performed eight spot-mapping sessions per plot from 15 May to 15 June, 2005–2010 (two years pre-disturbance and four years post-disturbance) to quantify density of territorial Cerulean Warblers. We established four transects and placed observation stations every 50 m. We walked transects and stopped at stations to listen and record singing locations and note behaviors of male cerulean warblers following standard spot-mapping convention (Bibby et al. 2000). Especially important were records of counter-singing males, which allowed us to determine territorial boundaries. We counted territories as full if >1/2 of territory registrations were located on the treatment plot and as a 1/2 territory if >1/3 ≤1/2 of registrations occurred on the plot. We also used nest and banding data (see below) to augment our spot-mapping data and to validate our delineation and estimation of territory numbers.

We used repeated-measures ANOVA to compare male cerulean warbler density during pre-disturbance years on plots where we completed two years of pre-disturbance spot-mapping (2005–06). We performed pre-disturbance spot-mapping on MON and WYO sites in 2006 only, so these sites were not included in this pre-disturbance analysis. We found no significant year effects ($F_{1,16} = 0.05$; $P = 0.41$) or year x treatment interaction ($F_{3,16} = 0.16$; $P = 0.49$). Therefore, we used mean pre-disturbance density (average of 2005 and 2006) as a starting point for all subsequent analysis for 5 sites and 2006 density at two sites.

We estimated the change in territory density from pre- to post-disturbance by calculating

$$Density\ ratio\ (DR) = \ Post\ density/Pre\ density$$

where we defined density as the number of territorial males/10 ha. Two plots were unoccupied pre-disturbance so we replaced zero values with 0.25 (the lowest recorded number of territories other than zero) to estimate DR. This replacement value results in more conservative rates of increase than in reality, but made very little difference in our estimates. DR did not meet parametric assumptions of normality and equal variance, so we performed a log transformation, after which log DR met those assumptions (Shapiro-Wilks $\lambda > 0.9$, Levene's test $P > 0.05$). We compared log DR among treatments using a repeated measures mixed-model ANOVA with treatment, year, and treatment x year as fixed effects and site and site x year as random effects (PROC MIXED in SAS). When we found a significant main effect for treatment, we performed pre-planned contrasts to evaluate differences between each disturbed treatment and controls. We found no statistical difference in log DR among buffers of the three treatment types in any year (one-way ANOVA; $P > 0.30$ in all years), so we used the mean annual density of the three buffers in our analysis as an additional treatment group called 'buffers'.

Age structure and body condition

We captured male cerulean warblers at five sites (RB, SQ, REMA, LW, and WYO) to assess age structure and body condition of individuals occupying territories on each treatment. To capture individuals, we erected mist nets within territories, broadcast territorial songs and call notes, and displayed a male cerulean decoy. After capture, we aged males as second-year (SY; first breeding season) or after-second-year (ASY) by plumage (second-year birds retain brownish juvenile alula and primary coverts; Pyle 1997). We measured right wing length to the nearest 0.5 mm (using a straight wing rule) and mass to the nearest 0.01 g (using a digital scale). We used body mass alone as our indicator of body condition because of recent concerns about using unverified indices to quantify body condition (Schamber et al. 2009, Labocha and Hayes 2011). We also calculated wing-mass residuals and found them highly correlated to body mass (r = 0.92); we performed analyses with both measures and found no change in inference.

We compared age structure of male cerulean warblers (% SY) among treatments using Pearson's chi-squared tests. We assessed age structure among treatments within each region as well as all sites pooled. To increase sample sizes, we also compared age structure of birds captured in all disturbed treatments (light, intermediate, and heavy disturbances pooled, n = 85) with birds captured in buffers and controls pooled (n = 119).

We evaluated potential differences in male body condition using a two-way mixed general linear model with age, treatment, and age x treatment specified as fixed factors and year and site as random factors. We inspected body mass for normality and equality of variance and found no deviation from normality or signs of heteroscedascity. Age x treatment was non-significant (P > 0.20), so we removed it and re-ran the GLM. To increase sample sizes, we performed a second analysis in which we pooled birds captured in all disturbed treatments (light, intermediate, and heavy disturbances, n = 48) and compared them to birds captured in both buffers and controls (n = 49). For individuals captured in more than one season, we randomly selected one capture event to use in analysis to avoid pseudo-replication. Sample sizes differ between analyses because we only included birds captured at REMA, SQ, and RB from 2008–10 in the body condition analysis (due to equipment inaccuracy at our West Virginia sites).

Reproduction

We searched for nests between late April and June, 2008–2010 (all post-disturbance), to estimate nest success, count the number of fledglings produced, and determine causes of nest failure. We used female behavioral cues during building and incubation, and to a lesser extent male vocalizations and behavior, to locate the majority of nests. Because we were more efficient at locating nests on disturbed treatments (females and nests were easier to detect and often existed at higher densities), we stratified our search efforts by increasing the time spent nest searching on controls and buffers in an attempt to locate an equal proportion of nests on each treatment. We monitored nests every 1–3 d until fledging or confirmed nest failure occurred. From nestling day six until fledging, we monitored nests daily for 30–45 min to determine nest fate and accurately count the number of nestlings which fledged. We used spotting scopes equipped with 20 – 60X magnification eyepieces to monitor nests after hatching (mean nest height was ~19 m). We were unable to examine the contents of nests directly and, therefore, only considered nests 'active' if we observed parental activity at the nest (indicating eggs or nestlings presence), as is standard in cerulean warbler breeding studies (D.A. Buehler, *personal communication*). We considered any nest that fledged >1 cerulean warbler young to be successful. For nests which failed, we attempted to determine the cause of failure in all cases, however we were unable to determine this in most cases, so all failed nests were included in our analysis. Additionally, we did not distinguish between initial and re-nesting attempts.

We analyzed daily nest survival rates (DSR) of cerulean warbler nests (exposure days) by comparing logistic exposure models in Program MARK to evaluate which factors were most strongly related to daily nest survival. This method uses a generalized linear model with binomial distribution for each day (nest fate = 1 if failed, 0 if successful) in relation to covariates that may affect nest survival. The exposure method of estimating nest survival is preferable to simply calculating apparent nest success (# of successful nests/total nests found), because, as Mayfield (1961) first noted, nests that fail early in the nesting cycle are less likely to be discovered, so apparent nest success will almost always be overestimated. We first compared models including the spatial factors of region (RGN) and site (SITE). We found strong support for region as the spatial factor that best explained variation in DSR (when compared with region, site $\Delta AIC_c = 5.59$, Table 1.1), and therefore we used this variable in all other possible models. We then compared all additive combinations of region, year (YEAR), and treatment (TRT), as well as a year x treatment (YEAR x TRT) to test for temporal variation in potential treatment effects. We also included a constant survival model (NULL) for a total of 10 candidate models (See Table 1.1). We found only one nest at MON, so this site was not included and as we observed no difference in nest survival among the buffers of the three treatment types (Program CONTRAST, chi-square test; $\chi^2_2 = 1.73$; $P = 0.42$) we therefore pooled all buffer nests into one treatment group simply called ‘buffers’. We used a sine link to model constant survival and a logit link to evaluate models that included covariates. We compared and ranked models using a corrected version of Akaike’s Information Criteria for small sample sizes (AIC_c), where the minimum AIC_c indicates the most influential of the models considered. We considered models with $\Delta AIC_c < 2$ to have strong support (Burnham and Anderson 2002).

To compare nest success among different levels of influential factors, we calculated entire period nest survival by raising DSR for each level to a power equal to the average length of the nest cycle (25 d). We report entire period survival rates (hereafter, simply ‘nest success’) throughout the rest of this paper for ease in interpretation.

We approximated entire nesting period variance and standard error using the delta method, following Powell (2007):

$$SE_{Total} = nest\ cycle\ length * SE_{Daily} * DSR^{(25-1)}$$

Because our units of interest were plots rather than individual nests, we decided *a priori* to compare nest success between each disturbance type and controls, within each region, and with years pooled and separately, using Program CONTRAST, which uses a modified chi-square analysis to identify differences in nest success among groups (Hines and Sauer 1989). We performed this analysis with both untransformed nest success rates and arcsin-square-root-transformed rates and found inferences unaffected, so we used untransformed nest success.

We compared the number of fledglings produced per successful nest among treatments using a mixed model ANOVA with treatment specified as a fixed factor and, because we observed differences in DSR between the northern and southern regions (see results), region as a random effect. We pooled all years for this analysis because of a lack of difference among years (One-way ANOVA, $F_{2,152} = 1.05$, $P = 0.35$). We only included nests where we were able to accurately count the number of fledglings produced (based on nest visibility).

We used JMP (v9.0) and SAS (v9.2) statistical software packages (SAS Institute Inc., Cary, NC) for analyses. For all statistical tests, we considered differences to be significant at $P \leq 0.05$ and marginally significant at $0.05 \leq P \leq 0.10$. We report untransformed means ± 1 SE in all figures and text.

Source-sink modeling

We used a deterministic population model to illustrate the effects of the various treatments in relation to source-sink dynamics, similar to Buehler et al. (2008). Input parameters included nest success, number of young produced/successful nest, after-hatch-year (AHY) and hatch-year

(HY) survival, proportion of individuals that attempt to re-nest after failing, and number of re-nesting attempts. We used nest success and number of fledglings estimates from this study and we used two published annual adult survival rates: 54% from Ontario (Jones et al. 2004) and 65% from Venezuela, on their wintering grounds (Bakermans et al. 2009). We compared the effect of each of these rates, and assumed that annual survival was equal on all treatments and sites. We lacked data on juvenile survival, so we assumed that juvenile survival was 50% of adult survival, a value commonly reported in the literature (May and Robinson 1985, Noon and Sauer 2001). We also assumed that 100% of females whose initial nests failed attempted to re-nest up to a maximum of three times (a number that was frequently observed in the field, T.J. Boves, *personal observation*). These last assumptions result in a model that is conservative with respect to the identification of sink populations (i.e., sink populations are truly sinks)..

RESULTS

Territory density

Pre-disturbance densities on plots were extremely variable, ranging from 0 – 17 territories/10 ha ($\bar{x}$ = 4.60 ± 0.43 terr/10 ha). In 2010, the last year of data collection, mean density had increased 17.6% to 5.58 ± 0.35 terr/10 ha (0 – 23 terr/10 ha). Mean density on controls (calculated from 4 post-disturbance years) increased post-disturbance at only one (of seven) sites, and as of 2010, total number of territories on controls decreased by 6.2% (Figure 1.2). Mean density on buffers increased post-disturbance at 3 sites, and as of 2010, total number of territories decreased by 5.2%. Mean density on light, intermediate, and heavy treatments increased post-disturbance at 6 sites each and, as of 2010, total number of territories increased overall by 25.5, 115.3, and 119.5%, respectively.

We found a main treatment effect ($F_{4,24}$ = 4.33, P = 0.009), but also a treatment x year effect ($F_{12,90}$ = 2.44, P = 0.008), so we performed pre-planned contrasts to evaluate differences between treatments and controls for each year independently (Figure 1.3). In light treatments, log DR was marginally greater than in controls in 2008 ($F_{1,24}$ = 3.46, P = 0.08), significantly greater in 2009 ($F_{1,24}$ = 4.63, P = 0.04), but exhibited no difference in 2007 ($F_{1,24}$= 0.38, P = 0.55) nor in 2010 ($F_{1,24}$ = 2.54, P = 0.12). In intermediate treatments, log DR was greater than controls in 2007 ($F_{1,24}$ = 8.41, P = 0.008), 2008 ($F_{1,24}$ = 10.80, P = 0.003), 2009 ($F_{1,24}$ = 13.16, P = 0.001), and 2010 ($F_{1,24}$ = 18.12, P = 0.0003). Log DR was significantly greater on heavy treatments than on controls in 2009 ($F_{1,24}$ = 4.40, P = 0.05) and 2010 ($F_{1,24}$ = 5.42, P = 0.03), but did not differ from controls in 2007 ($F_{1,24}$ =*1.44, P* = 0.25) or 2008 ($F_{1,24}$ =*1.28 P* = 0.27). Log DR did not differ between buffers and controls in any year (all $F_{1,24}$ < 1.50; all P > 0.20).

Age structure and body condition

We captured and aged 204 male Cerulean Warblers; 27% were SY birds, 73% ASY. There was no difference in age structure between regions (χ^2_1 = 1.09, P = 0.30, Figure 1.4). With all sites pooled, age structure did not differ among individual treatments (χ^2_4 = 1.63, P = 0.80), or when all disturbances were pooled and compared with controls and buffers (χ^2_1 = 0.45, P = 0.51). When assessing each region separately, no difference in age structure existed among individual treatments (northern region: n = 105, χ^2_4 = 2.89, P = 0.54; southern region: n = 99, χ^2_4 = 4.01, P = 0.40, Figure 1.4) or when comparing all disturbances pooled with controls and buffers pooled (northern region: χ^2_1 = 1.10, P = 0.29; southern region: χ^2_1 = 0.06, P = 0.81).

When all treatments were analyzed separately, we found no effect of treatment on body condition via body mass ($F_{4,87}$ = 1.11, P = 0.36, Figure 1.5). However, after pooling all disturbed treatments and buffers with controls, males on disturbed treatments were in better condition than males in controls and buffers ($F_{1,90}$ = 6.58, P = 0.01, Figure 1.5). Body condition also differed by age (SY males = 9.15 ± 0.07, n = 26; ASY males = 9.44 ± 0.04, n = 71, $F_{1,90}$ = 12.13, P = 0.0007).

Reproduction

The additive model of the three factors (RGN + YEAR + TRT) was the only model with any support in explaining DSR (Table 1.1). Of the three individual factors, region was the most influential (however, ΔAIC_c = 15.26). DSR was greater at southern sites (RB and SQ) than at northern sites (REMA, DB, LW, and WYO; χ^2_1 = 43.69, P < 0.0001; Figure 1.6). Therefore, we pooled nests from respective regions (southern sites: n = 208, northern sites: n = 205) to further examine treatment effect and annual variation.

At southern sites, annual nest success ranged from 0.48 ± 0.06 (2009) to 0.67 ± 0.05 (2010, Figure 1.7). When pooling nests from all three years (Figure 1.8), nest success was greater on controls than on light (χ^2_1 = 15.02, P < 0.0001), intermediate (χ^2_1 = 4.41, P = 0.04), or heavy treatments (χ^2_1 = 15.02, P < 0.0001), but there was no difference between controls and buffers (χ^2_1 = 1.89, P = 0.17). Annually, nest success was greater on controls than heavy treatments in 2009 (χ^2_1 = 26.07, P < 0.0001) and greater than light treatments during 2009 (χ^2_1 = 33.73, P < 0.0001) and 2010 (χ^2_1 = 5.64, P = 0.02, Figure 1.9a).

At northern sites, annual nest success ranged from 0.22 ± 0.04 (2009) to 0.40 ± 0.06 (2010, Figure 1.7). When pooling nests from all three years (Figure 1.8), nest success was marginally greater on controls than on light treatments (χ^2_1 = 3.50, P = 0.06) or buffers (χ^2_1 = 3.12, P = 0.08). On an annual basis, nest success did differ between control or any treatment or buffers (Figure 1.9b).

Cerulean Warblers at southern sites produced more fledglings/successful nest ($\bar{x}$ = 3.29 ± 0.07) than at northern sites ($\bar{x}$ = 2.48 ± 0.12; $F_{1,148}$ = 35.21, P < 0.0001). On southern sites, number of young produced among treatments did not differ ($F_{4,100}$ = 1.50 P = 0.21, See Figure 9). On northern sites, number of young differed marginally among treatments ($F_{4,46}$ = 2.65, P = 0.06), with buffer nests, on average, producing 46.7% more fledglings than nests on light treatments (buffers: $\bar{x}$ = 2.73 ± 0.15, n = 22, light: $\bar{x}$ = 1.86 ± 0.69, n = 7, see Figure 1.10).

The cause of nest failure was directly observed or inferred from evidence at 36 nests (Figure 1.11). Predation was the main cause of nest failure (61.0% of these 36 nests) with the next closest apparent disease or starvation (16.7%). However, the majority of failed nests (n = 174) were abandoned immediately for unknown reasons, indicating that predation was most likely, but abandonment of eggs due to cowbird parasitism cannot be ruled out.

Source-sink model

Our graphical model shows that given an AHY annual survival rate of 54%, only controls on the southern sites had levels of reproduction sufficient to maintain a stable (or source) population (Figure 1.10). If annual survival was increased to 65%, all treatments at southern sites would act as sources. We found no treatment at northern sites which could maintain a stable population given these two adult survival rates; all would require either much greater annual survival or reproductive output, immigration from other locations, or an adjustment in model assumptions to persist.

DISCUSSION

Contemporary second-growth forests may not provide quality habitat for some late-successional species, especially if those species are adapted to natural disturbance regimes that have been altered or suppressed within contemporary Appalachian forests. Here we first documented attraction to experimental disturbance by a late-successional forest avian species, the Cerulean Warbler, in mature forest ecosystems in the Appalachian Mountains. Individuals occupying disturbed habitats were also in better condition than those occupying controls and buffers. However, despite these apparent positive impacts of disturbance, nest success was lower on all disturbed treatments than on controls on the highly-productive southern sites, and on light treatments (and buffers) on the northern sites. We found no evidence that the costs of reduced nest survival were negated by increases in the number of young produced/successful nest. Therefore, we conclude that these disturbances, at the spatial and temporal scales that we examined, may function as ecological traps for Cerulean Warblers (Battin 2004). However, this designation is dependent on several assumptions concerning demographic parameters and life history traits including adult and post-fledgling survival, patterns of long distance dispersal, and alternate options of habitat selection, which we discuss below.

Territory density

The density response we observed is congruent with correlative studies which report that Cerulean Warblers are associated with canopy disturbances within mature forests (e.g., Wood et al. 2006, Bakermans and Rodewald 2009). Attraction was greatest after intermediate and heavy disturbance, suggesting that ceruleans are more highly attracted to habitat disrupted by fire, large blow-downs, landslides, or other severe natural disturbances, rather than smaller single tree-fall gaps caused by tree senescence, for instance. The response to intermediate disturbances was often unexpectedly strong. For example, on the intermediate treatment at LW, density increased from 0.25 terr/10 ha (pre-disturbance) to 23 terr/10 ha as of 2010. Increases after intermediate disturbances on other sites were more modest; perhaps because of pre-disturbance saturation. At RB, pre-disturbance density was at a (likely) near-saturation level of 17 terr/10 ha. Density increased post-disturbance, but only to a maximum of 20.5 territories in 2010. At such densities, it would seem unlikely that many more males could inhabit the area, no matter how attractive the habitat, particularly given reported territory sizes for ceruleans of 0.96 ± 0.18 ha in Ontario (Barg et al. 2005) and 0.9 ± 0.1 ha in Missouri (Robbins et al. 2009). However in West Virginia, territory sizes were substantially smaller at 0.37 ± 0.07 ha (Perkins 2006).

Body condition

Males that occupied disturbed habitats were in better condition (greater body mass) than those inhabiting buffers and controls. This result is compatible with our observed density response; however, it was not necessarily expected given the ecology of ceruleans. Cerulean Warblers often forage in the overstory, most often gleaning insects off leaves (George 2009). Our disturbed treatments (esp. intermediate and heavy) had a markedly reduced foliage area for foraging purposes. Additionally, because densities on disturbed treatments were greater, energy requirements for defending against conspecifics (and heterospecifics) would have been expected to increase as well (Dobbs et al. 2007). We do not know how settlement bias impacted this pattern (if individuals on disturbed treatments were in better condition initially or of higher quality), but we observed no difference in age structure among treatments, suggesting that birds in the disturbed treatments were better able to maintain their condition in these disturbed treatments. Canopy gaps can alter the composition of the arthropod community (Gorham et al. 2002, Greenberg and Forrest 2003) and ceruleans may be better adapted for foraging on species inhabiting broken canopies. George (2009) found that ceruleans increased their use of aerial foraging maneuvers after partial timber harvests occurred. These behavioral changes may reflect an altered arthropod community and behavioral plasticity in foraging strategies or inherent differences in the individuals selecting differing habitats.

Age structure

The lack of a clear difference in age structure among treatments runs counter to our expectations. Assuming older birds are dominant (Fretwell and Lucas 1970, Arcese and Smith 1985, Edler and Friedl 2010), experienced males (ASY) should out-compete inexperienced males (SY) and settle in preferred habitat more often. The Cerulean Warbler's propensity for long-distance breeding dispersal as adults would seem to make this even more likely (Girvan et al. 2007) as they do not exhibit the high rate of breeding site fidelity of other migratory passerines (Greenwood and Harvey 1982). Instead, the lack of difference in age structure which we observed may have been related to several factors, including the opportunity for extra pair copulations (EPC). Older, more-experienced males settling in preferred habitat may allow inexperienced individuals to occupy territories in close proximity to improve the older males' likelihood of gaining EPC from the younger males' mates (Weatherhead and Boag 1997, Double and Cockburn 2000). Despite being socially monogamous (Hamel 2000), EPCs may be quite common in the Cerulean Warbler mating system (Barg et al. 2006), but little data currently exist.

Reproductive success

Despite preference for, and improved body condition associated with, disturbances, reproductive output/pair declined in many of the treatments. A possible buffer to the fitness costs of decreased nest success could have been an increase in the number of young produced/successful nest, but we found no difference in this parameter across treatments. Maladaptive habitat selection was most obvious on our southern sites, where reproductive disparities among treatments were greater and statistically apparent. On northern sites, factors apparently unrelated to our habitat manipulations reduced nest success to levels where local habitat alterations had less impact, however nest success still was greater on controls than light treatments and buffers in this region.

Additionally, our sample size from heavy treatments on the northern sites was very low ($n = 5$ nests), so our power to detect statistical differences using chi-squared tests was limited.

Most failed nests were abandoned without apparent cause (nest intact with no sign of parents), but this sudden abandonment suggests that predation was the likely cause of failure for the majority of nests, as opposed to starvation or disease which would be indicated by observable changes in nestling and parental behavior. Predation is also well-documented as the major cause of nest failure for many avian species (Martin 1993, Newton 1998). Non-exclusive factors which may have increased predation rates after disturbance include an increase in predator abundance (Robinson and Robinson 1999), density-dependent nest predation (Schmidt and Whelan 1999), a decrease in available nest sites and nest-concealing foliage (Martin 1993, Liebezeit and George 2002), and maladaptive parental behavior during nest construction and feeding which may attract predators (Eggers et al. 2008, Lima 2009). Predators may be attracted to disturbances themselves (Robinson and Robinson 1999) or the soft edges which disturbances create (Batáry and Báldi 2004). Indirect predator effects in the form of “risk effects” may have also hindered reproduction (Creel et al. 2007). Direct and anecdotal evidence suggests that all of these factors in concert may have led to the greater nest failure rates we documented on disturbed treatments. For instance, light treatments, where nest success was lowest in both regions, appeared to harbor more diurnal mammalian predators (than any other treatment on RB and SQ, T.J. Boves, *unpublished data*), lacked nest-concealing canopy foliage (compared to controls), were occupied by greater densities of Cerulean Warblers (vs. controls), and did not elicit major adjustments in nest construction or provisioning strategies (T.J. Boves, *unpublished data*). Outside of predation, we documented several other factors that may have increased nest failure on disturbed treatments including increased inter- and intraspecific competition for food, nest material, or mates;

increased impacts of severe weather; increased susceptibility to disease; and increased thermal stress (Boves et al. 2011, Boves and Buehler *In Revision*).

Only three nests failed because of brood parasitism by Brown-headed Cowbirds, despite the fact that brood parasitism is a major contemporary cause of nest failure for many eastern North American passerines, including Cerulean Warblers in some parts of their range (Robbins et al. 1992). Some research suggests that selective harvesting practices may increase cowbird abundance (Annand and Thompson 1997, Thatcher 2007), but other evidence indicates that parasitism itself does not increase after partial harvests, especially in highly forested landscapes (Robinson et al. 1993, Robinson and Robinson 1999, Duguay et al. 2001). Cowbirds appeared to be more abundant on disturbed treatments (esp. intermediate and heavy; Newell 2010, J. Sheehan, *unpublished data*), however we documented cowbird nestlings at only four nests (<1% of all nests; 2 in light treatments, 1 in intermediate, 1 in buffer), two of which also fledged cerulean young (and were therefore considered successful). Thus, in these highly forested Appalachian landscapes, Brown-headed Cowbirds do not currently appear to be a major cause of Cerulean Warbler nest failure, even after anthropogenic disturbance. However, we were unable to determine how many nests were abandoned because of the presence of cowbird eggs, a behavior which occurs in some Neotropical migrants, (Robinson et al. 1995).

Anthropogenic disturbances as ecological traps

In this study, (1) males preferred all disturbed treatments over controls, (2) nest success differed among habitat types (particularly on southern sites), and (3) nest success was significantly lower on all three disturbed treatments at southern sites and on light treatments at northern sites. Therefore, all disturbed treatments on southern sites and light treatments on northern sites met the criteria necessary for designation as ecological traps. This type of maladaptive habitat selection can have dire consequences for population viability (Kokko and Sutherland 2001). Ecological traps may be more detrimental to a population's viability than sink habitats because traps may actually attract more individuals whereas sink habitats should be avoided (Kristan 2003). Several ecological traps created by timber harvests have recently been identified for Olive-sided Flycatchers (*Contopus cooperi*) breeding in selectively logged forests in Montana (Robertson and Hutto 2007) and Rusty Blackbirds (*Euphagus carolinus*) breeding in regenerating clear-cuts in northern New England (Powell et al. 2010).

While the evidence we collected indicates that anthropogenic disturbances acted as ecological traps, to fully determine if a habitat functioned as a trap, additional information is needed. Additional factors that could also affect the fitness of individuals breeding in a given setting include annual and post-fledging survival. Annual survival rates could have been greater for birds occupying disturbed habitats as individuals that occupied these areas may have been better able to withstand the rigors of migration by virtue of improved body condition (Newton 1993, Morrison et al. 2007). Post-fledgling survival may also be enhanced in disturbances. The post-fledging period is often as dangerous as the nestling period (Kershner et al. 2004, Low and Pärt 2009) and dense understory vegetation provided by canopy disturbance has positive effects on post-fledging survival in ground-nesting species such as Ovenbirds (*Seiurus aurocapilla*, Streby and Andersen 2011) and Worm-eating Warblers (*Helmitheros vermivorum*, Vitz and Rodewald 2011), but had no impact on survival of a midstory species, Rose-breasted Grosbeak (*Pheucticus ludovicianus*, Moore et al. 2010). Timing of reproduction may also play a role, as young fledged from successful nests on disturbed treatments, on average, five days later than on controls (disturbed habitat mean fledging date = 12 June; control mean fledging date = 7 June). However, evidence for an effect of seasonal timing on juvenile survival is also ambiguous; late fledging individuals were less likely to survive to reproductive age in Great and Coal Tits (*Parus major* and *P. Ater*; Naef-Daenzer et al. 2001), but more likely to survive in Wood Thrushes (*Hylocichla mustelina*; Anders et al. 1997) and Lark Buntings (*Calamospiza melanocorys*, Adams et al. 2006). Further research concerning the post-fledgling period is warranted for Cerulean Warblers and other upper canopy-nesting species, although this work will be challenging because of difficulties in capturing nestlings and fledglings.

Why might ceruleans prefer habitats in which they fail to maximize reproduction? Under evolutionarily-relevant historical conditions, canopy disturbances caused by fire or natural treefalls in old-growth forests may have created conditions where Cerulean Warblers were able to achieve high levels of fitness. In anthropogenic-disturbed habitats, such as our treatments, the environmental cues associated with high fitness apparently still elicit the same habitat selection behavior, however other conditions, contemporary in nature, have also been altered, thereby decoupling the habitat cues from historical fitness levels. This decoupling would be easiest to explain if brood parasitism was largely responsible for nest failures, as cowbirds are relatively new additions to eastern forest ecosystems (Mayfield 1965). However, because brood parasitism had minimal impact on reproduction in our study, this mechanism does not appear to be relevant. Therefore, the mismatch is most likely related to nest predation. Predation pressures (abundance or species composition) may be altered because of contemporary factors such as landscape-scale fragmentation (Stephens et al. 2003). If broad-scale factors are responsible, then the source of disturbance (natural or anthropogenic) may be irrelevant as any interior disturbance may result in the formation of an ecological trap. Jones et al. (2001) reported a decrease in cerulean nest success a year after an ice storm in Ontario, Canada, however densities also decreased markedly in that study, likely producing a sink rather than an ecological trap. Alternatively, despite our best intentions, forests disturbed by human activity may only superficially resemble naturally disturbed forests, and may actually differ in terms of tree age-class distribution (DeLong and Tanner 1996), increased soil disturbance (Spies et al. 1994), or a lack of standing dead trees or snags (Hutto 1995). These artificial modifications may result in differing predation pressures, arthropod composition (Short and Negrón 2003), or other factors that may make it difficult for ceruleans to assess habitat quality correctly. In the future, 24-hour video surveillance of cerulean nests will be necessary to better understand the causes of nest failure and the adaptiveness of their behavior.

All documented responses to treatments were short-term in nature (1-4 years); how birds will respond in the future is unknown. We may have already begun to see an adjustment in habitat selection behavior in 2010. While densities increased in 2008 and 2009 on the light treatments, by 2010 the density response to the light treatment was no longer statistically different than the controls. Birds may have begun to track variation in breeding success and adjusted their habitat selection decisions to match local conditions. This phenomenon has been observed before in avian species (Reed et al. 1999, Doligez et al. 2008). If habitat selection behavior is dynamic, and relatively low levels of nest success persist on disturbed treatments, densities on light (and possibly other) treatments may eventually drop below densities on the controls, but this hypothesis will require further study. An alternative explanation is that canopy closure had begun to occur on the light treatments, and attraction to the structural features of the vegetation had already begun to decline.

Source-sink dynamics and management implications

The source-sink dynamics of Cerulean Warblers in our study can be viewed at two spatial scales. At a broad scale, only our southern sites, both located in the Cumberland Mountains, would be expected to act as sources. When compared with estimates of fecundity from other locations, this region is the most productive documented breeding locale range-wide (Buehler et al. 2008), and its importance has been noted before (e.g., Buehler et al. 2006). At a finer scale, and assuming an annual survival rate of 54%, only undisturbed forest in the Cumberland Mountains would be expected to act as source habitat. This would seem to highlight the importance of maintaining these southern montane forests with minimum levels of fragmentation and anthropogenic disturbance, an unlikely scenario given the myriad of human activities scheduled to occur in the area over the next decade (Bulluck 2007, D.A. Buehler, *personal communication*). However, if we assume an adult annual survival rate of 65%, *all* treatments in the Cumberland Mountains become *global* source habitats, despite acting as *local* ecological traps. Therefore, a fundamental question which affects interpretation of the data is: what alternative breeding locations do birds forego to breed on the attractive disturbed forest stands? The answer to this question depends largely on dispersal and habitat selection decisions made by individuals. Ceruleans appear to be quite aberrant in their patterns of dispersal. As adults, while most migratory passerines exhibit relatively high site fidelity (Greenwood and Harvey 1982, Weatherhead and Forbes 1994), ceruleans disperse long distances with much more regularity (Girvan et al. 2007). If ceruleans do in fact regularly engage in long distance dispersal as adults (putatively searching for recently disturbed, mature forest habitat), the creation of attractive disturbed habitats in the Cumberland Mountains may be beneficial to the overall sustainability of the global cerulean population because it may increase densities of birds in this highly productive region. However, for this management strategy to be successful, it would require that birds attracted to disturbed habitats in the Cumberlands would have otherwise attempted to breed in less productive regions (e.g., Ohio, West Virginia, or elsewhere) or not at all, rather than breeding in more productive, adjacent undisturbed forest in the Cumberlands.

On the northern sites, emulating relatively severe disturbances did not result in major declines in nest success locally (when compared with local controls), however if disturbances attract birds to this region from more distant locations where their fecundity may have been greater (e.g., the Cumberland Mountains), a global ecological trap could be created. Alternatively, if many individuals attracted to disturbances would have otherwise failed to reproduce at all, anthropogenic disturbances could have a positive effect on the global population, even if fecundity in these disturbances is reduced.

As such, to increase, or even maintain, Cerulean Warbler populations into the future, managing the spatial distribution of managed forest stands may be a useful component of the overall conservation strategy. A balance between creating disturbances in stands where existing forest structure is unsuitable and cerulean density is low, and limiting disturbance on those stands where forest structure is currently appropriate and cerulean density is high, will need to be reached. Determining where appropriate forest structure currently exists may be accomplished by performing systematic bird surveys (to directly assess density) or by applying predictive models which use vegetative and topographic measurements (similar to Buehler et al. 2006, Bakermans and Rodewald 2009). Whichever method is used, successful application of management will likely require a continued cooperative effort throughout the Appalachians to provide habitat for a maximum number of breeding pairs across their range while also maintaining the most highly productive forested regions (such as in the Cumberland Mountains). Future studies examining long distance dispersal patterns of ceruleans inhabiting various disturbed treatments in both the highly and less productive regions (via stable isotope analysis) may help inform this situation further. In addition, we believe continued monitoring of these field sites to assess the persistence of the trends we have observed would be very informative.

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APPENDIX

Model	**AIC_C**	**ΔAIC_C**	**k**	***w***
S(RGN+YEAR+TRT)	1518.32	0.00	8	0.96
S(RGN+YEAR)	1526.25	7.92	4	0.02
S(RGN+TRT)	1526.38	8.05	6	0.02
S(RGN)	1533.58	15.26	2	0.00
S(SITE)	1539.17	20.85	2	0.00
S(RGN+YEAR+TRT+YEAR*TRT)	1540.58	22.26	23	0.00
S(YEAR+TRT)	1543.39	25.06	7	0.00
S(YEAR)	1551.49	33.16	3	0.00
S(TRT)	1559.92	41.59	5	0.00
S(YEAR+TRT+YEAR*TRT)	1564.59	46.26	22	0.00
S(NULL)	1567.25	48.92	1	0.00

Table 1.1. Summary of model selection results for factors influencing daily survival of Cerulean Warbler nests. Models with a lower ΔAIC and a greater AIC_c weight have greater support.

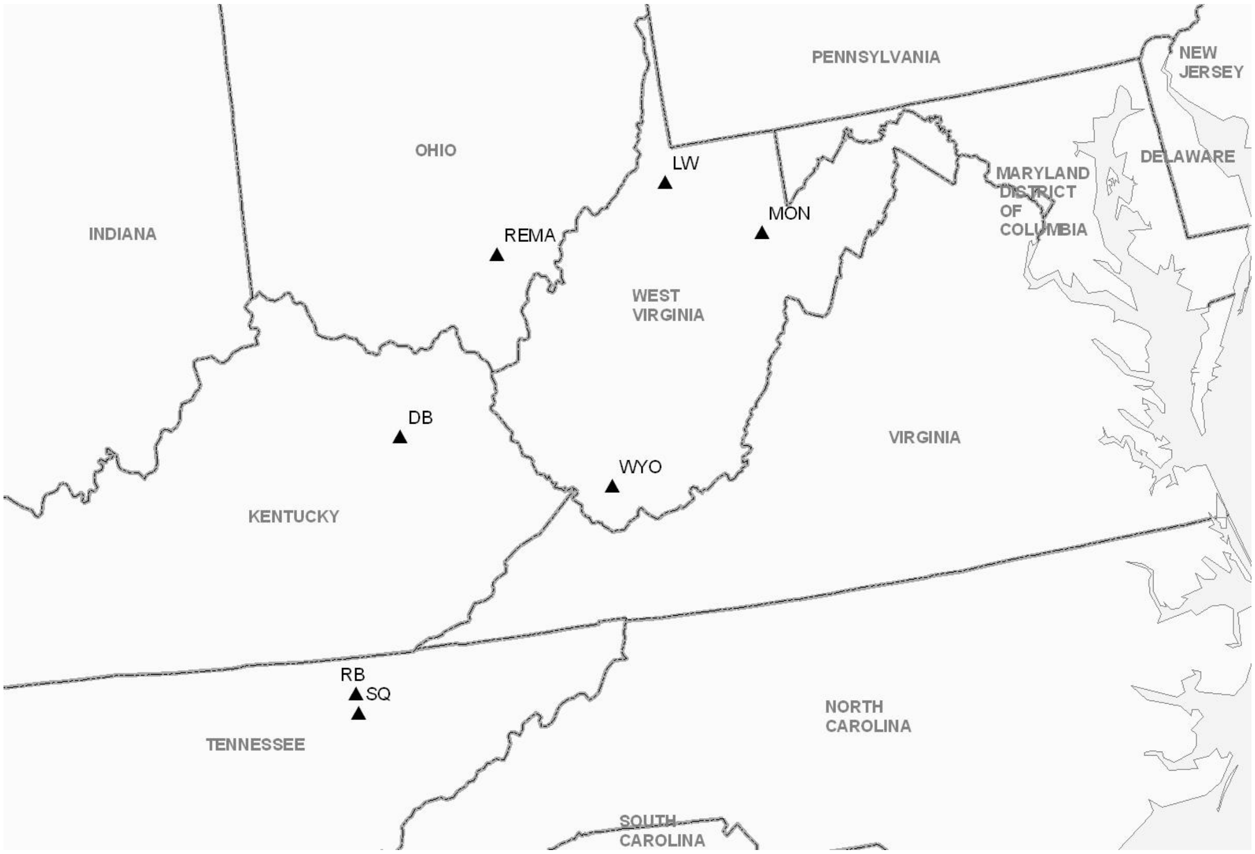


Figure 1.1. Map displaying locations of seven study sites in the Appalachian Mountains. All sites are located within the core of the Cerulean Warbler breeding range.

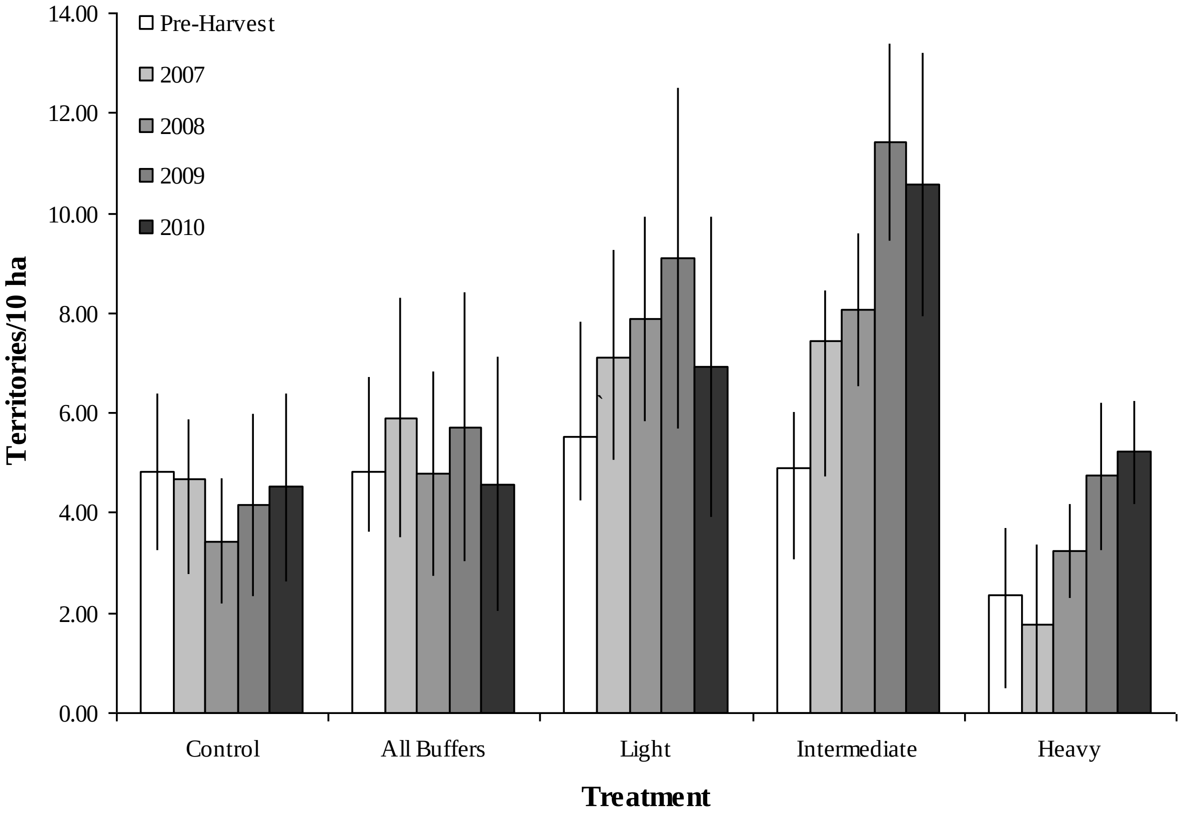


Figure 1.2. Mean densities ± 1 SE of Cerulean Warbler territories on disturbed treatments, controls, and buffers from pre-disturbance years (mean of 2005–06) to four years post-disturbance.

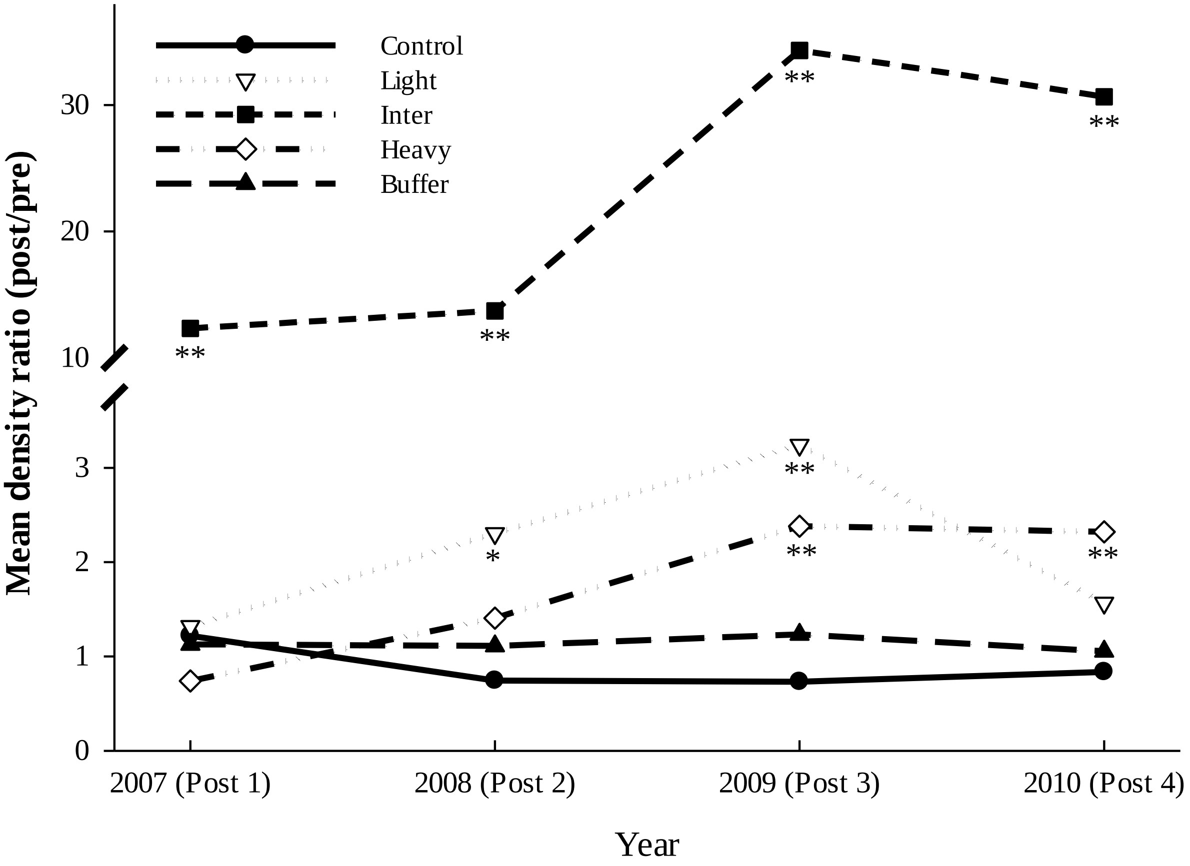


Figure 1.3. Mean density ratio of male Cerulean Warblers (calculated as post-disturbance density/pre-disturbance density) in various treatments. Double asterisks below markers indicate significant differences (α = 0.05) between control and the respective treatment for that year (repeated measures ANOVA, using log density ratio as response variable). Single asterisks indicate marginal annual differences (α = 0.10) between control and treatment. Density ratio = 1 reflects a stable population; all values above 1 indicate increased density, all values below indicate density reduction.

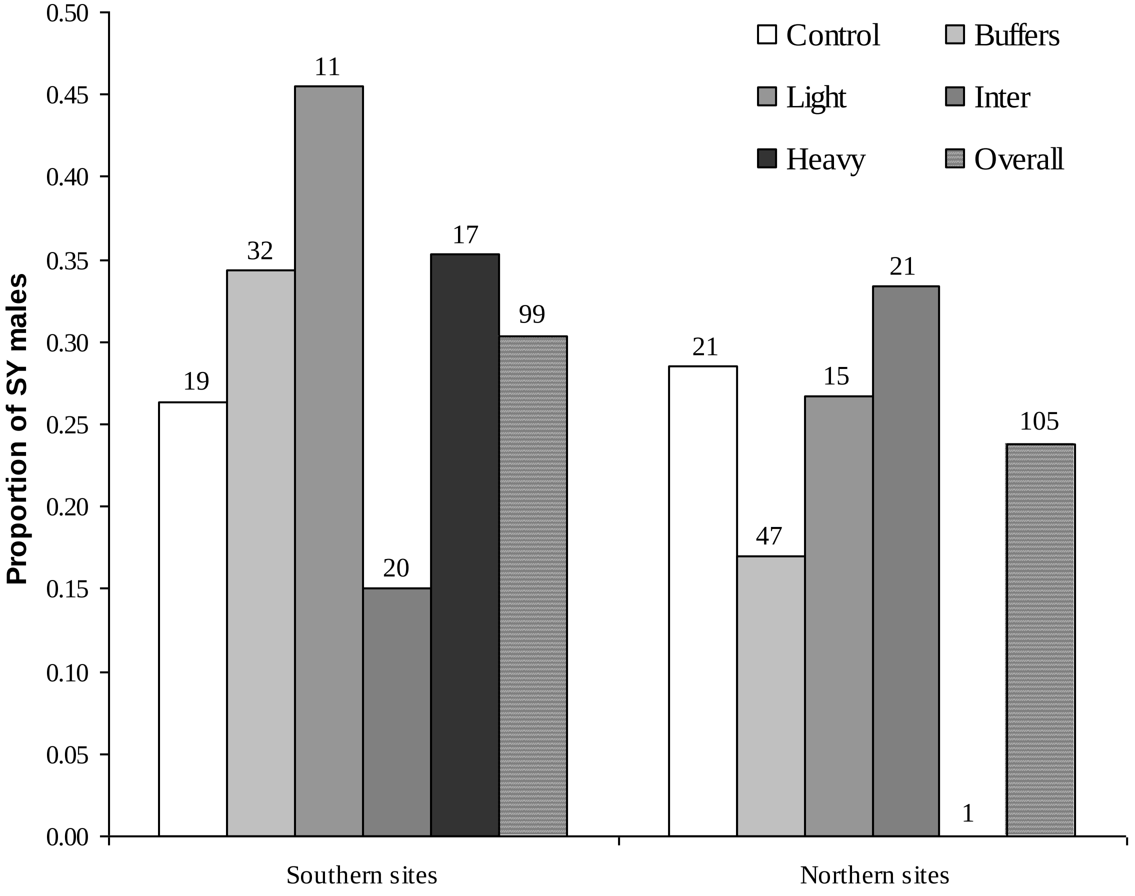


Figure 1.4. Age structure of male Cerulean Warblers on various treatments expressed as the proportion of second-year (SY) males captured. Numbers above bars indicate the total number of birds caught in the respective region and treatment from 2007–10.

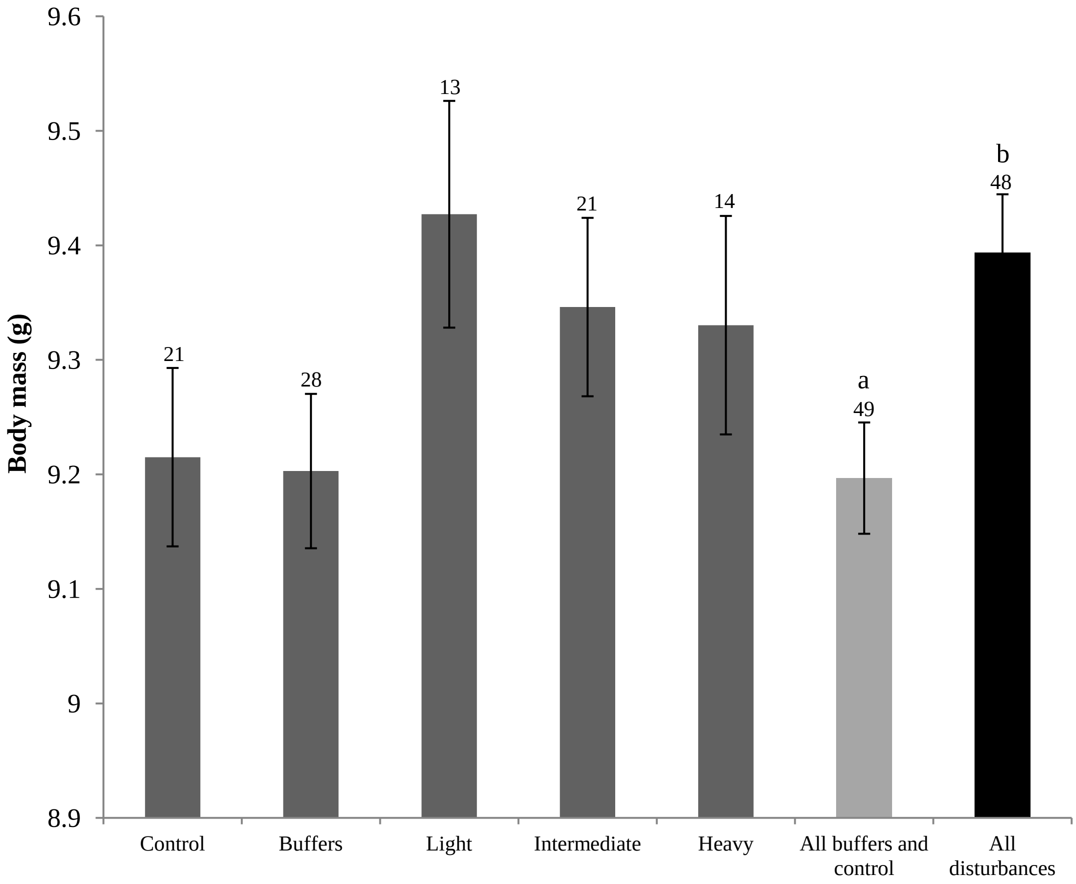


Figure 1.5. Body condition (via body mass) of male Cerulean Warblers by treatment, 2008–10. Sites, years, and age classes were pooled. Numbers above bars indicate sample size. Error bars represent ± 1 SE. Differing letters indicate significant difference at $\alpha = 0.05$ when compared in a mixed general linear model with age and treatment included as fixed effects site and year and site included as random effects.

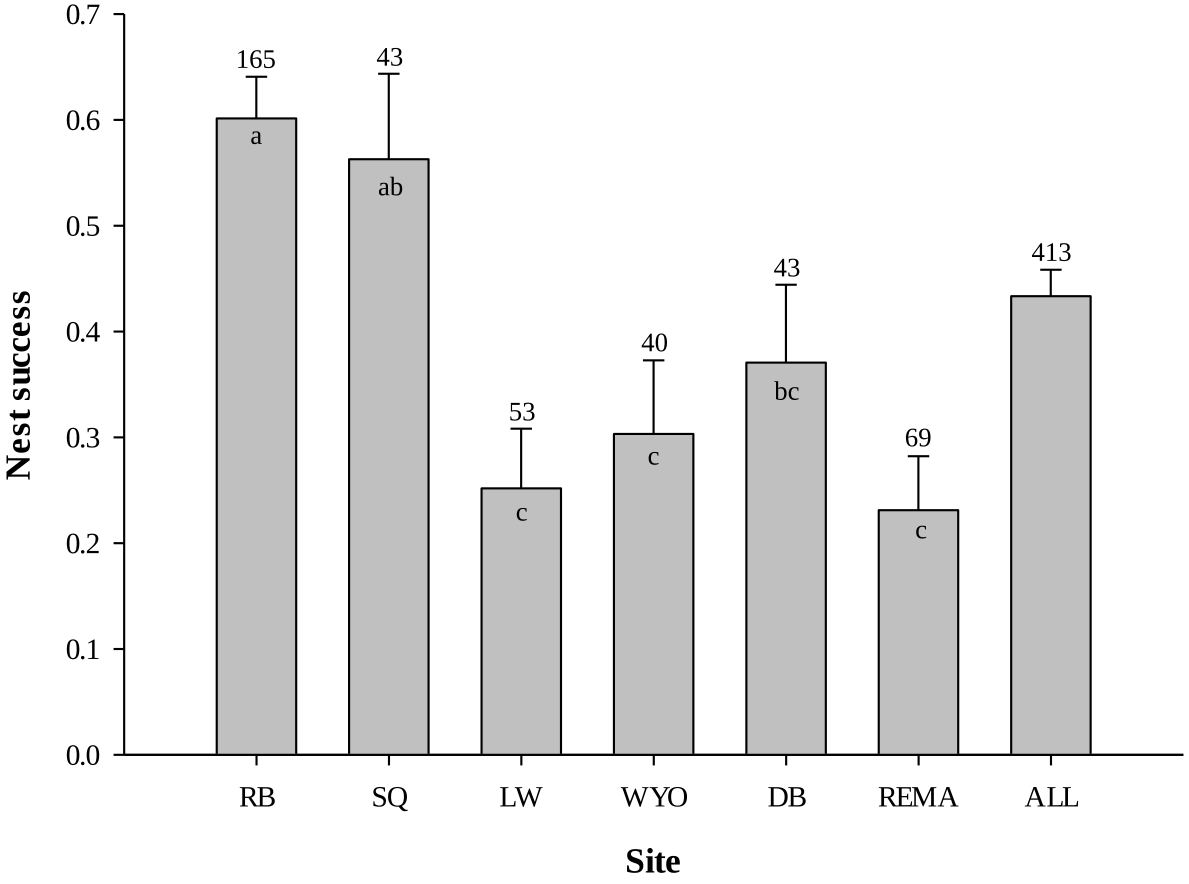


Figure 1.6. Cerulean Warbler nest success by site, all treatments combined, 2008–10. Numbers above bars indicate number of nests monitored. Differing letters indicate significant difference at α=0.05 among sites (based on CONTRAST χ^2 test). Error bars represent 1 SE.

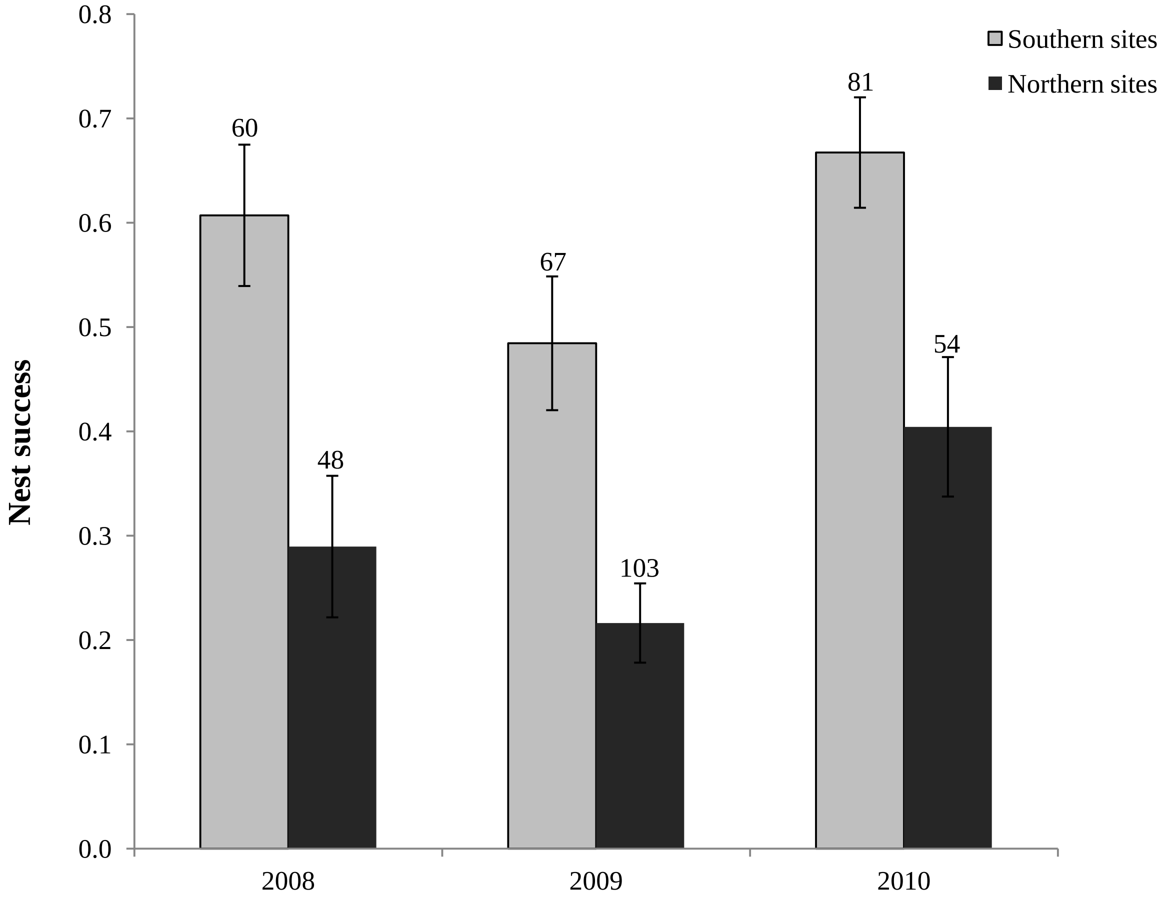


Figure 1.7. Cerulean Warbler nest success by year, all treatments combined. Numbers of above bars indicate numbers of nests monitored. Error bars represent ±1 SE.

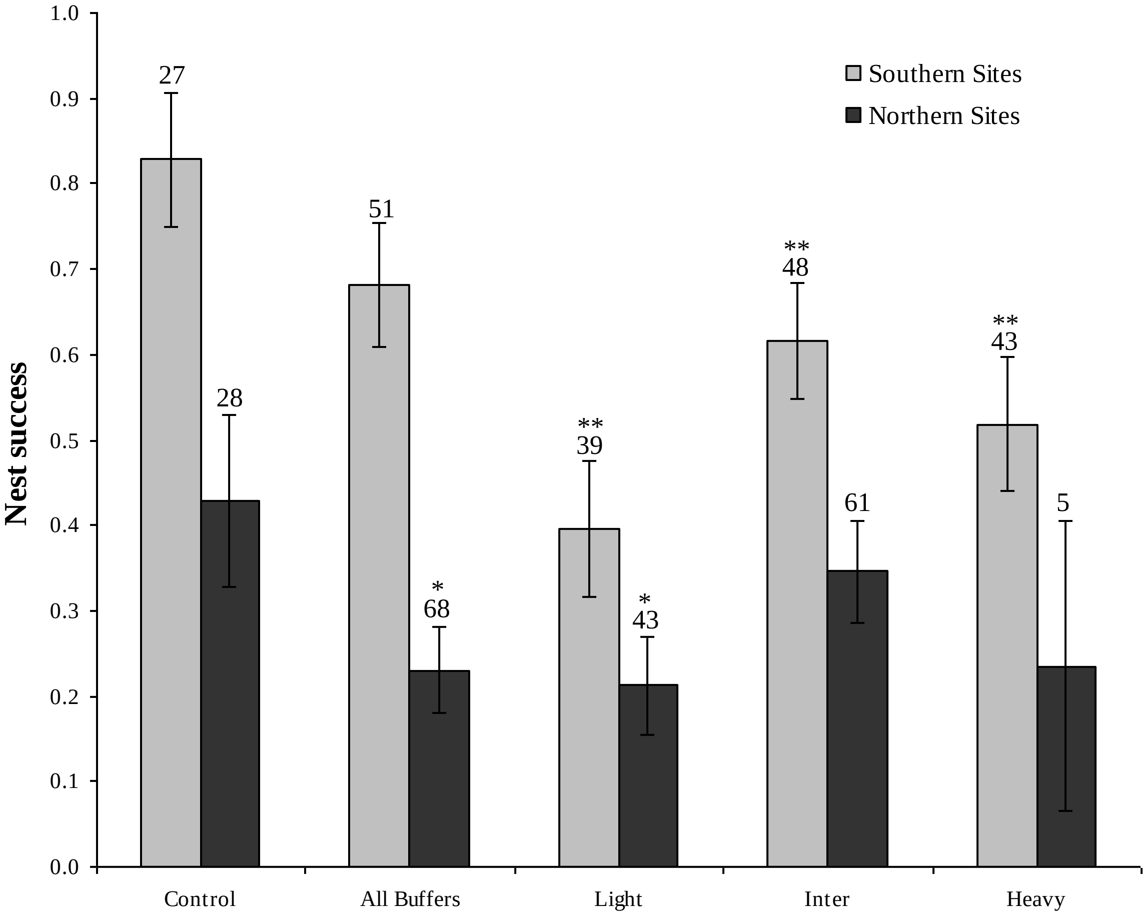


Figure 1.8. Cerulean Warbler nest success by treatment, all post-disturbance years combined. Numbers above bars indicate numbers of nests monitored. Double asterisks indicate significant differences (α=0.05) between control and respective treatment, each region analyzed independently (based on CONTRAST χ^2 test). Single asterisks indicate treatment types that differed marginally (α=0.10) from controls. Error bars represent ±1 SE.

Figure 1.9a.

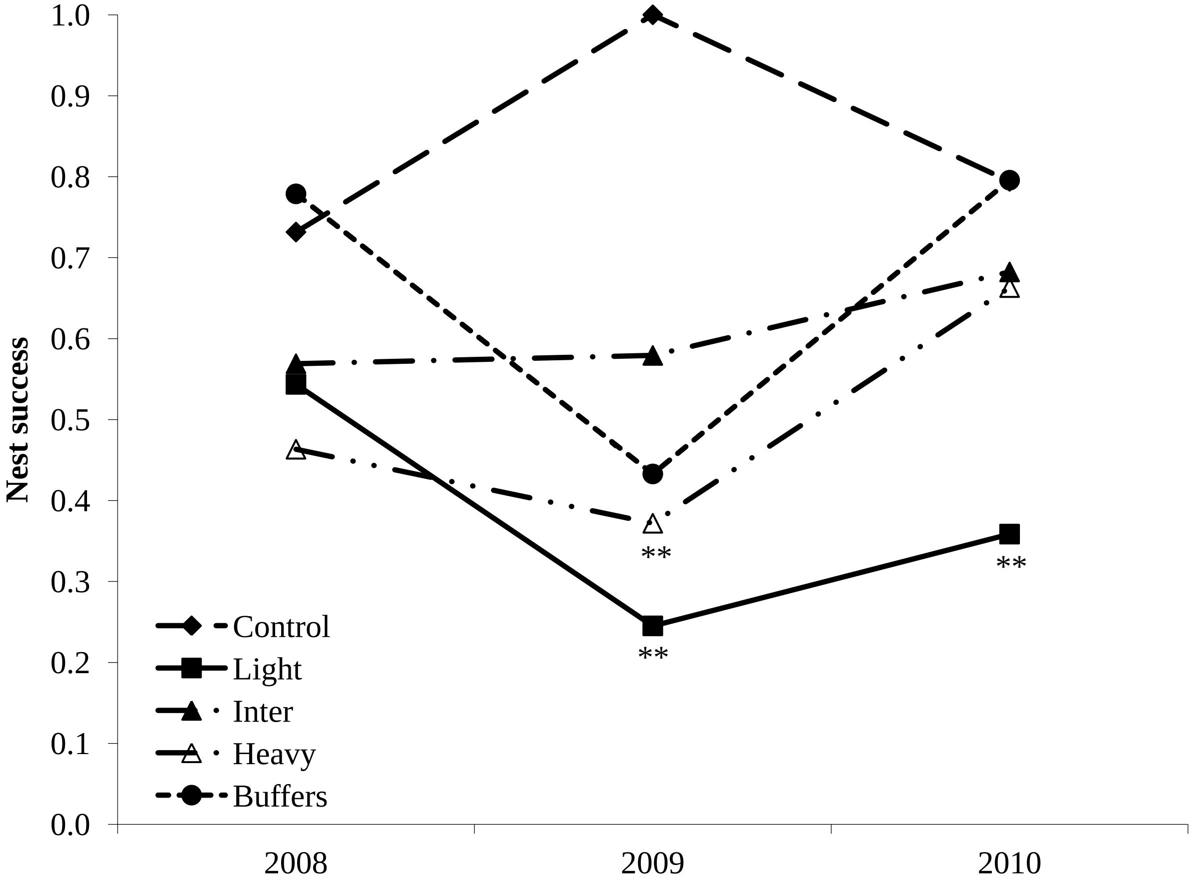
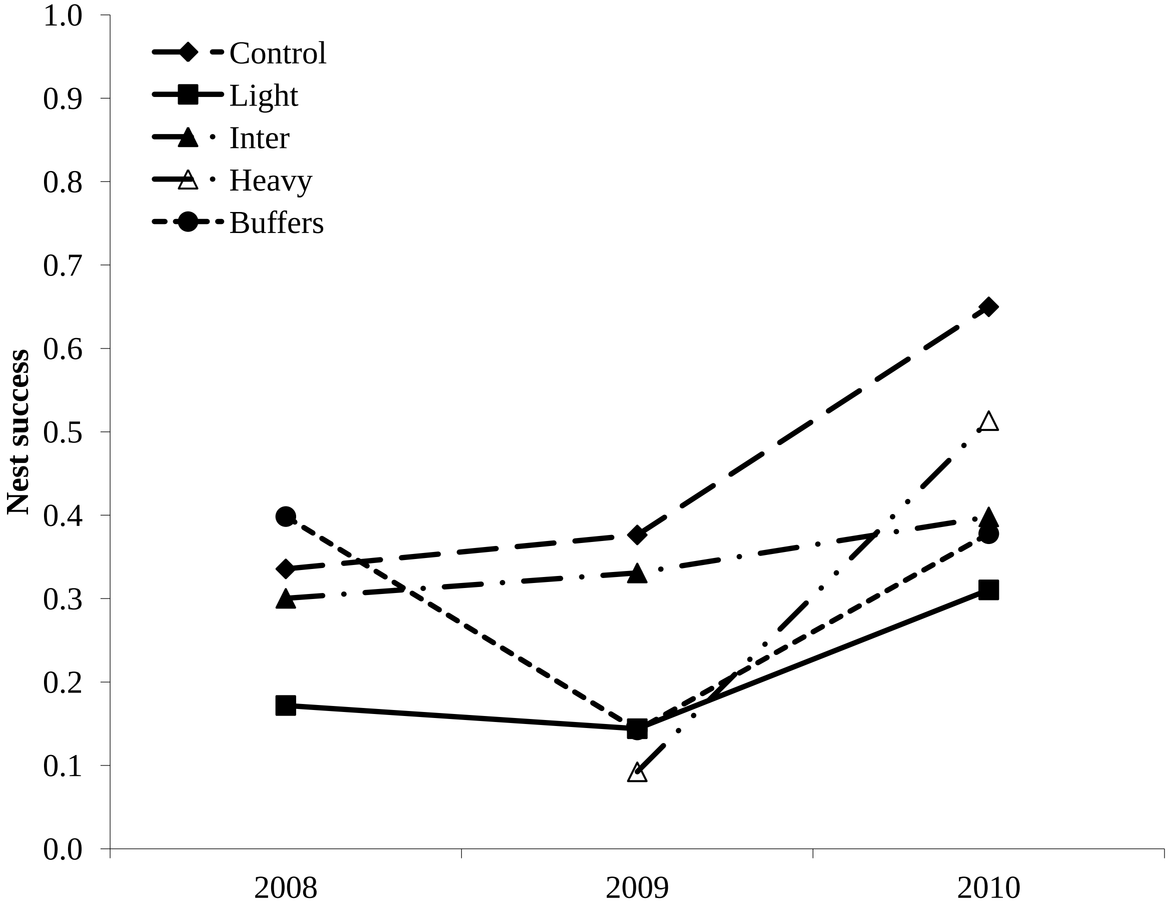


Figure 1.9a-b. Cerulean Warbler nest success by treatment and year at (a) southern sites (RB and SQ) and (b) northern sites (REMA, DB, LW, WYO). Double asterisks indicate statistical difference at α=0.05 between control and individual treatment, each year analyzed separately (based on CONTRAST χ^2 test).

Figure 1.9b.



Figures 1.9a-b. Nest success by treatment and year at (a) southern sites (RB and SQ) and (b) northern sites (REMA, DB, LW, WYO). Double asterisks indicate statistical difference at $\alpha=0.05$ between control and individual treatment, each year analyzed separately (based on CONTRAST χ^2 test).

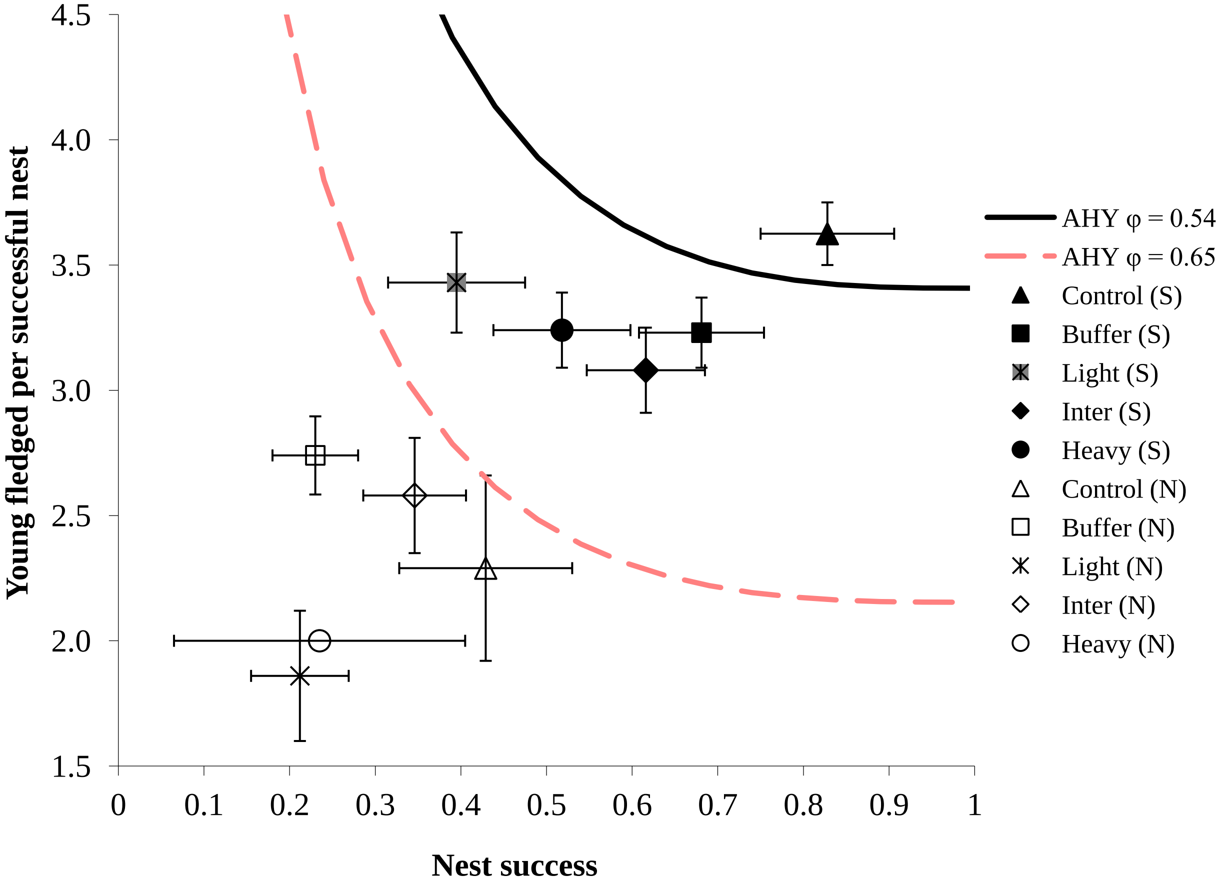


Figure 1.10. Source-sink graphical model using point estimates of nest success rates and mean number of young fledged/successful nest on various treatments at both southern (S) and northern (N) sites, 2008–10. Error bars indicate ±1 SE. Two lambda threshold curves are displayed, each based on a published annual survival rate: (1) from Ontario (54% AHY survival; Jones et al. 2004), and (2) from Venezuela (65% AHY survival; Bakermans et al. 2009). Points to the left or below the threshold curve, for each given survival rate, represents decreasing, or sink populations, and points to the right of the curve represent increasing, or source populations.

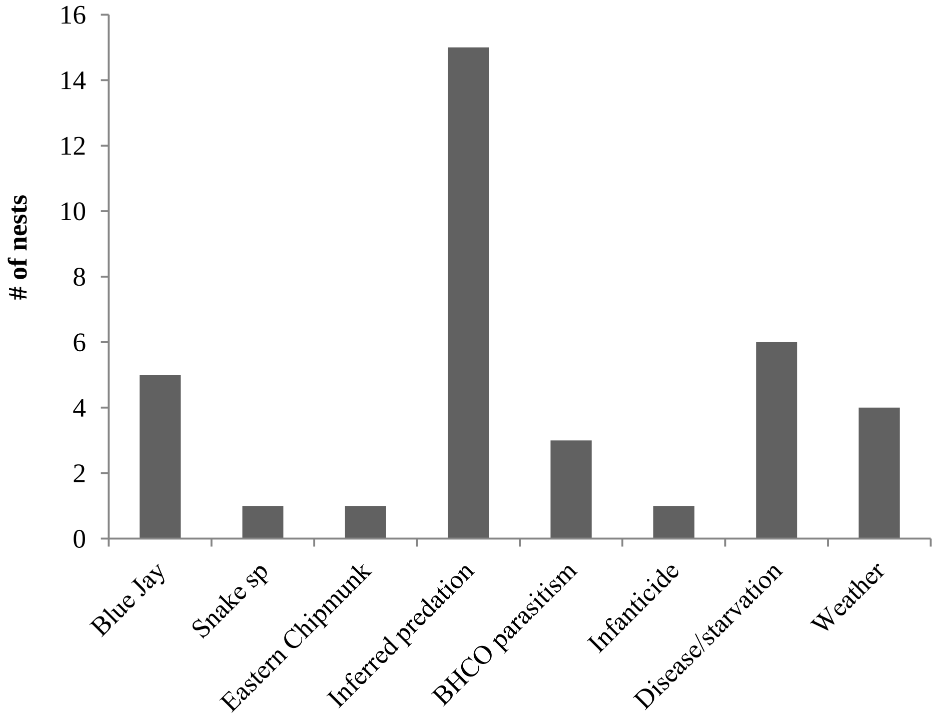


Figure 1.11. Causes of nest failure for Cerulean Warblers in the Appalachian Mountains from 2008–2010. Inferred predation refers to failed nests that we observed with structural damage that was likely caused by a predation event. An additional 174 nests were abandoned suddenly for unknown reasons.

CHAPTER 2: SPATIAL VARIATION OF MULTI-SCALE HABITAT SELECTION AND ADAPTIVENESS OF HABITAT DECISIONS MADE BY CERULEAN WARBLERS ACROSS A DISTURBANCE CONTINUUM

Abstract. Habitat selection studies have often been limited in that they cover relatively small geographic areas, do not examine habitat selection at multiple scales, and do not assess adaptiveness of habitat decisions. These limitations are particularly problematic for declining species in need of conservation and management. Cerulean Warblers (*Setophaga cerulea*) are among the fastest declining songbirds in North America and the core of their range has contracted into a relatively small area in the Appalachian Mountains. In this study, we worked with state and federal agencies and forest industry to implement disturbance treatments in forest stands at six widely-spaced study areas in the Appalachian Mountains. We used three different timber harvesting treatments to examine the variation and scale (from territory to nest-site) at which Cerulean Warblers select and use structural and floristic habitat features. We then compared habitat decisions to nest survival to assess the adaptiveness of the behavior. Selection for structural habitat features patterns differed substantially across study areas, especially at the territory scale. Male cerulean warblers at two study areas (the more-fragmented landscapes) selected micro-habitat features that reflected more closed-canopy, undisturbed forest conditions: relatively high basal area and overstory canopy cover. Males at other study areas preferred features, such as decreased basal area and increased understory cover, which were impacted positively by disturbance. Selection by females at the nest-patch and nest-site scale was more consistent across study areas, with females selecting for increased tree sizes, decreased basal area, decreased midstory cover, and increased understory cover, and similar floristic components. Preferred nest trees included white oak (*Quercus alba*), cucumber magnolia (*Magnolia acuminata*), and sugar maple (*Acer saccharum*), whereas northern red oak (*Quercus rubra*) and red maple (*A. rubrum*) were avoided. The apparent adaptiveness (measured by nest survival) of habitat selection decisions varied with study area. Nest selection behavior was maladaptive at three study areas and neutral at three, whereas territory selection was adaptive at two study areas, maladaptive at two, and neutral at two. Consequently, conservation strategies for Cerulean Warblers should be regionally-specific and should address both floristic and structural habitat characteristics. Care should also be taken to minimize the creation of maladaptive habitat that may have negative population consequences.

INTRODUCTION

Uncovering patterns in the process of habitat selection by avian species has long been a central goal of ornithological research (MacArthur 1962, Fretwell 1972, Cody 1985). Habitat selection studies, however, are often limited because they cover relatively small geographic areas and fail to examine habitat selection at multiple scales (Jones 2001). This limited scope can be problematic because patterns of habitat selection are often assumed to be fixed, while in reality they may apply only at specific scales and patterns may differ over large geographic areas (Whittingham et al. 2007, Fortin et al. 2008, Bamford et al. 2009). These inconsistencies are particularly important when studying species of conservation concern because extrapolation of habitat associations to other scales or regions may result in inappropriate conservation strategies. Thus, large-scale, replicated studies with experimental habitat manipulation are necessary to better inform managers on strategies to conserve high priority avian species (Donovan et al. 2002).

The Cerulean Warbler (*Setophaga cerulea*) is an example of a species in which a lack of congruency in habitat selection may be critical. Cerulean Warblers are among the fastest declining passerines in North America (Ziolkowski et al. 2010). Populations of this Nearctic-Neotropical migrant songbird declined by 3.2% per year from 1966 to 2003; this trend worsened to -4.6%/yr from 2003–2008 (Ziolkowski et al. 2010). Because of these sharp declines, Cerulean

Warblers are designated a “first-priority” species for conservation action by the U.S. Fish and Wildlife Service and Partners in Flight (U.S. Fish and Wildlife Service 2008) and “vulnerable” to extinction by BirdLife International (BirdLife International 2010). Cerulean Warbler habitat selection is known to vary substantially across the breeding range in the deciduous forests of the eastern United States. For example, at the range-wide scale, habitat selection is bi-modal. Ceruleans select bottomland riparian forests in areas such as the Mississippi Alluvial Valley while using high elevation forests along ridgetops and upper slopes in the Appalachian Mountains (Hamel 2000). However, within the relatively homogenous Appalachian Mountain region, where >70% of the remaining population breeds (Hamel and Rosenberg 2007), information regarding habitat selection at finer scales (particularly at nest-site scale), regional variability, and the adaptive nature of the behavior of habitat selection is lacking.

Our knowledge of Cerulean Warbler micro-habitat associations in the Appalachian Mountains has changed greatly over just the past two decades. For over a century, ceruleans were thought to breed exclusively in mature deciduous forests with predominantly closed canopies and open understories (Wilson 1811, Lynch 1981, Robbins et al. 1992). A growing body of evidence, however, suggests that in the Appalachians, and other locations, ceruleans often occupy mature forest characterized by diverse canopy structure and disturbance (Oliarnyk and Robertson 1996, Hamel 2000, Bakermans and Rodewald 2009). These types of canopy conditions can occur naturally in the Appalachians, based on topography (e.g., steep slopes), and historically have been enhanced by disturbances such as fire, wind or ice storms, insect outbreaks, or natural tree senescence, particularly in old-growth forests (Lorimer 1980). Alternatively, similar conditions can be created by using forest management techniques such as partial timber harvesting or prescribed burning (Long 2009). As many natural interior forest disturbances have become quite rare in the Appalachians (Lorimer and Frelich 1994), managed disturbances may create breeding habitat for Cerulean Warblers (Rodewald 2004, Bakermans and Rodewald 2009).

Avian habitat selection may occur in a hierarchical manner (Johnson 1980, Orians and Wittenberg 1991, Gaillard et al. 2010). Male Cerulean Warblers arrive on their breeding grounds before females (the range of which we be consider first-order selection, sensu Johnson 1980) and select and defend territories within the forest tract (i.e., second-order or territory selection). Within a week after males, females arrive and select either a male or a territory (or a combination of both), and within that territory, select a patch appropriate for raising a brood (i.e., third-order, or nest-patch, selection). Females, occasionally with help from males, then select a specific location in a single tree (within the nest patch) to build nests and raise broods (i.e., fourth-order selection). Evaluation of each of these scales is vital to understanding the overall behavioral process of habitat selection and to make successful management decisions on behalf of this species.

As habitat selection is, at least partly, behavioral in nature, it can be influenced by many factors including topography, vegetation structure (physiognomy) and composition (Holmes and Robinson 1981, Martin 1993, Deppe and Rotenberry 2008), conspecific attraction (Betts et al. 2008), interspecific competition (MacArthur 1958, Sherry and Holmes 1988), previous experience (Davis and Stamps 2004), predation risk (Martin 1993, Morosinotto et al. 2010), and food availability (Whittingham et al. 2006). While each of these factors may play a role in the process of habitat selection by Cerulean Warblers, vegetation structure and composition (hereafter, floristics) are the most amenable variables for management (MacArthur 1962, Wiens and Rotenberry 1982, Scott et al. 2002).

Although understanding the environmental features responsible for habitat selection is important, how habitat selection behaviors influence fitness should also be evaluated. If birds select breeding habitats via natural selection, birds that breed in the most preferred habitats should experience increased fitness (Williams and Nichols 1984). In anthropogenically-modified habitats, however, maladaptive habitat selection has been documented in many taxa (Battin 2004). Because habitat selection can be maladaptive, it is important to incorporate fitness components (survival, reproductive output, or both) in studies of habitat selection (Jones 2001). In avian species, components of fecundity such as nest success and the number of young produced are also important component measures of fitness that can be estimated accurately and then compared with habitat selection patterns to determine adaptiveness.

The goals of this study were threefold: (i) In experimentally-disturbed forests of the Appalachian Mountains, we investigated which structural and floristic habitat features influence habitat selection of Cerulean Warblers at multiple scales, (ii) we evaluated how habitat selection varied across the core of their range, and (iii) we evaluated how habitat features influenced reproductive success and assessed adaptiveness of habitat decisions. The information gained in this study is important to improve our ability to make appropriate local and regional management decisions for Cerulean Warbler conservation.

METHODS

Study areas

The study was conducted during the breeding seasons of 2008–2010 at six widely-spaced study areas in the Appalachian Mountains, all within the Central Hardwoods' mixed-mesophytic forest region (Fralish 2003), that corresponds to the core of the Cerulean Warbler range (Figure 2.1). These study areas were: Royal Blue Wildlife Management Area, TN (RB), Sundquist Wildlife

Management Area, TN (SQ), Raccoon Ecological Management Area, OH (REMA), Daniel Boone National Forest, KY (DB), Lewis Wetzel Wildlife Management Area, WV (LW), and Wyoming County Forest, WV (WYO), a large, privately-owned forest tract. We selected study areas based on the presence of Cerulean Warbler breeding populations and the potential to implement partial timber harvests. All study areas were embedded within a matrix of mature forest; mean percent forest cover within 10 km of the study area center was 83 ± 2.8% SE (range = 74–95, 2001 NLCD). Mean elevation was 550 ± 80 m (range = 250–850 m). Plant composition differed slightly among study areas, but common overstory tree species included tulip poplar (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), various hickories (*Carya* spp.), and white and chestnut oak (*Q. alba, Q. montana*). Common avian conspecifics included American Redstart (*S. ruticilla*), Black-throated Green Warbler (*S. virens*), Blackburnian Warbler (*S. fusca*), Red-eyed Vireo (*Vireo olivaceous*), and Scarlet Tanager (*Piranga olivacea*). Likely nest predators included Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), *Accipiter* spp., Eastern Chipmunk (*Tamias striatus*), Flying Squirrel (*Glaucomys volans* and *sabrinus*), Gray Squirrel (*Sciurus carolinensis*), and Black Rat Snake (*Elaphe obsoleta*). Brown-headed Cowbirds (*Molothrus ater*), which are often brood parasites of ceruleans, were uncommon but present at all study areas.

Habitat manipulations

We worked with state and federal agencies and forest industry to implement canopy disturbances of varying intensities on four stands (replicated at each of the six study areas) using commercial harvesting techniques. These manipulations were designed to emulate natural processes that spanned the range of potential mature forest disruptions while also representing common silvicultural practices of the region. At each study area, three 10-ha stands were harvested to meet pre-determined ranges of residual basal area and were broadly designated as light (or least intense disturbance), intermediate, and heavy (or most intense disturbance). In addition, we monitored ceruleans in 50-ha of undisturbed forest, which included a 20-ha control plot and six 5-ha buffers on either side of harvests, for a total coverage area of 80-ha at each study area. Light harvests mimicked mature forests disturbed by numerous small treefall gaps (typical of those caused by tree senescence, wind, etc.) and were harvested using traditional single-tree selection methods. We reduced basal area (BA) and overstory canopy cover on these stands by approximately 20% (residual BA = 21.1 ± 1.2 m^2/ha; residual CC = 60.9 ± 5.5%). Intermediate harvests mimicked more severe natural disturbances such as fire, blow-downs, or larger tree fall gaps; we reduced BA and CC by approximately 40% (residual BA = 14.1 ± 1.2 m^2/ha; residual CC = 45.5 ± 6.4%). Heavy harvests emulated even more severe natural disturbances such as large blow-downs, ice-storms, landslides, or more intense fire; we reduced BA and CC by 75% (residual BA = 6.5 ± 1.1 m^2/ha; residual CC = 18.2 ± 4.3%). We removed all understory and midstory stems >5 cm DBH on the intermediate and heavy harvests. We left control plots undisturbed throughout the life of the study (BA = 27.7 ± 0.7 m^2/ha; CC = 73.2 ± 5.2%). Overstory species composition was largely unchanged by the harvests and residual stands on the intermediate and heavy treatments were comprised of dominant and co-dominant trees. While we refer to harvest designations for explanatory purposes here, we were not interested in the response to the harvests per se, but rather in identifying relationships with specific habitat features. Therefore, hereafter we refer only to the continuous habitat variables themselves which capture more variation than categorical designations, and we do not refer to these harvests by name again. Plots were located on north or east-facing slopes to maximize cerulean presence (Buehler et al. 2006, Wood et al. 2006) and to control for potential interactions between aspect and behavioral response. Harvesting was performed in the fall of 2006 and spring of 2007, >1 year before we began collecting data, reducing the potential impacts of site fidelity on habitat selection patterns and allowing treatments to initiate vegetative response.

Territory delineation

We used the combined input from three methods to locate and delineate territories selected by male Cerulean Warblers. First, we spot-mapped each stand on eight mornings between 15 May and 15 June (2008–2010), during which we recorded locations of singing males and other territorial behaviors (Bibby et al. 2000). Second, we searched intensively for nests on all plots between late April and early July of each year and attempted to find all nests. Finally, we banded 122 males at five study areas (RB, SQ, LW, WYO, and REMA) using mist nets, a male Cerulean Warbler decoy, and territorial song playback equipment. Each male captured was fitted with a unique combination of color bands, which made it possible to distinguish among individuals in the field.

Nest searching and monitoring reproductive success

During each breeding season, we searched for nests between late April and late June. We used behavioral cues of females during building and incubation, and to a lesser extent male vocalizations and behavior, to locate the majority of nests. Because we were more efficient at locating nests on harvested stands (females and nests were easier to detect), we stratified our search efforts in an attempt to locate an equal proportion of nests on each treatment. We were unable to find all nests, however we believe our stratified search effort yielded a similar proportion of nests in each harvest type (we found nests for approximately 60% of all territories across all study areas). And as we used female behavior to lead us to nests, we believe our sample of nests is representative of the population and not biased by visibility. We monitored nests every 1–3 d until fledging or confirmed nest failure occurred. From nestling day six until fledging, we monitored nests daily for >45 min to accurately determine nest fate. We used spotting scopes equipped with 20–60X magnification eyepieces to monitor nests after hatching (the average nest height was approximately 19 m). We were unable to examine the contents of nests and we therefore only considered nests ‘active’ if we observed the female incubating, as has been standard in Cerulean Warbler breeding studies (D.A. Buehler, *personal communication*). We considered any nest that fledged > 1 Cerulean Warbler young to be successful.

Habitat measurements

We measured habitat characteristics at three point locations: random (R), territory (T), and nest (N) points. Random points provided us with a measure of overall habitat availability from which males selected territories (second-order, or territory selection). We established 80 random points/study area/year (using ArcGIS 9.2, ESRI Products, Redlands, CA), stratified by treatment so that we included 10 points/10-ha harvest type, 10 points/10-ha buffer, and 20 points/20-ha control plot. Because our study areas were all within deciduous forest with appropriate topography, elevation, and forest type, we considered all areas on our plots to be available for selection by male Cerulean Warblers. We placed territory points at either (a) a location of increased male foraging activity or, if this information was not available, (b) at the geographic center of each mapped territory. We established nest points directly under each nest and recorded nest-patch (third-order selection) and nest-site (fourth-order) measurements from this point. At all three point types, we measured habitat variables that we believed were important proximate factors for habitat selection at one or more spatial scale(s), based on previous literature and our understanding of Cerulean Warbler ecology. These variables included: slope (degrees), aspect (transformed following Beers et al. 1966), BA (m^2/ha), diameter at breast height (DBH) of all trees >10 cm within basal area prism plot (cm), distance (m) to nearest natural or artificial canopy gap within 100 m, overstory canopy height (m), and understory (0.5–3 m), midstory (3–12 m), and overstory canopy cover (>18 m). We also identified the species (or species group) of all trees within the BA prism plot. We measured slope and canopy height using a clinometer and BA using a 2.5× factor metric prism. We took canopy cover readings within a 0.04-ha area (situated around a point center) with an ocular tube at 21 points in 4 cardinal directions. At each nest point, we also measured nest-site specific variables: nest tree DBH (cm), nest tree height (m), nest height (m), distance from nest to bole and outer edge of tree (m), and distance from nest to top of crown (m).

Analytical methods: habitat selection

We used MANOVA to test for significant multivariate habitat differences between: (1) random and territory points (for territory selection) and (2) territory and nest-patch points (for nest-patch selection). We included the 10 habitat variables that we chose *a priori*. The first eight variables were related to physiognomy: average DBH of trees (in prism plot), maximum DBH of trees (in prism plot), BA, average canopy height, distance to nearest canopy gap, and understory, midstory, and overstory cover. Two variables were related to topography: slope and Beers aspect. We examined data for univariate and multivariate normality, equality of covariances, and collinearity. We arcsin-square root transformed all canopy cover proportions and log-transformed distance to nearest gap. To calculate the log of distances of zero we added 0.5 m. After transformations, we still detected minor departures from multivariate normality and heteroscedasticity (Box's M Test, $P < 0.001$), so we evaluated significance using Pillai's Trace statistic, which is robust to violations of assumptions (Scheiner 2001). We found little evidence of collinearity among variables, except between maximum and average DBH (All Pearson's $r < 0.5$). We first performed a MANOVA in which we treated point type, study area, and point type x study area as fixed effects. We found a strong point type x study area interaction (*Pillai's trace* = 0.16, df =100 and 28340, $P < 0.0001$) and, therefore, we analyzed each study area independently using the same approach; we also included year as a random effect at each area. If we found significance in a MANOVA, we subsequently performed univariate ANOVAs to identify sources of variation. We considered $P < 0.05$ as indication that selection for a habitat variable occurred, but recognize that multiple tests could result in inflated type I error rates, so we also evaluated significance after controlling type I error rate at 0.05 using the Dunn-Sidak method (Gotelli and Ellison 2004).

In addition to MANOVA, we evaluated the consistency of habitat selection across our study areas using a meta-analysis approach. We calculated raw mean differences (*D*) across study areas between point types for each variable at two orders of selection (territory: R vs. T, and nest patch: T vs. N). As the control in the calculation, we used the point type that provided the measure of habitat availability (random points for territory selection and territory points for nest-patch selection). Thus, a positive *D* indicated selection for greater values of a habitat feature and a negative *D* indicated selection for lesser values of a feature. We constructed confidence intervals around the average *D* using a random effects model because we assumed effects to be heterogeneous across study areas, a likely scenario in ecological research (Gurevitch and Hedges 2001). We considered *D* to be significantly different from zero if the 95% confidence intervals (CI) did not include 0.

Regional variation in habitat characteristics

In addition to evaluating habitat selection (i.e., the disproportionate use of habitat features relative to availability), we also used MANOVA to assess the variability of territory, nest-patch, and nest-site habitat features used (without regards to availability) by male and female ceruleans across our six study areas. We examined data at each scale for univariate and multivariate normality and equality of covariances. For features at territory and nest patches, we arcsin-square root transformed all canopy cover proportions and log-transformed distance to nearest gap to address non-normality. For nest-site characteristics, both assumptions were met. We included year as a random effect and evaluated significance using Pillai's Trace statistic for territory and nest-patch characteristics and Wilk's λ for nest-site characteristics. Subsequent to finding significant differences in the MANOVA, we performed univariate ANOVAs and considered geographic differences to exist when $P < 0.05$, after adjusting for multiple comparisons using the Dunn-Sidak method where k = 10 for territory and nest-patch variables ($\alpha = 0.0052$) and 5 for nest-site variables ($\alpha = 0.01$).

Selection for floristics

We assessed multi-scale selection for tree species, or tree groups in the case of hickories (*Carya* spp.) and the red oak group (subgenus Erythrobalanus), at each individual study area and all areas combined by comparing multinomial confidence intervals (CI). We only included tree species (or groups) that made up > 4% of available trees (derived from random points) or > 4% of nest trees. Species that comprised the remainder of trees were combined in a group designated as "other". The number of tree species or groups that we included varied by study area and ranged from 8 to 11. We compared tree composition at random points to tree composition at territory points (territory selection), and territories to nest patches (nest-patch selection) and nest trees (nest-site selection) by constructing and comparing CI calculated using the Goodman method for deriving multinomial CI, a method which controls the type I family-wise error rate (May and Johnson 1997). When CI did not overlap (95% CI for all study areas combined, 90% for individual areas) at the respective scale of selection, we considered selection to have occurred. We used 90% CI for individual study areas because the Goodman method is sensitive to sample size, which was relatively low for nest trees at some study areas. We found 90% CI for tree species at random points to overlap across all years (at all study areas and overall) and therefore we averaged annual random point CI to estimate availability. For territory, nest patch, and nest tree, we pooled trees across years. We performed all habitat selection analyses using NCSS (Version 7.1.19, Kaysville, UT) and SAS (Version 9.2, SAS Institute, Cary, NC) software. For ease of interpretation, we report untransformed data in all text and tables and means ± 1 SE unless otherwise noted.

Nest survival

We analyzed daily nest survival rates (DSR) of 410 Cerulean Warbler nests (6,384 nest exposure days) by comparing logistic exposure models in Program MARK to evaluate factors most related to daily nest survival. This method uses a generalized linear model with binomial distribution for each interval (nest fate = 0 if successful, 1 if failed) in relation to covariates that may be related to nest survival. The exposure method of estimating nest survival is preferable to simply calculating apparent nest success (# of successful nests/total nests found), because, as Mayfield (1961) first noted, nests that fail early in the nesting cycle are less likely to be discovered, so apparent nest success will almost always be biased high.

To assess the adaptiveness of habitat selection and to limit the number of models evaluated, we applied a hierarchical approach to modeling nest survival based on *a priori* hypotheses we derived from our nest-site selection results (Dinsmore et al. 2002). We used corrected Akaike's information criterion (AIC_c) to compare candidate model fit. Habitat selection differed among study areas, so we analyzed the association of covariates with DSR at each study area independently. At each study area, we developed three suites of models; after analyzing each level, we carried all models that had a ΔAIC_c value < 2 over to the next suite of models. Our first suite included univariate models of habitat covariates that were significant in our analysis of territory selection (study area-specific). Our second suite included univariate models which incorporated covariates that were significant at the scale of nest-patch selection, and our third suite included our five nest-site covariates (of which we did not analyze selection) and up to two covariates representing nest tree species that were selected for or against. In this final suite, we also included a null model (constant survival) and a saturated additive model which included all individual covariates with $\Delta AIC_c < 2$. The final number of candidate models w/ $\Delta AIC_c < 2$ varied by study area and ranged from 1 to 8. We assessed adaptiveness of habitat selection by comparing the sign of the slope of each univariate nest-survival model in the final suite (β coefficient) with the direction of habitat selection for that variable (at the respective scale). If the sign of the slope and direction of habitat selection were consistent (e.g., a positive association for selection and a positive association with DSR), we considered habitat selection adaptive. If the signs were opposing (e.g., a negative association for selection but a positive association with DSR), we considered the behavior maladaptive. We used raw covariate values because standardization did not affect numerical optimization (Rotella 2007).

RESULTS

Territory selection: habitat structure

We measured habitat characteristics within 936 territories across all study areas from 2008–2010; habitat measurements pooled across study areas are summarized in Table 2.1. Multivariate habitat selection occurred at the territory scale at all six of our study areas (*Pillai's Trace*, all $P < 0.05$). All habitat features measured influenced selection at one or more study areas (Table 2.2). Selected habitat features differed among study areas, as did the direction of selection. Four variables (average DBH, basal area, overstory canopy cover, and canopy height) were *positively* related to cerulean habitat selection at one or more study areas but *negatively* related to habitat selection at other study areas (even after Dunn-Sidak adjustments). Territories were characterized by large-diameter trees at four study areas (RB, REMA, LW, and WYO), but at SQ, average DBH of trees at territory points was lesser than DBH at random points (All $P < 0.0052$). Territories at RB and SQ had lesser basal area than at random points, whereas territories at DB and REMA had greater basal area than random points. At three study areas (DB, REMA, and LW), territories had greater overstory canopy cover than at random points, but at SQ, the reverse pattern existed. At three study areas (REMA, LW, and WYO), territories had trees taller than at random points, whereas at SQ males selected territories with lower canopy heights than canopy heights at random points. The males at REMA and SQ selected habitat characteristics in contradictory manners more often than any other pair of study areas, with opposing selection patterns for all four variables. Males at REMA and DB and at RB and LW, on the other hand, selected territory characteristics more similarly than any other pairs of study areas, with consistent selection for three variables. At REMA and DB, territory selection was positive for basal area, Beers aspect, and overstory canopy cover. At RB and LW, territory selection was positive for average DBH, and negative for mid-story canopy cover and distance to the nearest gap.

Our meta-analysis showed a relationship between two variables and territory selection (Table 2.3). Beers aspect had a positive association (*D* = 0.100, 95% CI= 0.0137 to 0.186) and distance to nearest gap had a negative association (*D* = -8.19 m, 95% CI = -12.400 to -3.979) with territory selection.

Nest-patch selection: habitat structure

We found 479 nests from 2008–2010; pooled nest-patch measurements are summarized in Table 2.1. Female Cerulean Warblers demonstrated multivariate selection for habitat structure at the scale of nest patch at all study areas except for WYO (*Pillai's Trace*, all $P < 0.05$). The habitat features selected for differed among study areas, but the direction of the habitat associations differed for only one feature: canopy height (Table 2.2). Females chose nest patches with higher canopies (than available territory points) at DB and SQ, whereas at REMA and LW nest patches with lower canopies were selected for.

Our meta-analysis showed nest-patch selection to be less variable than territory selection. Four variables were associated with nest-patch selection across study areas: average DBH, basal area, midstory canopy cover, and understory canopy cover (Table 2.3). Average DBH had a positive association (*D* = 1.41 cm, 95% CI = 0.442 to 2.37), basal area had a negative association (*D* = -1.56 m^2/ha, 95% CI = -2.69 to -0.42), midstory canopy cover had a negative association (*D* = -0.047, 95% CI = -0.090 to -0.0031), and understory canopy cover had a positive association (*D* = 0.032, 95% CI = 0.0060 to 0.057).

Regional variation of habitat characteristics

Without accounting for availability, habitat characteristics of territories varied among study areas (*Pillai's Trace* = 1.06, F = 24.71, df = 50 and 4615, $P < 0.0001$) and all individual habitat features differed significantly (all $P < 0.0001$, Table 2.2). We refer only to the extremes of each habitat characteristic here. Males at SQ occupied territories consisting of the smallest diameter trees (DBH), whereas males at LW occupied territories consisting of the largest trees (+28%, Table 2.2). Males at WYO occupied territories with the lowest basal area, whereas males at REMA occupied territories with the greatest basal area (+35%). Males at DB occupied territories with the lowest understory component, whereas males at SQ occupied territories with greatest understory component (+216%). Males at LW occupied territories with the lowest midstory component, whereas males at SQ occupied territories with greatest midstory component (+59%). Males at WYO occupied territories with the lowest overstory component, whereas males at SQ occupied territories with greatest overstory component (+29%). Males at LW occupied territories closest to a canopy gap, whereas males at REMA occupied territories furthest from a canopy gap (+167%). Males at REMA occupied territories with the shortest canopy, whereas males at WYO occupied territories with the highest canopy (+13%). Males at REMA occupied territories on the most gradual slopes, whereas at males at WYO occupied territories on the steepest slopes (+88%). Males at REMA occupied territories on the least productive slopes, whereas males at SQ occupied the most productive slopes (Beers aspect increased by 48%).

Characteristics of nest patches also varied among study areas (*Pillai's Trace* = 1.25, F = 15.51, df = 50 and 2335, $P < 0.0001$) and all individual habitat features differed significantly (all $P < 0.0001$, Table 2.2). Females at SQ used nest patches composed of the smallest trees (DBH), whereas females at LW used nest patches composed of the largest trees (+23%, Table 2.2).

Females at WYO used nest patches with the lowest basal area, whereas females at REMA used nest patches with the greatest basal area (+58%). Females at DB used nest patches with the lowest understory component, whereas females at RB and SQ used nest patches with the greatest understory component (+211%). Females at LW used nest patches with the lowest midstory component, whereas at females at SQ used nest patches with the greatest midstory component (+76%). Females at DB used nest patches with the lowest overstory component, whereas females at RB used nest patches with greatest overstory component (+59%). Females at LW used nest patches that were closest to a canopy gap, whereas females at REMA used nest patches that were furthest from a gap (+1197%). And females at LW used nest patches composed of the shortest canopy, whereas females at RB used nest patches with the tallest canopy (+22%). Females at REMA used nest patches located on the most gradual slopes, whereas females at WYO used nest patches located on the steepest slopes (+76%). Females at LW used nest patches on the least productive slopes, whereas females at RB used nest patches on the most productive slopes (Beers aspect increased by 69%).

Characteristics of nest sites varied among study areas (*Wilk's* $\lambda = 0.67$, $F = 6.40$, df = 30 and 1874, $P < 0.0001$). Nest-tree DBH and distance from bole to nest did not differ regionally ($P > 0.05$), but the other three characteristics all differed ($P < 0.003$; Table 2.4). Females at DB placed their nests closest to the ground, whereas females at SQ placed their nests at the highest location in trees (+26%, Table 2.4). Females at REMA placed their nests closest to the top and horizontal edge of the tree crown, whereas at WYO females placed their nest more than twice as far from the top, and at RB females placed their nests 40% further from the horizontal edge of the crown.

Floristics

Tree species composition at territory points varied little when compared with composition at random points. When we pooled all study areas, species composition in territories differed from random points in that red maples were selected against (avoided) and sugar maples were selected for (preferred, Figure 2.2). At individual study areas, ash spp. (*Fraxinus* spp.) and chestnut oaks were avoided at one area each, red oaks were preferred at one area, and tulip poplars were preferred at one area and avoided at another (Table 2.5). At nest patches, white oaks were preferred and sugar maples were avoided when all study areas were combined (Figure 2.2). At two study areas, tulip poplars were more common in nest patches than at territory points (Table 2.5).

White oaks, sugar maples, and cucumber magnolias (*Magnolia acuminata*) were all preferred as nest trees (used more often than expected by availability in territories), whereas red oaks and red maples were avoided when all study areas were combined (Figure 2.2). At individual study areas, tulip poplars were used more often than expected by availability at one area and black cherries (*Prunus serotina*) were used less than expected at one area (Table 2.5).

Influence of habitat features on nest survival and adaptiveness of habitat selection

The habitat features that were related to daily nest survival and the adaptiveness of Cerulean Warbler habitat selection behavior differed by study area (Table 2.6). At three study areas, habitat selection behavior appeared mainly maladaptive; nest survival at RB, REMA, and DB areas was negatively related to the habitat characteristics selected by ceruleans at both the territory and nest scale. At RB, BA, average DBH, distance to gap, and midstory cover all negatively impacted DSR, indicating maladaptive behavior, however β-coefficient 95% CI did overlap 0. At REMA, the use of preferred white oak as a nest tree was negatively related to DSR and β-coefficient 95% CI did not overlap 0, indicating strong maladaptive behavior. At LW and SQ, territory selection behavior appeared to be adaptive (despite being opposite at the two study areas), as candidate models ($\Delta AIC_c < 2$) had coefficients with signs which matched the direction of territory selection for the variables involved, but β 95% CI overlapped 0. However, nest-patch selection behavior was maladaptive for these same characteristics at these study areas. At SQ, territory selection for overstory canopy cover, basal area, and average DBH was adaptive as these habitat features were related to DSR in the same direction as selection at the territory scale. At WYO, the only model with $\Delta AIC_c < 2$ included the distance to the edge of nest tree foliage, a nest-site feature which we did not test for habitat selection, so we were unable to determine if this habitat selection behavior was adaptive.

DISCUSSION

We assessed spatial variation of habitat selection patterns based on the disproportionate selection of structural and topographical habitat features and floristics by Cerulean Warblers at multiple scales across the Appalachian Mountains. In addition, we evaluated the adaptiveness of these habitat decisions; habitat preferences are assumed to be adaptive as long as they have some genetic basis (Jaenike and Holt 1991). Plastic behavioral responses to spatial heterogeneity can lead to inappropriate conservation strategies if fixed habitat selection is assumed. Habitat characteristics varied greatly across the region at all scales. When compared to availability, habitat selection of structural features by females at the scale of nest patch and site was more consistent than habitat selection by males at the territory scale. Habitat selection based on floristics occurred predominantly at the nest-site scale and was largely consistent across our study areas. Given the patterns of selection documented, Cerulean Warblers made several weakly maladaptive decisions when selecting habitat, particularly at the nest-patch and nest-site scale, but adaptiveness of their decisions was also regionally variable.

Territory selection

The variation detected at the territory scale suggests that habitat selection behavior by male Ceruleans is quite plastic. One possible explanation for this variability is that rather than simply relying on information provided by local, or micro-habitat, features, males may also use landscape information to make finer-scale decisions about territory selection. At REMA and DB, study areas located in the two most-fragmented, least-heavily forested landscapes (74 and 75% forest cover, respectively, within 10-km), males selected habitat characteristics normally associated with closed canopy, undisturbed mature forest: greater basal area and greater overstory cover. At other study areas, where surrounding forest cover was greater, attraction to habitat attributes enhanced by disturbance was more evident, with males selecting for territories with lower basal area, greater understory cover, and in closer proximity to canopy gaps (than available). These results suggest that landscape structure (with an unknown threshold of fragmentation or “patchiness”), may partly govern the decision strategies ceruleans use to select territories. At DB, apparent selection for features related to decreased canopy disturbance may have partially been a function of the availability of habitat features, as the overall forest at this study area was more open (see random points in Table 2.2). However, males at DB also occupied territories with the lowest understory cover component, a feature which is directly correlated with disturbance severity, further suggesting that males at this study area were selecting for relatively closed canopy conditions.

Regional flexibility in habitat decisions has been noted previously in several avian species. Bamford et al. (2009) showed that models of habitat associations of two vulture species were not transferable among six regions in southern Africa. And Nur et al. (2008) found that the influence of habitat variables on avian species' occupancy varied across several watersheds of the Sacramento and San Joaquin valleys of California.

Spatial variation in habitat selection strategies are ultimately influenced by differences in predation and brood parasitism, food resources, micro-climate, or interspecific competition among study areas. To evaluate the importance of these various factors at our study areas, we can compare environmental pressures at our two most disparate areas: SQ and REMA. The types of predators varied between these two study areas: Blue Jays were much more prevalent at REMA than at SQ, whereas raptors and flying squirrels were more prevalent at SQ (F.A. Newell and T.J. Boves, *unpublished data, personal observation*). Blue Jays are visual predators that threaten cerulean eggs and nestlings, and are likely better able to locate nests in the open canopy conditions that were avoided by ceruleans at REMA. In contrast, flying squirrels (which also threaten eggs and nestlings) and raptors (which threaten adults and juveniles) are more suited to undisturbed forest conditions that were avoided by Cerulean Warblers at SQ (Vanderwel et al. 2009). There was also likely an increased threat of Brown-headed Cowbird parasitism and landscape-scale, fragmentation-related predation at REMA as this study area was surrounded by agricultural lands (Young and Hutto 1999, Chalfoun et al. 2002). Although we found little evidence of actual brood parasitism (<1% of nests at REMA contained cowbird nestlings, 0% at SQ), the risk of parasitism at REMA may have prompted males to select territories in more concealed habitats (Hobson and Sealy 1989). Geographic differences in habitat selection can also be influenced by variation in interspecific competition and aggression (Martin and Martin 2001, Price and Kirkpatrick 2009). At REMA, Eastern Wood-Pewees were major antagonistic competitors whereas Black-throated Green Warblers were absent, while at SQ, Black-throated

Green Warblers were major competitors and wood-pewees were nearly absent (F. A. Newell, T. J. Boves, *unpublished data*). Additionally, wood-pewees preferred open canopy conditions that ceruleans avoided at REMA, whereas Black-throated Green Warblers preferred the closed-canopy conditions that ceruleans avoided at SQ (Newell 2010, T.J. Boves, *unpublished data*). Although anecdotal in nature, these observations suggest that spatial variation in competition may influence the patterns of habitat selection observed (MacArthur and Levins 1964, Sherry and Holmes 1988). Finally, micro-climate conditions did not appear to vary greatly between the two study areas and we cannot speculate about differences in food availability because it was not estimated.

Although variability among study areas was apparent, we observed some similarities in territory selection. Males, regardless of landscape context, selected territories closer to canopy openings than expected (based on availability), similar to previous studies (Oliarnyk and Robertson 1996, Bakermans and Rodewald 2009). Productive slopes were also preferred, another habitat feature often associated with Cerulean Warblers and appears to be among the most important features across their Appalachian range (Buehler et al. 2006, Wood et al. 2006). Although aspect is not likely the ultimate factor of interest for use by ceruleans, this topographical feature is often correlated with other important habitat attributes and may act as a cue for selection, especially early in the season when foliage expansion is limited. Preference for productive exposures may be related to food availability, tree growth and floristics, or micro-climate (or a combination of these factors). Slope aspect likely impacts arthropod (Tolbert 1975) and tree communities (Doolittle 1958). Trees on productive slopes also grow faster and larger (Fekedulegn et al. 2003) because of increased moisture and nutrient availability (Rosenberg et al.

1983). The climate profile of these slopes may also affect energy budgets and thermoregulation of adult and juvenile Cerulean Warblers.

Nest-patch and nest-site selection

At nest patch and nest site scales, habitat selection was strong for several structural and floristic components and variability among study sites was minimal. This lack of variation might be expected because nest-site choice is evolutionarily conservative in many avian species (Martin and Roper 1988, Martin 1993, but see Eggers et al. 2006, Lomáscolo et al. 2010). Overall, females chose nest patches with large, well-spaced trees, increased understory cover, decreased midstory cover, a large white oak component, and a decreased sugar maple component (when compared with available conditions at territory points). These conditions are generally found within, or near the edges of canopy disturbances in mature forests and where small-scale canopy disturbances have occurred in the past. In such conditions, basal area is reduced, understory vegetation has increased, and woody vegetation has not yet reached the midstory. Canopy disturbances promote regeneration of less shade-intolerant species, such as white oaks, and discourage growth of shade tolerant species such as sugar maples. From a behavioral perspective, incubating and brooding female ceruleans will often drop vertically from nests before flying horizontally, presumably to mislead predators as to their nest location (Jones and Robertson 2001, T. J. Boves, *personal observation*). This behavior may be an adaptation for nest sites characterized by less densely packed overstory trees and a sparse midstory.

At the nest-tree scale, females exhibited strong, consistent selection for floristic components with little variability among study areas. Females preferred white oaks, sugar maples, and cucumber magnolias and avoided red oaks and red maples as nest trees. This spatially consistent selection for nest-tree species suggests that fitness benefits have been historically linked to the use of these specific tree species in the Appalachians. In addition to the obvious management implications, the pattern of floristic selection was striking because of two unexpected patterns: (1) the avoidance of sugar maples at the nest patch, but preference for sugar maples at territories and as nest trees, and (2) the preference for white oaks and sugar maples, and avoidance of red oaks and red maples as nest trees. The inconsistency of selection for sugar maples at different scales is congruent with the concept of preference for a mosaic of disturbed and undisturbed mature forest habitat by ceruleans. As sugar maples are disturbance averse, shade-adapted trees, they can be out-competed in openings by oaks or other shade-intolerant species (Godman 1965, Trimble 1973). Sugar maples, however, can become dominant overstory trees in closed-canopy forests that have remained undisturbed for long periods of time (Godman 1965). If disturbances are localized and undisturbed forest is adjacent, conditions may exist in which sugar maples do not dominate but are still present in small numbers on protected micro-sites at the edge of canopy disruptions. Females may prefer sugar maples as nest trees because of their phenology and foliage profile. Leaf emergence occurs earlier on sugar maples than most potential nest tree species in the Appalachians (Lopez et al. 2008). Because of their high shade-tolerance, sugar maples produce leaves in thick bunches that may increase nest concealment and stabilize nests in windy conditions (T.J. Boves, *personal observation*). Finally, overstories dominated by sugar maples will often suppress midstory development, a habitat feature that is preferred by breeding females.

The conflicting selection of congeneric oak (white preferred vs. red avoided) and maple species (sugar preferred vs. red avoided) by females may be related to differences in bark morphology, foliage structure, or leaf chemistry. Mature sugar maples and white oaks have rougher, flakier bark on limbs and branches compared to their red oak and maple counterparts

(Blakeslee and Jarvis 1972). These characteristics may increase the stability of nests built in white oaks and sugar maples, particularly in adverse weather conditions. Sugar maples are more shade tolerant and therefore typically produce many more twigs and leaves than do red maples, further increasing the potential stability and concealment advantages for nests built in this species. Both of the preferred species produce leaves containing lower concentrations of tannins, which in turn affect the invertebrate herbivores that ceruleans rely on for food. Decreased chemical defense may help explain why white oaks harbor a greater abundance of insects in the summer than red oak species (Forkner et al. 2004). George (2009) found a similar pattern in a foraging study of ceruleans; white oaks were preferred while red oaks were avoided. Similar effects on herbivores have been observed for sugar and red maples, with red maples being less palatable to lepidopteran larvae such as forest tent caterpillars (Nicol et al. 1997). These plant-insect relationships may make the presence of white oaks and sugar maples attractive, as their relative abundance and proximity may reduce the area from which ceruleans need to search for prey. Interestingly, sugar maples are considered an “infrequent associate” with the white oak-black oak-northern red oak forest type (Type 52, Eyre 1980), suggesting that forests which support a combination of sugar maple and white oaks in close proximity are relatively rare.

Adaptiveness of Habitat Selection

The great variety of habitat features related to nest survival at our study areas may help explain why habitat selection patterns differed geographically. As birds are subjected to different pressures across their range, they may modify their habitat selection behavior appropriately to respond to the specific selective forces present at a location, assuming they have the genetic capacity to do so (Lima 2009). These forces could be related to predation, food availability, competition, or climate. Adaptive habitat selection (which we observed consistently only at SQ) would be expected if selective pressures associated with environmental cues from an ecologically relevant time period are still linked in a similar fashion. Maladaptive habitat selection behaviors (observed at RB, REMA, and DB) would be expected if environmental cues that were once coupled with fitness are no longer as tightly coupled. Nest-patch and nest-site selection were more maladaptive than territory selection, which would be predicted given the often conservative, and possibly less flexible, nature of nest-site selection. Even universally selected habitat features appeared to be maladaptive in some cases. At DB, increased Beers aspect (indicating more productive slopes), was related (albeit weakly) to a decrease in daily nest survival. This was the only study area where that pattern was evident, but it is unexpected to see a universal preference appear maladaptive at any study area. Additionally, at REMA nests placed in white oaks (consistently preferred nest tree) were more likely to fail.

Conservation and management implications

Our results provide evidence that topography, vegetation structure, and floristic composition are all important features for habitat selection by Cerulean Warblers in the Appalachian Mountains. In addition, our data suggest that a ‘one-size fits all’ management strategy across the Appalachians will likely be unsuccessful at sustaining Cerulean Warblers. Instead, land owners and managers will need to account for local conditions when managing for ceruleans, possibly related to landscape-scale land configuration. The paradox for conservation is that some contemporary habitat selection patterns appear to be maladaptive, at least in terms of nest survival. Therefore, if we choose to manipulate forests in a way that only considers producing features that are attractive to ceruleans, we may have unintended effects by creating habitat that is attractive, yet unable to sustain populations. Conversely, habitat features that may lead to nest survival might not be as attractive to ceruleans for territory establishment. It is possible that the negative impacts some habitat features appeared to have on reproduction may be temporary or offset by a positive impact on adult or post-fledgling survival, but we currently have no evidence to support these speculations. Our findings also highlight the importance of spatial replication in ecological studies. If this study was performed at a single study area, as is often the case, the results may have been assumed, incorrectly, to be transferrable to the entire breeding range of Cerulean Warblers.

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APPENDIX

Habitat variable	**R (*n* = 1437)**	**T (*n* = 931)**	**N (*n* = 480)**
Avg DBH (cm)	39.23 ± 0.26	41.50 ± 0.31	43.58 ± 0.43
Max DBH (cm)	62.90 ± 0.47	63.97 ± 0.50	65.07 ± 0.69
Basal area (m^2/ha)	22.04 ± 0.27	21.56 ± 0.32	20.69 ± 0.44
Understory canopy cover (%)	0.38 ± 0.01	0.39 ± 0.01	0.47 ± 0.01
Midstory canopy cover (%)	0.52 ± 0.01	0.47 ± 0.01	0.45 ± 0.01
Overstory canopy cover (%)	0.64 ± 0.01	0.66 ± 0.01	0.69 ± 0.01
Distance to gap (m)	21.20 ± 0.66	12.29 ± 0.49	14.18 ± 1.02
Canopy height (m)	28.02 ± 0.15	29.11 ± 0.19	29.54 ± 0.25
Slope (degrees)	23.14 ± 0.24	22.37 ± 0.31	23.18 ± 0.44
Beers aspect	1.31 ± 0.02	1.46 ± 0.02	1.46 ± 0.03

Table 2.1. Cerulean Warbler habitat measurements at random (R), territory (T) and nest patch (N) points pooled across six study areas in the Appalachian Mountains, 2008–2010.

	Royal Blue, TN (RB)			**Sundquist, TN (SQ)**			**REMA, OH (REMA)**		
Habitat variable	**R (*n* = 242)**	**T (*n* = 253)**	**N (*n* = 187)**	**R (*n* = 240)**	**T (*n* = 89)**	**N (*n* = 51)**	**R (*n* = 246)**	**T (*n* = 89)**	**N (*n* = 88)**
Avg DBH (cm)	41.65 ± 0.55	**44.47 ± 0.54 (++)**	**46.56 ± 0.69 (+)**	39.76 ± 0.47	**36.21 ± 0.92 (- -)**	37.80 ± 0.96	39.65 ± 0.51	**42.31 ± 0.84 (+)**	42.55 ± 0.79
Max DBH (cm)	66.31 ± 0.98	67.06 ± 0.96	68.30 ± 1.06	62.46 ± 0.99	**52.77 ± 1.56 (- -)**	54.69 ± 2.19	63.78 ± 0.96	66.78 ± 1.47	66.15 ± 1.31
Basal area (m^2/ha)	24.07 ± 0.61	**21.70 ± 0.64 (-)**	20.99 ± 0.77	24.51 ± 0.67	**20.26 ± 1.05 (- -)**	21.25 ± 1.51	22.55 ± 0.66	**25.99 ± 1.09 (++)**	25.06 ± 0.79
Understory canopy cover (%)	0.48 ± 0.02	**0.57 ± 0.02 (++)**	0.59 ± 0.02	0.54 ± 0.01	0.58 ± 0.03	0.59 ± 0.03	0.33 ± 0.02	0.34 ± 0.02	0.37 ± 0.03
Midstory canopy cover (%)	0.56 ± 0.02	**0.48 ± 0.02 (- -)**	**0.43 ± 0.02 (-)**	0.62 ± 0.02	0.65 ± 0.03	0.58 ± 0.04	0.48 ± 0.02	0.51 ± 0.03	**0.57 ± 0.03 (+)**
Overstory canopy cover (%)	0.77 ± 0.02	0.74 ± 0.02	0.78 ± 0.01	0.83 ± 0.02	**0.75 ± 0.03 (- -)**	0.75 ± 0.03	0.63 ± 0.02	**0.71 ± 0.03 (++)**	0.74 ± 0.02
Distance to gap (m)	19.68 ± 1.52	**13.53 ± 1.01 (- -)**	13.71 ± 1.36	20.40 ± 1.40	**9.03 ± 2.64 (-)**	10.46 ± 0.92	20.49 ± 1.60	20.49 ± 2.56	33.34 ± 3.62
Canopy height (m)	30.43 ± 0.29	30.67 ± 0.27	31.06 ± 0.32	30.68 ± 0.36	**28.92 ± 0.72 (-)**	**32.00 ± 0.92 (+)**	25.13 ± 0.20	**27.21 ± 0.38 (+)**	26.19 ± 0.32
Slope (degrees)	24.14 ± 0.45	23.34 ± 0.40	23.7 ± 0.50	24.10 ± 0.44	23.40 ± 0.88	24.92 ± 1.18	15.36 ± 0.56	16.79 ± 0.97	**18.58 ± 1.04 (+)**
Beers aspect	1.68 ± 0.03	1.68 ± 0.02	1.71 ± 0.03	1.70 ± 0.02	1.69 ± 0.05	1.55 ± 0.08 (-)	0.93 ± 0.05	1.14 ± 0.08 (+)	1.31 ± 0.07

Table 2.2. Cerulean Warbler habitat measurements at random (R), territory (T), and nest (N) points at six study areas in the Appalachians, 2008–2010. To evaluate habitat selection, we compared T with R for territory selection; N with T for nest-patch selection. Significance of point type (MANOVA, Pillai's Trace Statistic) was < 0.05 at all study areas (at both scales of selection, except for nest patch at WYO). Direction and significance of selection for individual variables is indicated by bold and + or -; + indicates selection for the variable was positive, - indicates selection for the variable was negative. Significance at α = 0.05 is indicated by a single + or -; significance at α = 0.0052 (following Dunn-Sidak adjustment) is indicated by ++ or - -. When assessing use only, all habitat characteristics differed among study areas at both the territory and nest-patch scale (ANOVA, All $P < 0.0001$).

Table 2.2 (cont'd)

	Daniel Boone, KY (DB)			**Lewis Wetzel, WV (LW)**			**Wyoming County, WV (WYO)**		
Habitat variable	**R (*n* = 238)**	**T (*n* = 231)**	**N (*n* = 48)**	**R (*n* = 237)**	**T (*n* = 193)**	**N (*n* = 63)**	**R (*n* = 234)**	**T (*n* = 76)**	**N (*n* = 43)**
Avg DBH (cm)	36.88 ± 0.67	36.90 ± 0.50	38.64 ± 1.26	43.35 ± 0.67	**46.31 ± 0.72 (++)**	47.80 ± 1.00	33.98 ± 0.76	**38.63 ± 0.92 (++)**	38.90 ± 1.51
Max DBH (cm)	57.80 ± 1.12	59.54 ± 0.89	59.57 ± 1.89	68.48 ± 1.23	69.83 ± 1.05	70.95 ± 1.91	58.44 ± 1.39	61.94 ± 1.54	58.62 ± 2.31
Basal area (m^2/ha)	18.93 ± 0.57	**22.47 ± 0.57 (++)**	20.36 ± 1.23	20.45 ± 0.67	19.64 ± 0.68	**16.82 ± 0.94 (-)**	21.63 ± 0.66	19.26 ± 0.91	**15.83 ± 1.08 (-)**
Understory canopy cover (%)	0.19 ± 0.01	0.18 ± 0.01	0.19 ± 0.03	0.34 ± 0.02	0.36 ± 0.02	0.42 ± 0.03	0.38 ± 0.01	0.39 ± 0.02	0.50 ± 0.04
Midstory canopy cover (%)	0.46 ± 0.02	0.43 ± 0.01	**0.37 ± 0.03 (-)**	0.49 ± 0.02	**0.41 ± 0.02 (-)**	**0.33 ± 0.03 (-)**	0.48 ± 0.01	0.50 ± 0.02	**0.40 ± 0.04 (- -)**
Overstory canopy cover (%)	0.51 ± 0.03	**0.62 ± 0.02 (++)**	**0.55 ± 0.01 (-)**	0.51 ± 0.02	**0.59 ± 0.02 (++)**	**0.53 ± 0.02 (-)**	0.57 ± 0.02	0.58 ± 0.03	0.49 ± 0.03
Distance to gap (m)	17.21 ± 1.49	13.40 ± 1.14	**8.55 ± 0.68 (- -)**	16.32 ± 1.29	**7.67 ± 0.87 (- -)**	**2.57 ± 0.56 (- -)**	32.91 ± 2.31	**9.23 ± 1.68 (- -)**	**3.60 ± 0.96 (-)**
Canopy height (m)	27.87 ± 0.84	27.85 ± 0.39	**30.28 ± 0.36 (++)**	26.39 ± 0.30	**28.88 ± 0.50 (++)**	**26.29 ± 0.72 (- -)**	27.61 ± 0.49	**30.86 ± 0.75 (++)**	30.77 ± 1.05
Slope (degrees)	22.16 ± 0.70	19.93 ± 0.62 (-)	20.21 ± 1.54	23.27 ± 0.38	22.66 ± 0.68	22.42 ± 1.15	30.18 ± 0.58	31.53 ± 1.46	32.74 ± 2.03
Beers aspect	1.22 ± 0.05	**1.44 ± 0.04 (++)**	1.50 ± 0.09	1.15 ± 0.04	**1.31 ± 0.45 (+)**	**1.01 ± 0.08 (- -)**	1.14 ± 0.04	1.24 ± 0.08	1.19 ± 0.11

Table 2.2. Cerulean Warbler habitat measurements at random (R), territory (T), and nest (N) points at six study areas in the Appalachians, 2008–2010. To evaluate habitat selection, we compared T with R for territory selection; N with T for nest-patch selection.

	Territory selection		**Nest-patch selection**	
Habitat variable	***D***	**95% CI**	***D***	**95% CI**
Avg DBH (cm)	1.55	[-0.66, 3.75]	**1.41**	**[0.44, 2.37]**
Max DBH (cm)	0.07	[-3.47, 3.63]	0.35	[-1.27, 1.97]
Basal area (m^2/ha)	-0.44	[-3.06, 2.18]	**-1.56**	**[-2.69, -0.42]**
Under CC (%)	0.024	[-0.0065, 0.055]	**0.032**	**[0.0060, 0.057]**
Mid CC (%)	-0.024	[-0.064, 0.016]	**-0.047**	**[-0.090, -0.0031]**
Over CC (%)	0.028	[-0.035, 0.091]	-0.018	[-0.063, 0.028]
Canopy ht (m)	1.016	[-0.24, 2.27]	0.28	[-1.11, 1.67]
Dist to gap (m)	**-8.19**	**[-12.40, -3.98]**	-1.27	[-4.91, 2.37]
Slope (°)	-0.47	[-1.41, 0.47]	0.58	[-0.33, 1.49]
Beers aspect	**0.10**	**[0.014, 0.19]**	-0.042	[-0.68, 0.08]

Table 2.3. Meta-analysis results of Cerulean Warbler habitat selection at six study areas in the Appalachian Mountains, 2008–2010. We report average D and 95% CI at two scales of selection: territory and nest-patch. Significant effects are indicated in bold.

		Nest tree DBH (cm)				**Nest height (m)**				**Dist to top of crown (m)**				**Dist to bole (m)**				**Dist to foliage edge (m)**			
Study area	**N**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**
DB	**48**	42.56	2.54	14.60	80.00	18.51	0.81	10.40	30.50	9.64	0.72	1.00	24.40	3.44	0.27	0.65	7.90	2.05	0.16	0.40	5.40
LW	**63**	43.92	1.89	10.10	85.30	18.80	0.76	6.10	32.54	9.67	0.70	0.40	22.00	3.90	0.30	0.50	12.00	2.25	0.17	0.40	6.00
RB	**187**	44.04	1.12	12.10	95.50	19.32	0.37	7.60	35.00	9.82	0.32	0.00	25.00	3.80	0.11	0.50	9.00	2.38	0.10	0.10	9.80
REMA	**87**	45.55	1.49	19.00	90.00	19.78	0.55	5.00	32.00	6.23	0.39	0.50	17.00	3.52	0.17	0.00	8.00	1.67	0.12	0.00	6.00
SQ	**51**	43.36	1.79	20.60	62.10	23.40	1.01	9.00	35.00	8.80	0.85	1.50	36.25	4.38	0.27	1.00	10.00	2.13	0.15	0.50	5.80
WYO	**43**	43.01	1.94	20.32	62.50	20.61	0.99	8.84	35.36	13.28	1.07	2.14	33.55	3.61	0.26	0.75	9.00	2.29	0.30	0.00	11.00
All	**479**	**43.99**	**0.67**	**10.10**	**95.50**	**19.80**	**0.26**	**5.00**	**35.36**	**9.33**	**0.24**	**0.00**	**36.25**	**3.77**	**0.08**	**0.00**	**12.00**	**2.17**	**0.06**	**0.00**	**11.00**

Table 2.4. Cerulean Warbler nest-site characteristics at six study areas in the Appalachian Mountains, 2008–2010. Nest-site locations varied among study areas (MANOVA, Wilk's λ=0.68, *P* < 0.0001) and nest height, distance to top of crown, and distance to foliage edge varied (ANOVA, All *P* < 0.003). We detected no difference in nest tree DBH and distance from nest to bole among sites (ANOVA, *P* > 0.05).

Territory	DB	REMA	RB	SQ	LW	WYO
Ash spp	**A**	x	x	x	x	x
Basswood	x	x	=	=	=	x
Black Cherry	x	x	=	x	x	x
Black Locust	x	x	x	=	x	x
Chestnut Oak	=	=	=	**A**	=	=
Cucumber Magnolia	x	x	=	x	x	=
Hickory spp	=	=	=	=	=	=
Red Maple	x	=	=	=	=	=
Red Oak Group	=	=	=	=	**P**	=
Sugar Maple	=	=	=	=	=	=
Tulip Poplar	**P**	=	**A**	=	=	=
White Oak	=	=	=	x	=	=
Other	=	=	=	=	=	=

Table 2.5. Multi-scale habitat selection in relation to floristic composition by Cerulean Warblers at six study areas in the Appalachian Mountains, 2008–10. Tree species (or tree groups) that made up >4% of either random or nest trees at a study area were included in analysis. Selection determination was based on comparison of 90% (individual study area) or 95% (all sites combined) Goodman multinomial CI between available and selected points (at each respective scale). 'A' indicates avoidance of a species, 'P' indicates preference for a species, '=' no selection for the species, and 'x' indicates that a species did not meet the proportional threshold at a study area.

Table 2.5 (cont'd)

Nest patch	**DB**	**REMA**	**RB**	**SQ**	**LW**	**WYO**
Ash spp	=	x	x	X	x	x
Basswood	x	x	=	=	=	x
Black Cherry	x	x	=	x	x	x
Black Locust	x	x	x	=	x	x
Chestnut Oak	=	=	=	=	=	=
Cucumber Magnolia	x	x	=	x	x	=
Hickory spp	=	=	=	=	=	=
Red Maple	x	=	=	=	=	=
Red Oak Group	=	=	=	=	=	=
Sugar Maple	=	=	=	=	**A**	=
Tulip Poplar	**P**	**P**	=	=	=	=
White Oak	=	=	=	x	**P**	=
Other	=	=	=	=	=	=

Table 2.5. Multi-scale habitat selection in relation to floristic composition by Cerulean Warblers at six study areas in the Appalachian Mountains, 2008–10.

Table 2.5 (cont'd)

Nest site	**DB**	**REMA**	**RB**	**SQ**	**LW**	**WYO**
Ash spp	=	x	x	x	x	x
Basswood	x	x	=	=	=	x
Black Cherry	x	x	**A**	x	x	x
Black Locust	x	x	x	=	x	x
Chestnut Oak	**=**	**=**	**=**	**=**	**=**	**=**
Cucumber Magnolia	x	x	**P**	x	x	**=**
Hickory spp	**=**	**=**	**A**	**=**	**=**	**=**
Red Maple	x	**=**	**=**	**=**	**=**	**=**
Red Oak Group	**A**	**A**	**A**	**=**	**=**	**=**
Sugar Maple	**=**	**=**	**P**	**=**	**=**	**=**
Tulip Poplar	**=**	**P**	**=**	**=**	**=**	**=**
White Oak	**P**	**P**	**P**	x	**P**	**=**
Other	**=**	**A**	**=**	**=**	**=**	**=**

Table 2.5. Multi-scale habitat selection in relation to floristic composition by Cerulean Warblers at six study areas in the Appalachian Mountains, 2008–10.

Study area	**Model**	**AICc**	**ΔAICc**	**k**	**β**	**Lower 95%**	**Upper 95%**	**Scale of selection**	**Selection adaptive?**
RB	**S(BA)**	489.52	0.00	1	0.020	-0.006	0.05	T	No
	S(Dist nest to crown)	489.65	0.13	2	0.044	-0.02	0.10		
	S(Dist to gap)	489.67	0.15	2	0.012	-0.006	0.03	T	No
	S(Null)	489.91	0.39	2					
	S(Avg DBH)	491.06	1.54	2	-0.01	-0.04	0.01	T	No
	S(Dist nest to foliage edge)	491.13	1.62	2	-0.08	-0.25	0.09		
	S(Mid cover)	491.40	1.89	2	0.35	-0.62	1.32	T, NP	No, No
	S(Nest ht)	491.51	1.99	2	-0.02	-0.07	0.03		
SQ	**S(Canopy ht)**	138.82	0.00	2	-0.06	0.14	0.02	T, NP	Yes, No
	S(Dist nest to foliage edge)	138.85	0.03	2	-0.32	-0.70	0.05		
	S(Nest ht)	138.98	0.17	2	-0.06	-0.14	0.02		
	S(Null)	139.25	0.43	1					
	S(Nest tree DBH)	139.55	0.73	2	-0.03	-0.07	0.01		
	S(Over cover)	139.60	0.78	2	-1.56	-4.11	0.99	T	Yes
	S(Avg DBH)	140.44	1.62	2	-0.03	-0.11	0.04	T	Yes
	S(BA)	140.45	1.63	2	-0.02	-0.08	0.03	T	Yes
LW	**S(Nest ht)**	256.42	0.00	2	0.059	-0.0001	0.12		
	S(Canopy ht)	257.64	1.22	2	0.048	-0.007	0.10	T, NP	Yes, No
WYO	**S(Dist nest to foliage edge)**	195.35	0.00	2	0.27	-0.02	0.56		
REMA	**S(Nest tree preferred)**	249.92	0.00	2	-0.90	-1.72	-0.07	NS	No
DB	**S(Aspect)**	186.40	0.00	2	-0.61	-1.38	0.16	T	No
	S(Null)	187.29	0.89	1					

Table 2.6. Final candidate models from Cerulean Warbler nest survival analysis at individual study areas in the Appalachian Mountains, 2008–2010. Only candidate models with substantial support ($\Delta AIC_c < 2$) are displayed. Beta (β) indicates direction of influence of a covariate on nest survival (e.g., + β indicates positive effect of covariate on nest survival). Scale of selection refers to the scale at which a habitat feature affected habitat selection (T = territory, NP = nest patch, NS = nest site). 'Adaptive selection' indicates if the direction of selection for the variable (at the respective scale of analysis) was consistent with the influence that the covariate had on nest survival (e.g., + for selection and + for survival was considered adaptive). Nest-site structural characteristics were not tested for selection so their adaptiveness was not evaluated

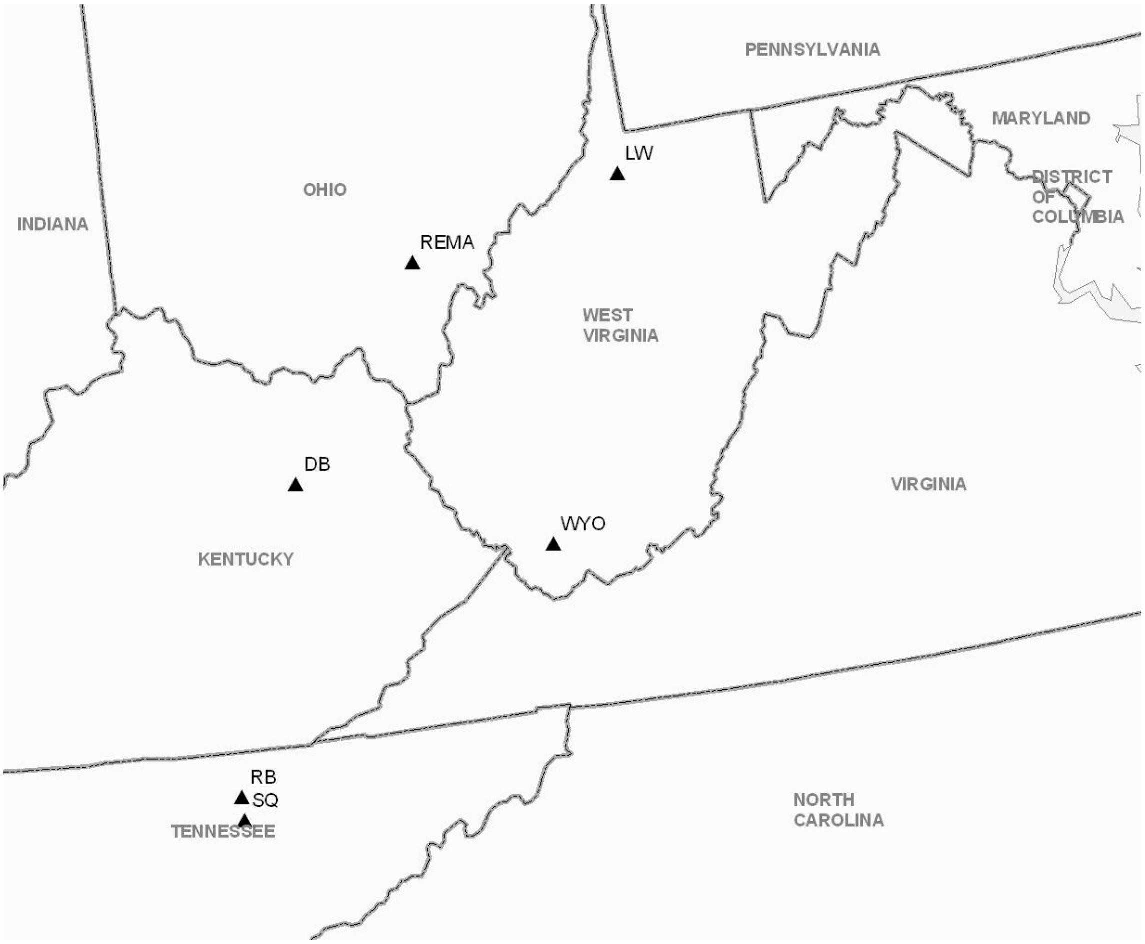

Figure 2.1. Locations of study areas across the Appalachian Mountains, all within the core of the Cerulean Warbler range.

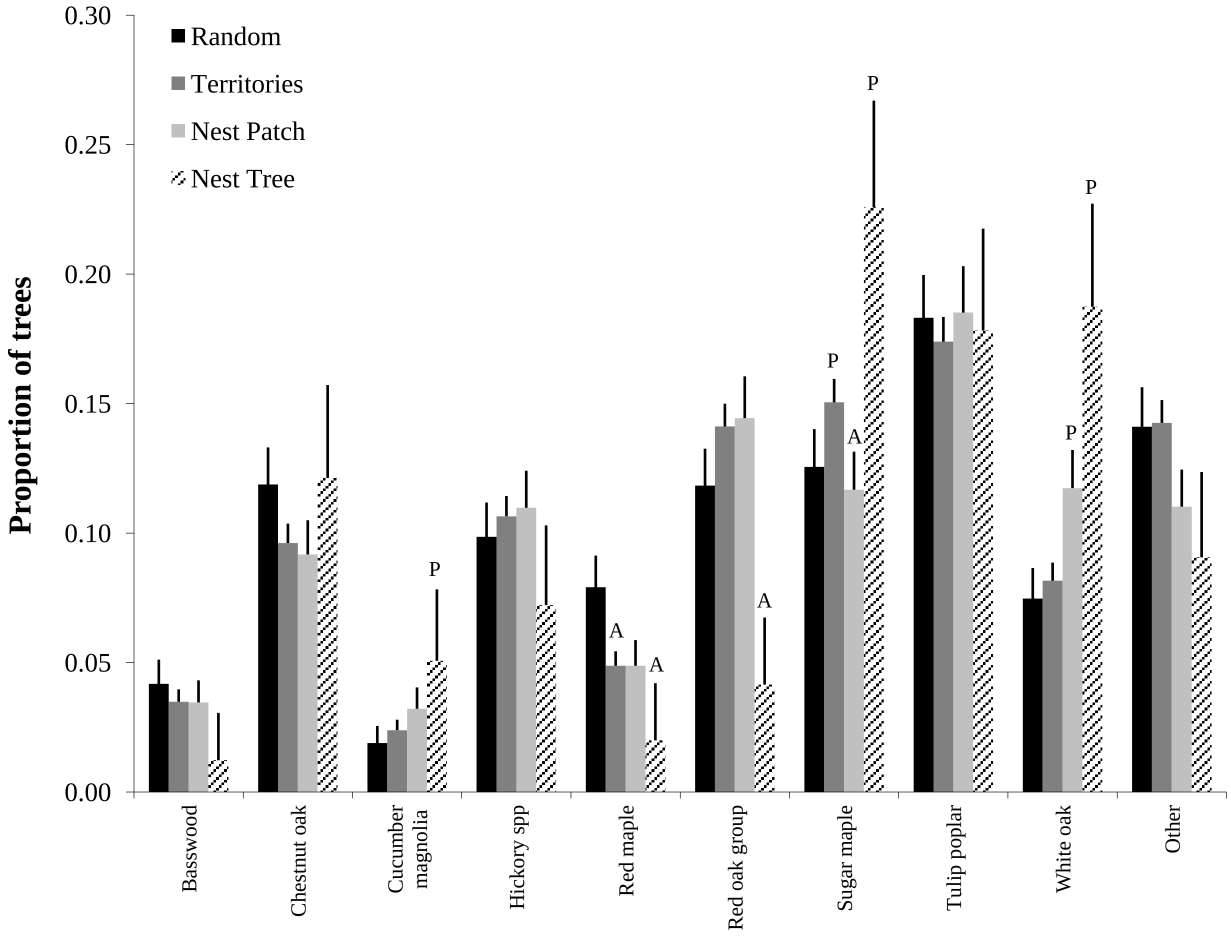

Figure 2.2. Multi-scale selection for tree species by Cerulean Warblers at all study areas (pooled) in the Appalachian Mountains, 2008–10. Red oak group includes northern red (*Quercus rubra*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oak, and hickory species include mockernut (*Carya tomentosa*), bitternut (*C. cordiformis*), pignut (*C. glabra*), and shellbark (*C. laciniosa*) hickory. Error bars represent Goodman 95% multinomial confidence intervals (Goodman 1965). Selection for tree species at respective scales was evaluated by comparing 95% CI of random points with territory points, territories with nest patches, and territories with nest trees. “P” indicates selection for a tree species (preference) and “A” indicates selection against (avoidance) at the representative scale of selection.

CHAPTER 3: INFORMATION CONTENT AND HABITAT CONTINGENCY OF MULTIPLE PLUMAGE ORNAMENTS IN A CANOPY-DWELLING SONGBIRD, THE CERULEAN WARBLER

Abstract. The honest indicator theory of sexual selection postulates that males display ornaments, such as colorful plumage in birds, to provide reliable information about individual quality (phenotypic or genotypic attributes related to fitness) during female mate choice and intrasexual competition. Multiple ornaments may convey different messages because they are produced by different metabolic mechanisms and/or because environmental heterogeneity may influence the magnitude and direction of the relationship between ornament expression and quality. In this study, we examined the information content of potential plumage ornaments of various metabolic origins in a population of free-living Cerulean Warblers, an obligate canopy-dwelling songbird. We also evaluated the impact of environmental heterogeneity on the honesty of plumage ornaments by assessing relationships between plumage and quality across a range of forest conditions. We caught and analyzed 55 male Cerulean Warblers (SY = 17, ASY = 38) and found that individuals displayed several plumage ornaments that signal phenotypic qualities likely related to survival and reproductive success. All four of the plumage ornaments we assessed signaled male age to different degrees, thereby supporting the redundant message hypothesis. After controlling for age, we found evidence to support the multiple messages hypothesis as well. Birds with more exaggerated tail white ornaments grew their tail feathers in at a faster rate (measured via ptilochronology). Individuals that displayed more exaggerated structural rump plumage provided more parental care (measured via provisioning rates) and they also had decreased body mass at time of capture. In addition, eumelanic breast band width was positively related to body mass, but only in moderately open forest habitats which supported high cerulean densities, supporting the hypothesis that melanin-based plumage ornaments signal adaptations to stressful conditions. Furthermore, we documented non-random spatial distribution

of eumelanic breast band and tail white; both were found in their most exaggerated form in moderately open forest habitat.

INTRODUCTION

The honest indicator theory of sexual selection postulates that males display ornaments, such as colorful plumage in birds, to provide reliable information about individual quality (phenotypic or genotypic attributes related to fitness, Wilson and Nussey 2010) during female mate choice and intrasexual competition (Andersson 1994, Hill and McGraw 2006). Rather than possessing just one signal, male birds may possess multiple plumage ornaments. Three main hypotheses have been proposed to explain this phenomenon (Møller and Pomiankowski 1993). First, each individual ornament may reveal different information about the signaler to the receiver (multiple message hypothesis). Second, multiple ornaments may all convey similar information about the signaler to receivers, and together provide a more complete expression of quality than any one ornament does alone (redundancy hypothesis). Third, some ornaments may not actually convey any useful information, but instead are simply inexpensive to produce and exist in populations only because of a preference for them by females or as a signal for species recognition (unreliable signal hypothesis).

Birds may convey multiple messages because of differential costs related to the type and elaboration of plumage ornaments that an individual displays. Costs may be intrinsic or extrinsic (Searcy and Nowicki 2005). Intrinsic costs relate to the fact that plumage ornaments may be produced by different metabolic processes that vary in their physiological cost to an individual. Alternatively, some plumage ornaments may be inexpensive to produce, but external factors (such as increased intraspecific competition or predation) may discourage cheating and enforce honesty (Maynard Smith and Harper 2003). Melanin pigmentation is responsible for the blacks, browns, and grays found widely in avian feathers, eyes, and skin (McGraw 2006). Unlike carotenoids, which vertebrates cannot synthesize and must obtain through diet, melanin pigments can be produced *de novo* and are often strongly controlled by genetic factors (Majerus 1998, McGraw 2006). For this reason, melanin-based ornaments may not act as honest signals of condition (see Jawor and Breitwisch 2003). However, limiting intrinsic costs associated with melanogenesis may be related to the acquisition and processing of limited metals, amino acids, and testosterone (McGraw 2008), and/or pleiotropic effects associated with development of the melanocortin system (Ducrest et al. 2008, Roulin and Ducrest 2011). Extrinsically, eumelanic ornaments are often displayed as bold patches, or ‘badges’ which are often related to social status and intraspecific competition, and may also help enforce honesty of these ornaments (Møller 1987, McGraw et al. 2003, Senar 2006). Previous investigations of the honesty and information content of melanin-based ornaments as signals of quality have had mixed results. Melanin ornaments have been shown to co-vary with quality traits such as body condition (Parker et al. 2003), immuno-competence (Roulin et al. 2000), and parental ability (Norris 1990) in various species, whereas other studies have found no relationship between melanin-based ornaments and measures of condition (McGraw and Hill 2000, Hill and McGraw 2003). In addition, melanic ornaments may co-vary with quality measures only under specific conditions (Roulin et al. 2008a, Roulin et al. 2008b, Roulin 2009).

Structural ornaments make up another class of plumage ornaments and include feather patches which are blue, purple, or iridescent (Prum 2006). These colors differ from pigment-based colors as they are produced not simply by the deposition of pigments in feathers, but by the scattering of long wavelengths and the reflection of shorter wavelengths within a matrix of keratin rods and air vacuoles located around a basal layer of melanin within feathers (Prum

2006). In empirical studies, the information content of structural colors has been found to overlap that of melanin (depending on the species), as they also have been reported to signal different aspects of quality for many species of birds including condition (Siefferman and Hill 2005), parental effort (Siefferman and Hill 2003), and immune response (Griggio et al. 2010b). The honesty of structural ornaments has also been questioned , because of what some contend to be a lack of experimental evidence documenting sufficient constraining costs related to the production of these ornaments (Prum 2010, Peters et al. 2011, but see Siefferman and Hill 2005 and 2007). However, there is still much to understand about the production and maintenance of the nanoscale structures responsible for these colors. Potential mechanisms for structural colors to honestly indicate quality exist, most promisingly intrinsically via the impacts of stress on feather production (Peters et al. 2011) or extrinsically via social costs (Rémy et al. 2010).

Achromatic, or white, feather patches represent a slightly different form of structural plumage ornaments. These achromatic plumage ornaments are produced by the incoherent scattering of all wavelengths from unpigmented feather keratin (Prum et al. 1999). Because these ornaments require no pigment and appear quite inexpensive to produce, intrinsic costs appear to be minimal. However, the honesty of achromatic ornaments could be maintained extrinsically by handicaps related to maintaining and displaying white feathers, such as increased susceptibility to feather breakage or abrasion (Griggio et al. 2010a), increased antagonistic interactions with other males (Qvarnström 1997), and increased exposure to predators and parasites (Gustafsson et al. 1994, Dale and Slagsvold 1996). Furthermore, some recent evidence suggests that achromatic feathers may actually have some intrinsic production costs as well (McGlothlin et al. 2007, Griggio et al. 2010a).

In addition to the type of ornament displayed, another way multiple ornaments may convey different information is through the effects of environmental heterogeneity. Although some ornaments may convey consistent information about specific qualities of an individual, environmental context may influence the magnitude and direction of the relationship between ornament expression and quality (Roulin et al. 2008b, Cornwallis and Uller 2010). Honest signaling via ornamental plumage may be mediated by a variety of environmental conditions including androgen and corticosterone levels related to competition or other ecological stressors (Fargallo et al. 2007, Roulin et al. 2008a), food availability (Dreiss et al. 2010), climatic factors (Cockburn et al. 2008, Sirkiä et al. 2010), predation pressures (Rodewald et al. 2011), and prevalence of parasites (Vergara et al. 2011). The impact of environmental heterogeneity on plumage signals may occur across populations or large geographic scales (Dunn et al. 2008, Roulin et al. 2009) and across local habitats or environmental conditions (Roulin et al. 2008b, Sirkiä et al. 2010, Rodewald et al. 2011). For example, at the local scale, eumelanic coloration co-varied with body mass in Barn Owls (*Tyto alba alba*), but only when food resources were limited or when energy needs were increased (Roulin 2009). And in Red Grouse (*Lagopus lagopus scoticus*), the relationship between comb size and body condition was strongest in the most competitive environments (Martinez-Padilla et al. 2010). Additionally, phenotype (or genotype) x environment interactions may cause individuals to select habitats or conditions to which they are best adapted, and non-random distribution of the ornaments which signal these adaptations may exist (Kassen 2002, Sirkiä et al. 2010). While several studies have documented experimentally-derived environmental contingencies (e.g., stress, food limitation, and parasites) which affect ornament-quality relationships, it is unclear how prevalent these contingencies are in natural environments or how these relationships may impact habitat selection patterns.

At least partly because of ease of capture, most studies of signaling systems in free-living birds have concentrated on species which occupy open or suburban habitats, nest in cavities, or spend a large proportion of their time on, or near, the ground. There is a paucity of information regarding the information content of plumage ornaments in difficult-to-capture canopy obligate species, which have often evolved in different environments, both in terms of ambient light and selective pressures, than those species adapted to the environments mentioned. Additionally, most studies have been performed over a limited geographic area, where the full range of plumage variation may not be represented and the impacts of environmental heterogeneity may not be expressed (Cornwallis and Uller 2010). In this study, we investigated multiple potential ornaments of a canopy-dwelling songbird, the Cerulean Warbler (*Setophaga cerulea*), across a range of habitat contexts. We first asked if, and what kind of, information is conveyed by 4 potential plumage ornaments and evaluated the hypotheses of multiple ornaments in this species. Using free-living birds, we assessed the information content of a eumelanic breast band, structural blue forecrown and rump, and structural achromatic tail patches in relation to the experience and survival (age), condition at time of last molt on breeding grounds (via ptilochronology), current body condition (via body mass), and parental ability (via provisioning rates). Second, we evaluated the impact of environmental heterogeneity on the honesty of plumage ornaments by comparing relationships between plumage and quality across a range of forest conditions (covering much of the natural variability of conditions occupied by Cerulean Warblers). Third, we assessed spatial distribution of plumage ornaments to determine whether individuals distributed themselves in a non-random fashion in regards to their plumage expression.

METHODS

Study species

Cerulean Warblers are territorial, socially monogamous, mature forest songbirds that breed in the canopy of deciduous forests of the eastern United States (Hamel 2000). They are an ideal model organism to explore the relationships between ornamentation and quality of a canopy-dwelling songbird because they spend the majority of their life in the far reaches of the canopy, usually in large tracts of mature forest where light conditions differ greatly from that of the forest floor or understory, open fields, or suburban parks (Théry 2006). In this light environment, ceruleans have evolved plumage unique among congeners; they display several potential signals including a eumelanin-based breast band, achromatic white tail spots (hereafter referred to as ‘tail white’), and unique structural blue upper-parts (including a bright sky-blue forecrown and blue-green rump). As no previous study has investigated the color variability or signaling potential of Cerulean Warbler plumage, we selected to evaluate these plumage regions because of several lines of evidence suggesting their importance in signaling and social interactions. We assessed breast band width because it varies widely among individuals (Hamel 2000, T.J. Boves, *personal observation*), we observed cerulean males investigating the breast band of decoys when attempting to capture them, and melanin-based breast patches or stripes have been identified as honest signals and signals of status in other species (Senar 2006). We assessed tail white because it also varies in ceruleans as well as many other *Setophaga* spp. (Pyle 1997); ceruleans fan their tails in both inter- and intra-specific interactions, and white tail patches have been identified as signals of quality in other avian species (McGlothlin et al. 2007). We assessed the blue forecrown patch because it is the brightest area of the upper-parts (to the human eye) and varies among individuals (Hamel 2000), and we assessed the rump because it also varies among individuals (T.J. Boves, *personal observation*), particularly between age classes (Pyle 1997).

Ceruleans typically molt twice per year, but timing of molt differs by age class. Both hatch year (HY) and after-hatch-year (AHY) birds molt their rectrices on the breeding grounds. This happens soon after fledging in the case of HY birds and in mid-July to Aug for AHY birds. Both ages then undergo a partial molt on their South American wintering grounds where they replace crown, body, and (putatively) their rump feathers (Pyle 1997, F.A. Newell, *personal communication*), however the exact timing of the molt is not known. Therefore, we presumed that the ornaments we assessed were produced either on the wintering grounds (body, crown, and rump feathers) or on the breeding grounds (rectrices).

Study area and field procedures

We monitored and captured male Cerulean Warblers ($n = 55$) breeding in the North Cumberland Wildlife Management Area, Campbell County, TN, USA (36°12’ N, 84° 16’ W) from early May to mid-June in 2009 and 2010. We captured birds that were occupying forest stands that were partially harvested at various intensities as part of a forest management experiment during the fall of 2005 and spring of 2006. This manipulation provided a range of forest conditions from which ceruleans could select, ranging from undisturbed (closed canopy) to heavily disturbed forest (>70% reduction in canopy cover and basal area, hereafter BA). Previous research on this population of ceruleans has shown that the greatest breeding densities (i.e., preferred forest conditions) occur in mature forests where the canopy has been moderately disturbed and canopy openings exist (BA = 12 – 25 m^2/ha), but individuals can also be found occupying areas with greater and lesser canopy disturbance and stem density (T.J. Boves, *unpublished data*). Breeding densities ranged from 0.5 pairs/ha on unharvested controls to >2 pairs/ha on moderately-open forest stands. We attempted to capture individuals that occupied territories spanning the full range of conditions (BA range = 2.5 – 45 m^2/ha). To capture individuals, we erected mist nets within territories, broadcast territorial songs and call notes, and displayed a male cerulean decoy, which we attached to a line that we agitated to produce movement. After capture, we aged birds as second-year (SY; first breeding season) or after-second-year (ASY; ≥ 2nd breeding season) by plumage and molt limits (particularly useful is that SY birds retain brownish juvenile alula and primary coverts; Pyle 1997). We measured right wing length to the nearest 0.5 mm (using a straight wing rule) and mass to the nearest 0.01 g (using a digital scale). We fitted each bird with a unique combination of plastic colored leg bands to later identify individuals in the field without recapture.

Field methods: plumage measurements

Using tweezers, we collected approximately 10 feathers from each bird's forecrown (in front of the eyes) and rump (at the base of the tail just above the synsachrum). We also collected a single tail feather, the first left rectrix (R1), to measure tail growth bars. We stored feathers in glassine envelopes placed inside of manila coin envelopes in dry, dark, room temperature conditions.

We took three photographs of each bird in the field (all by the same individual, T.J. Boves, Figures 3.1a-b). We photographed the breast band by holding the bird with their back flush against a gray piece of cardboard with a reference ruler placed next to, and at the same depth as, the bird (for calibration purposes). We smoothed the breast feathers and positioned the bill to an approximate 30° angle from horizontal and took pictures using a Nikon Coolpix P5100 12.1-megapixel digital camera. We took separate photographs of each side of the tail as well. To do so, we spread the rectrices so that the broad white area on the distal part of each individual feather was fully exposed. We took tail photographs perpendicular to the surface of the tail and at a distance of approximately 25 cm.

Nest searching, provisioning, and habitat measurements

Cerulean Warblers build small open-cup nests high in the canopy of deciduous forests so we intensively searched for nests and evidence of pairing between late April and late June within each banded male's territory. We used female behavioral cues during building and incubation and, to a lesser extent, male vocalizations and behavior, to locate the majority of nests. Once we located a nest, we monitored it every 1–3 d to identify the male that was associated with a nest (all nests had only 1 male provisioning young). When we determined that a nest had a banded male associated with it, we monitored the nest until fledging, or until nest failure, was confirmed. On day 7–9 of the nestling stage, we monitored nests for >45 min to count the number of nestlings. We also recorded each nest for 2 hrs using Sony Handicam video-recorders and later analyzed video files to measure provisioning rates (visits/hr/nestling). We started recording between 0700 and 0800 on days when weather conditions were benign (little wind and no rain). We found no influence of the age of nestlings on the rate of provisioning ($F_{1,56} = 0.18$, $P = 0.67$), so we did not adjust for nestling age. To characterize habitat, we measured overstory canopy cover (>18 m) and BA at the area of greatest use within each male's territory using an ocular tube and a 2.5X metric BA prism. BA and overstory canopy cover were highly correlated ($r = 0.72$), so we used only BA, the more repeatable measure, in our analyses.

Lab methods: plumage measurements

To measure color variables for crown and rump ornaments, we formed artificial feather patches (for both rump and crown plumage) by laying feathers on black cardstock paper with minimal reflectance in a manner that mimicked how feathers lay naturally on the bird's body (Figures 3.1c-d). To determine the minimum number of feathers to use in our patches, we first created test patches using 1–10 feathers for 5 birds (for both body regions). We found that total reflectance increased with each additional feather up to 4 feathers for the rump, and up to 5 feathers for the crown, so we created all artificial patches using 1 extra feather for each patch (i.e., 5 feathers for the rump and 6 feathers for the crown). We used an Ocean Optics S2000 fiber-optic spectrometer (range = 250–800 nm; Ocean Optics, Dunedin, FL, USA) to generate reflectance data. We held a micron fiber-optic probe, housed within a rubber stopper to exclude all ambient light, at a 90° angle 1-mm from the feather patch. The feather patch was illuminated by deuterium (UV light source) and tungsten-halogen bulbs (visible-light source). We calibrated the spectrometer prior to data collection (and repeated between measurements as needed), using a white WS-2 reflectance standard (Labsphere Inc., North Sutton, NH, USA). We generated reflectance data relative to the standard using OOIBase32 spectral software. We incorporated a smoothing function using a boxcar value of 10 and each data point was the average of 20 spectral measurements. We obtained readings from three locations on each feather patch at wavelengths between 300–700 nm. We averaged the data from the three reflectance curves for all analyses. We extracted color variables using the color analysis software program CLR v1.05 (Montgomerie 2008) for each of the plumage patches. On average, reflectance for both the crown and rump peaked at approximately 490 nm (blue-green region, or hereafter, BG; Figures 3.3 and 3.4) and variability was greatest in this region (T.J. Boves, *unpublished data*), so we calculated BG chroma and BG hue for both crown and rump. BG chroma was calculated as the reflectance ratio $\sum R_i/\sum R_{300–700}$ where *i* was 435–534 nm. BG hue was calculated as the wavelength of maximum reflectance within the BG region (λR_{max}). Based on research from other birds that display structurally-based plumage coloration (Satin bowerbirds, *Ptilonorhynchus iolaceus,* Doucet and Montgomerie 2003, and Tree Swallows, *Tachicyneta bicolor*, Bitton and Dawson 2008), we considered males with lower hue (bluer) and greater BG chroma values to display more-exaggerated plumage.

To calculate breast band width we used ImageJ software (available from NIH at http://rsbweb.nih.gov/ij/). We considered the band to consist of the area of eumelanin pigmentation that connected the dark streaking on either side of the bird's breast (streaking was not included in our measurements, Figure 3.1a). We calibrated each photo (using the ruler we included in photos) and measured the mean vertical width at 8 evenly-spaced locations along the breast as well as at the maximum and minimum width. We then calculated the mean breast band width of these 10 measurements and used this as our measure of breast band width. Based on research from other birds that display melanin patches (Great Tit, *Parus Major*, Norris 1990, Hegyi et al. 2007), we considered males with wider breast bands to display more-exaggerated plumage.

We used ImageJ to measure tail white, which we defined as the mean ratio of white area to the total feather area (across all 12 rectrices). For each individual rectrix (R2-R6 on either side), we used the polygon selection tool to measure the broad white patches on the distal end of each feather, and then did the same for each entire feather. For R1, which we collected, we measured tail white from photographs taken in the lab. We calculated the ratio of white to total feather area and then averaged that ratio across all rectrices. When possible, we used all rectrices to calculate tail white, however when one feather was missing or broken, we used only the intact feathers (and assumed the missing feather had the same amount of white as the complementary feather from the other side of the tail). Based on research from other birds that display achromatic tail white (Dark-eyed Juncos, *Junco hyemalis*, McGlothlin et al. 2007), we considered males with more-extensive tail white to display more-exaggerated plumage.

Measures of quality

We used body mass alone as an indication of current body condition at the time of capture because of recent concerns about using unverified indices to quantify body condition (Schamber et al. 2009, Labocha and Hayes 2011). We also calculated wing-mass residuals and found them highly correlated to body mass ($r = 0.92$); we performed analyses with both measures and found no change in inference. To gauge condition at the time of molt, we used ptilochronology (Grubb 1989). We first measured the collected R1 feather using digital calipers. We then took a digital photograph of the feather under individualized lighting conditions that allowed us to best observe growth bars. Using ImageJ, we measured the average distance between seven tail growth bars closest to the proximal end of the feather (Figure 3.2). We assumed this distance was representative of condition at the time of tail molt such that males in better body condition grew tail feathers with wider growth bars (i.e. faster growth). We recorded provisioning rates of individuals for whom we located a nest that fledged young as the number of feeding visits/hr/nestling.

Statistical analyses

We first tested for correlations among plumage ornaments by performing pairwise correlation tests using the REML method (for age classes pooled and partitioned). For this and subsequent regression analyses, we examined partial residual vs. fitted values, performed Shapiro-Wilk’s and D’Agostino tests, and examined scatterplots to assess linearity and parametric assumptions. We log-transformed breast band width and crown BG chroma to address non-normality and heteroscedascity.

We used ANOVA to determine if potential ornaments differed by age class (SY vs., ASY) or year (2009 vs. 2010). We treated age, year, and age x year interactions as fixed factors. We found no significant effect of age x year (all $P > 0.10$), so we removed the interaction term from all analyses. For crown and rump, we performed ANOVAs for chroma and hue of the BG region. We examined variables for normality (using omnibus test) and equal variance (modified Levene's test); if we found the assumption of normality to be violated, we transformed data appropriately. We log-transformed crown BG chroma to address non-normality; all other variables met parametric assumptions.

To examine the relationships between potential ornaments (dependent variables) and measures of quality (body mass, tail growth, and provisioning rates; independent variables), we used multiple linear regression analysis. To avoid the problems of multi-collinearity and differing sample sizes, we assessed each plumage measurement and independent variable separately. We controlled for the potentially confounding variables of age and year by including them as binary independent variables as well as all two-way interactions. When interactions were non-significant ($P > 0.10$), we removed them from final models. We again log-transformed breast band width and crown BG chroma.

Because we performed multiple tests on each plumage ornament, the chance of committing a type I error increased with each test. To reduce the likelihood of committing a type I error, we used the false discovery rate method (Curran-Everett 2000). This method controls for the number of falsely rejected hypotheses rather than the family error rate and increases statistical power. We replaced α with a false discovery rate (f_F) of 0.05 which produced a critical significance level (d_i) by: $d_i = (i/k)*f_F$ for i of k comparisons, ordered by decreasing magnitude of P-values for each independent variable individually (e.g., d_i for independent variable with lowest P-value associated with specific ornament calculated using $i = 1$, $k = 3$; second lowest, $i = 2$, $k = 3$, etc.).

If the observed significance level (*P*-value) was < d_i for a given test, we considered the relationship significant. If $d_i < P \leq 0.05$, we considered the result marginally significant.

We tested for habitat contingency of information content of plumage ornaments by modeling plumage measures as dependent variables and age and measures of quality (mass, tail growth, and provisioning rate) as independent variables (separately), but we also included BA and BA x respective quality measure interactions as independent variables in all models. We considered signaling relationships to be contingent on habitat if BA x independent variable term was significant ($P < 0.05$). We tested for non-random distribution of plumage across habitats by fitting linear and quadratic regressions (based on previous research showing preference for moderately open habitat) of BA against each plumage measurement. We performed this analysis with and without age as an independent variable. We log-transformed breast band width and crown BG chroma. We performed all statistical analyses in JMP (v.9.02, SAS Institute, Cary, NC).

RESULTS

Plumage correlations

With age classes pooled, 9 of 15 pairwise correlations were significant ($P < 0.05$, Table 3.1). However, when age classes were partitioned, correlations were only significant within and between structural crown and rump color variables (Table 3.1). In SY birds, rump BG hue was positively correlated with crown hue ($r = 0.60$, $P = 0.01$) and negatively correlated with rump chroma ($r = -0.73$, $P = 0.0008$). In ASY birds, rump BG hue was negatively correlated with crown chroma ($r = -0.45$, $P = 0.006$) and rump chroma ($r = -0.56$, $P = 0.0003$) and positively correlated with crown hue ($r = 0.74$, $P < 0.0001$). Crown chroma was also negatively correlated with crown hue ($r = 0.66$, $P < 0.0001$). Thus, within age classes, breast band width and tail white were independent of all other plumage ornaments, however measurements of crown and rump were correlated (particularly in ASY birds).

Information content of plumage ornaments

Eumelanic breast band width, achromatic tail white, structural crown BG hue (Figure 3.3), rump BG hue (Figure 3.4), and rump BG chroma all differed between age classes (Table 3.2). After controlling for age and year of capture, tail white was positively related to feather growth rate at molt (*Std Beta* = 0.28, $F_{1,51}$ = 2.88, P = 0.006; Figure 3.5a). Rump BG chroma and hue were both related to provisioning rate (chroma positively, *Std Beta* = 0.35, $F_{1,20}$ = 2.80, P = 0.01; hue negatively, *Std Beta* = -0.43, $F_{1,20}$ = -2.97, P = 0.008, Figure 3.5b). Rump BG chroma was negatively related to body mass (*Std Beta* = -0.29, $F_{1,50}$ = -2.73, P = 0.009, Figure 3.5c). We found no relationship between log of breast band width (all $P > 0.20$), log of crown BG chroma (all $P > 0.10$), or crown BG hue (all $P > 0.09$) and any measure of quality (tail growth, body mass, provisioning rate).

Habitat contingency of information content of plumage ornaments

After including BA and BA x quality measure interactions as independent variables, the log of breast band width was positively related to body mass (*Std Beta* = 0.47, t_{50} = 2.76, P = 0.009), however the interaction term was also significant (*Std Beta* = -0.62, t_{53} = -3.11, P = 0.003). Thus, information content conveyed by breast band width was contingent on forest conditions. By splitting birds into three (somewhat) arbitrary groups (low BA = 2.3 – 14 m^2/ha, moderate = 16 – 24 m^2/ha, and high = 25 – 45), we depict these differences graphically (Figure 3.6). The linear relationship was positive and strongest in birds inhabiting moderately open forests (R^2 = 0.33 for medium BA), a weaker positive relationship existed within birds occupying very open forests (R^2 = 0.22 for low BA), and the weakest (and negative) relationship existed for birds living in dense closed-canopy forests ($R^2 = 0.04$ for high BA). We found no evidence for habitat-contingent relationships between measures of quality and either structural or achromatic plumage ornaments.

Distribution of plumage ornaments across habitats

There were no significant linear relationships between plumage ornaments and habitat (all $R^2 < 0.04$, all $P > 0.15$). However, after fitting a quadratic relationship between log breast band width and BA, we found a significant fit ($R^2 = 0.23$, $F_{2,52} = 14.14$, $P = 0.0004$, Figure 3.7a). We found a similar quadratic relationship between tail white and BA ($R^2 = 0.17$, $F_{2,52} = 10.11$, $P = 0.003$, Figure 3.7b). Therefore, birds with the largest eumelanic breast bands and greatest proportion of tail white occupied moderately open habitat, whereas birds with smaller breast bands and less tail white occupied more extreme forest conditions, very open (i.e., low BA) or dense, closed canopy forest habitat (high BA). When we included age as an independent variable, the quadratic relationship was still significant with log breast band width ($P = 0.02$), but no longer with tail white ($P = 0.40$).

DISCUSSION

Male Cerulean Warblers displayed several plumage ornaments that signaled individual quality. All ornaments were redundant in their signaling of age as older birds displayed more-exaggerated ornaments. Across all habitats, tail white and blue-green rump coloration conveyed unique messages; condition at molt was positively correlated with exaggerated tail white while parental effort was positively correlated with exaggerated rump coloration. In addition, breast band width was positively related to body mass, but only in habitats where basal area was at intermediate levels, providing support for the hypothesis of environmental contingency of melanin-based plumage signals (Ducrest et al. 2008, Roulin 2009, Dreiss et al. 2010).

Furthermore, spatial distributions of eumelanic (breast band width) and achromatic ornaments (tail white) were non-random; birds that displayed the most-exaggerated form were found in moderately open forest habitat.

Redundant messages

All plumage ornaments were related to age to some degree; older males displayed more-ornamented traits than did SY males. This raises a question: are male Cerulean Warblers constrained during molt or do they undergo delayed plumage maturation (DPM) as a life-history strategy? Many avian species exhibit DPM and most evidence now supports this process as an adaptive life-history strategy in which sub-adult birds delay maturation to reduce competition with older males during their first year of life and thereby increase lifetime fitness levels (Hawkins et al. In Press). DPM typically involves species in which sub-adults differ substantially from adults (from a human perspective), with little or no overlap in plumage coloration between age classes and/or delayed gonadal maturation. Sub-adult male (SY) ceruleans in the Cumberland Mountains, however, regularly secured mates and (presumably) sired offspring, were prone to intrasexual competition, and responded aggressively to territorial intruders (as this is how we were able to capture them). These SY individuals exhibited only subtle plumage differences with ASY individuals. In addition, although on average, plumage ornaments were more exaggerated in ASY birds, a few SY males displayed more exaggerated plumage than some older birds for all ornaments (see Table 3.1). As such, plumage differences between age classes may not exist simply because of an adaptive life-history strategy, but rather young birds may be constrained in some manner at the time of a male’s first (tail feathers) or second molt (crown, rump, and breast feathers). These constraints could arise because young birds are inexperienced and inefficient foragers (Wunderle 1991, Desrochers 1992), are prone to increased infection due to delayed immune system maturation (Buehler et al. 2009), have increased energy costs related to development, or are otherwise handicapped early in life. Other species where age-related color variation is related to factors other than DPM include House Finches (*Carpodacus mexicanus frontalis*, Hill 2002), Eastern Bluebirds (*Sialia sialis,* Siefferman et al. 2005), Western Bluebirds (*Sialia mexicana*, Budden and Dickinson 2009), and Chestnut-sided Warblers (*Setophaga pennsylvanica*, King et al. 2001). It is unknown whether plumage differences exist among age classes beyond ASY in ceruleans because aging methods for older age-class birds have not been developed.

Multiple messages

Although all ornaments redundantly signaled age, several ornaments conveyed unique information within age classes. Tail white was the only ornament that reflected individual condition during the last breeding season. Logically, the production of tail white must coincide with the molt of rectrices. Other ornaments, in contrast, are likely temporally decoupled from post-breeding molt and produced up to 3 months later on the wintering grounds, when individuals may be in a different nutritional state. Potential mates and competitors could assess tail white to gain information about long-term, or previous breeding, condition of males.

The honesty of tail white as a signal of quality may be enforced via intrinsic and extrinsic costs associated with displaying and maintaining the ornament (Dale and Slagsvold 1996, Qvarnström 1997, Fitzpatrick 1998). Furthermore, the ability to produce more exaggerated tail white may be related to adaptations to highly stressful or competitive environments. Dark-eyed Juncos (*Junco hyemalis*) were able to grow their tails faster, with larger white spots when given a subsistence diet during molt, however no ornament-condition relationship existed when provided with an enriched diet (McGlothlin et al. 2007). Furthermore, juncos with larger tail spots were better able to elevate testosterone levels when challenged with male competition (McGlothlin et al. 2008). Similarly, we observed a non-random spatial distribution of the expression of tail white, with birds displaying greater exaggeration more often occupying preferred moderately-open forest. Although these are preferred habitat conditions, greater intrasexual competition also occurs in these habitats as densities are extremely high (T.J. Boves, *personal observation*). These conditions may cause an increase in stress and potential decrease in available foraging time. A simple linear regression (with age classes pooled) confirms that birds with exaggerated tail white had greater numbers of conspecific neighbors (Figure 3.8a), supporting the hypothesis that birds with more tail white are capable of handling greater levels of aggression. However, this spatial distribution existed only when both age classes were pooled, and therefore experience (which also covaries with tail white) or social dominance may be more influential in the pattern of habitat selection and territory acquisition than any within-age class differences signaled by plumage ornaments.

Structural rump coloration was related to two different measures of quality: body mass and provisioning rate. Birds that displayed more exaggerated BG hues (i.e., lower wavelengths or bluer plumage), and more exaggerated chroma (greater proportion of their total reflectance in the BG color range), fed nestlings at greater rates. These results support the good parent hypothesis of sexual signaling (Møller and Thornhill 1998). Male ceruleans provide a large amount of parental care to nestlings, making, on average, 50% of total provisioning trips to the nest (T.J. Boves, *unpublished data*). Females may benefit from assessing the direct benefits that a potential partner might provide offspring. Previous studies investigating structural ornaments and their relationship with parental effort have had ambiguous results. Structural coloration was positively related to provisioning rates in male and female Eastern Bluebirds (Siefferman and Hill 2003, 2005), but no apparent relationship existed in Western Bluebirds (Budden and Dickinson 2009) and in Bluethroats (*Luscinia s. svecica*, Smiseth et al. 2001). This variability may be related to idiosyncratic species-specific signaling patterns or variation in the confidence of paternity in these different species or populations (Trivers 1972, Westneat and Sherman 1993). While ceruleans with greater BG chroma values provided more parental care, this color variable was negatively related to body mass, suggesting that these individuals may have expended more energy on parental care than on self-maintenance. By the nature of the measurement, chroma in one region of the spectrum is often negatively related to that of other regions. It is possible that a portion of the reflectance spectrum is positively related to body condition (potentially associated with a secondary peak in the UV region, Figure 3.4), but we did not assess other spectral regions in this study.

The crown plumage was the only ornament that did not appear to signal any phenotypic quality (including age), providing support for the third hypothesis of multiple ornaments (unreliable signal). This plumage may have evolved because of runaway selection on a female preference, however there are other qualities that could potentially covary with crown plumage (e.g., immuno-competence). This plumage may have also evolved for species recognition in small or large gap habitats; blue is an appropriate signal for conspicuousness in these habitats, as it contrasts highly with the ambient light (Théry 2006)

Habitat contingency

The habitat contingent relationship between breast band width and body mass supported the hypothesis that melanin-based ornaments may signal the capacity to handle stressful conditions (Ducrest et al. 2008, Roulin et al. 2008a, Roulin and Ducrest 2011). Melanic color expression in vertebrates is usually largely under genetic control (Majerus 1998) and is regulated by the melanocortin system, the same system of hormones responsible for regulating stress response, immune function, homeostasis, and aggression. This linkage may result in pleiotropic correlations between melanic plumage and these physiological processes (Roulin and Ducrest 2011). Male ceruleans able to produce large eumelanic ornaments may be better at handling physiological stress related to extreme weather, predators, or competitive interactions found in moderately-open forest conditions. We can only speculate on the specific environmental stressor(s) in this case, but these habitats did harbor the greatest densities of breeding territories as well as the greatest levels of intrasexual competition and aggression. The high breeding densities in moderately open forest habitats suggest that, overall, resources were plentiful, but only those individuals capable of handling the stress of competition and aggression were able to maintain their body condition in these habitats. Traits which improve competitive ability (which may be correlated with eumelanic plumage) should be under the strongest selection in high-density populations (Calsbeek 2009) and the honesty of melanin-based ornaments may be enforced by intrasexual competition as males are "challenged" by neighbors of different ranks (Møller 1987, Tarof et al. 2005). The increase in challenges by neighboring birds in the high density, moderately open forest habitats may have caused unsustainable stress levels (and hence loss of body mass) among individuals that lacked a more active melanocortin system. The time spent engaging in intrasexual competition may indirectly impact food availability by decreasing foraging time, further creating conditions in which darker individuals appear to be better adapted (Roulin 2009).

Several other studies have reported relationships between eumelanic ornaments and condition under specific environmental conditions. In Barn Owls (*Tyto alba*), eumelanic spotting co-varied with body mass only when the period since last feeding was long, indicating that darker individuals were better able to cope with a lack of food resources (Roulin 2009). More heavily-spotted Barn Owl nestlings were also able to grow faster than individuals with smaller spots, but only after experimental implantation of the stress hormone corticosterone (Roulin et al. 2008a). Moreover, in Alpine Swifts (*Apus melba*) the offspring of darker fathers grew faster only when brood size was experimentally increased (Roulin et al. 2008b).

Based on this habitat-contingent pattern, we tested for a non-random spatial distribution of this plumage and found a quadratic relationship between breast band width and basal area, with birds possessing the largest breast bands occupying the most preferred habitats (moderately open forests), a relationship that was present even after controlling for age. We also observed a positive linear relationship between breast band width and the number of adjacent territories (Figure 3.8b), with birds possessing the largest breast bands occupying territories with more neighboring competitors. Interestingly, these are the same spatial patterns that we documented for tail white (albeit not within age classes). This is somewhat surprising because these two ornaments are metabolically disparate, were not highly correlated, and would seemingly have different signaling capacities. However both signaled condition, only at differing time scales; tail white signaled condition from the previous breeding season (long term) and breast band width signaled current condition in specific contexts (short term).

Conclusions

We found support for the redundant and multiple message hypotheses of multiple ornaments in an obligate canopy-dwelling songbird, the Cerulean Warbler. Our results also support the hypothesis that eumelanic ornaments signal adaptation to specific environmental conditions as we documented a relationship between the breast band width and body condition only in moderately-open forest habitats where greater levels of competition existed. We also documented non-random distribution of phenotypes, as birds with larger eumelanic ornaments inhabited moderately open habitat more often. These results are novel as few studies have documented an ornament-condition contingency under natural conditions or whether a contingency of this type may impact habitat occupancy patterns. In addition, as our habitat conditions were produced by partial timber harvests, our results illustrate how human activities may impact selective environments and potentially influence the evolution of plumage ornaments and patterns of sexual selection. Finally, we caution that care should be taken when assessing ornament-condition co-variation at small spatial scales. If environmental heterogeneity is not present and/or interactions are not evaluated, a lack of relationship may be inferred.

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APPENDIX

All ages	**BB width (log)**	**Tail white**	**Crown BG chroma (log)**	**Crown BG hue**	**Rump BG chroma**	**Rump BG hue**
BB width (log)	1					
Tail white	**0.34**	1				
Crown BG chroma (log)	0.12	0.23	1			
Crown BG hue	-0.09	-0.15	**-0.56**	1		
Rump BG chroma	**0.32**	**0.50**	0.25	**-0.38**	1	
Rump BG hue	-0.26	**-0.43**	**-0.36**	**0.70**	**-0.75**	1
SY						
BB width (log)	1					
Tail white	0.04	1				
Crown BG chroma (log)	-0.03	-0.04	1			
Crown BG hue	0.26	-0.11	-0.34	1		
Rump BG chroma	-0.02	-0.06	-0.04	-0.27	1	
Rump BG hue	0.29	-0.02	0.08	**0.60**	**-0.73**	1
ASY			`			
BB width (log)	1					
Tail white	-0.14	1				
Crown BG chroma (log)	-0.02	0.11	1			
Crown BG hue	-0.08	0.16	**-0.66**	1		
Rump BG chroma	-0.04	-0.07	0.20	-0.32	1	
Rump BG hue	-0.07	0.050	**-0.45**	**0.74**	**-0.56**	1

Table 3.1. Pairwise correlations (estimated using REML method) between six plumage measurements for age classes pooled and within-age classes. Significant correlations at α = 0.05 are in bold.

	Age		ANOVA	
Plumage measure	**SY**	**ASY**	***F***	***P***
Breast band width (mm)	1.77 ± 0.16 (*n* = 17) Range = 0.90 – 3.11	2.44 ± 0.11 (*n* = 38) Range = 1.43 – 3.87	11.4	**0.001**
Tail white (%)	14.20 ± 0.46 (*n* = 17) Range = 9.13 – 17.09	19.11 ± 0.31 (*n* = 38) Range = 15.45 – 23.42	74.3	**< 0.0001**
Crown BG chroma (%)	31.03 ± 0.22 (*n* = 17) Range = 29.36 – 34.31	31.60 ± 0.15 (*n* = 37) Range = 29.88 – 32.84	4.7	**0.03**
Crown BG hue (nm)	492.07 ± 3.34 (*n* = 17) Range = 470 – 508	484.26 ± 2.27 (*n* = 37) Range = 451 – 513	3.6	0.06
Rump BG chroma (%)	27.31 ± 0.23 (*n* = 17) Range = 25.08 – 28.80	29.00 ± 0.15 (*n* = 38) Range = 26.86 – 30.97	36.2	**< 0.0001**
Rump BG hue (nm)	516.04 ± 3.56 (*n* =17) Range = 487 – 539	494.23 ± 2.38 (*n* = 38) Range = 461 – 523	24.8	**< 0.0001**

Table 3.2. Plumage measurements of breast band width, tail white, rump blue-green (BG) chroma (435–534 nm) and hue, and crown BG chroma and hue for second-year (SY) and adult (ASY) male cerulean warblers in the Cumberland Mountains, 2009–10. We included age and year as fixed factors and log-transformed crown BG chroma. We report untransformed means ± SE.

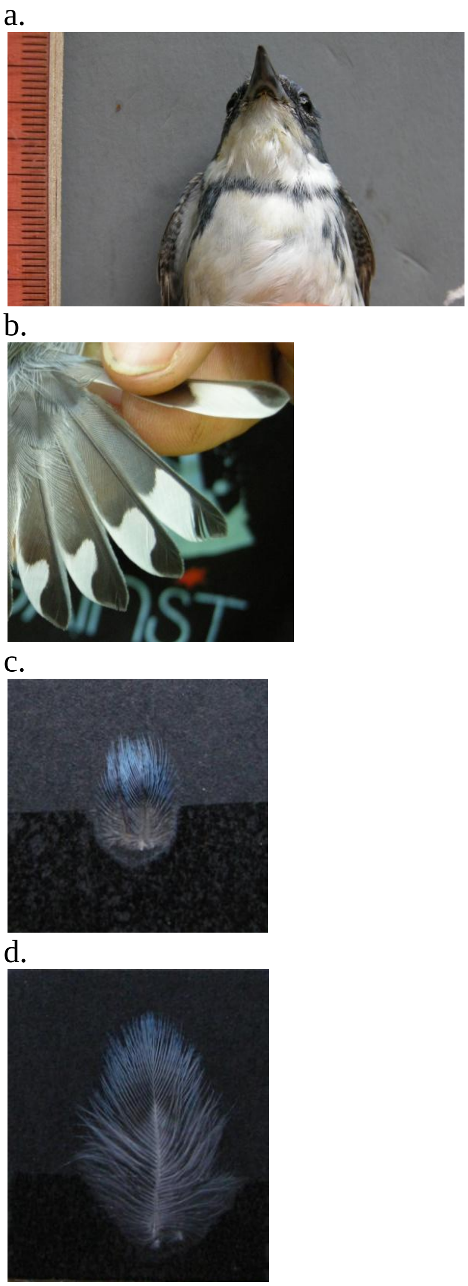

Figure 3.1a-d. Photographs depicting Cerulean Warbler ornaments evaluated. Figure 1a. depicts eumelanin breast band; 1b. depicts tail white; 1c. depicts crown feather patch; 1d. depicts rump feather patch.

Figure 3.2. Example of the use of ptilochronology to infer body condition at the time of tail molt. Growth bars are indicated by white vertical lines. We measured the average distance between the seven most proximal tail growth bars.

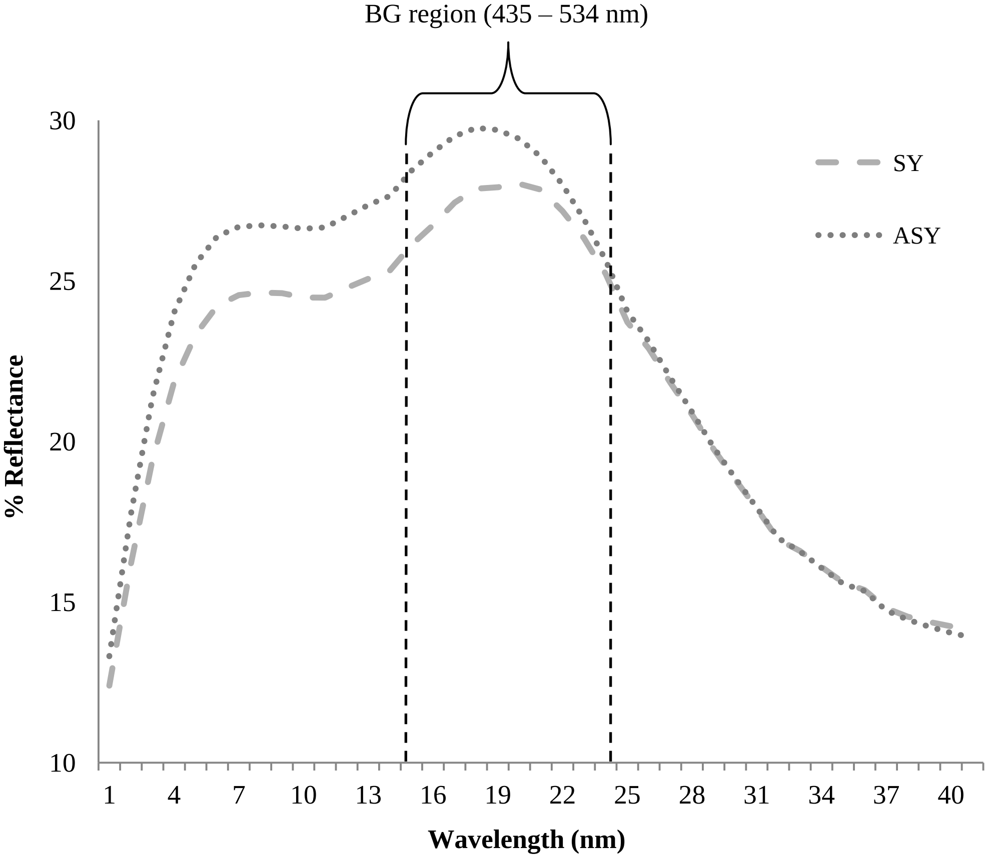

Figure 3.3. Crown reflectance spectrum from second-year (SY) and after-second-year (ASY) Cerulean Warblers captured in the Cumberland Mountains, TN, 2009–10. Blue-green (BG) region of spectrum used in analyses is highlighted.

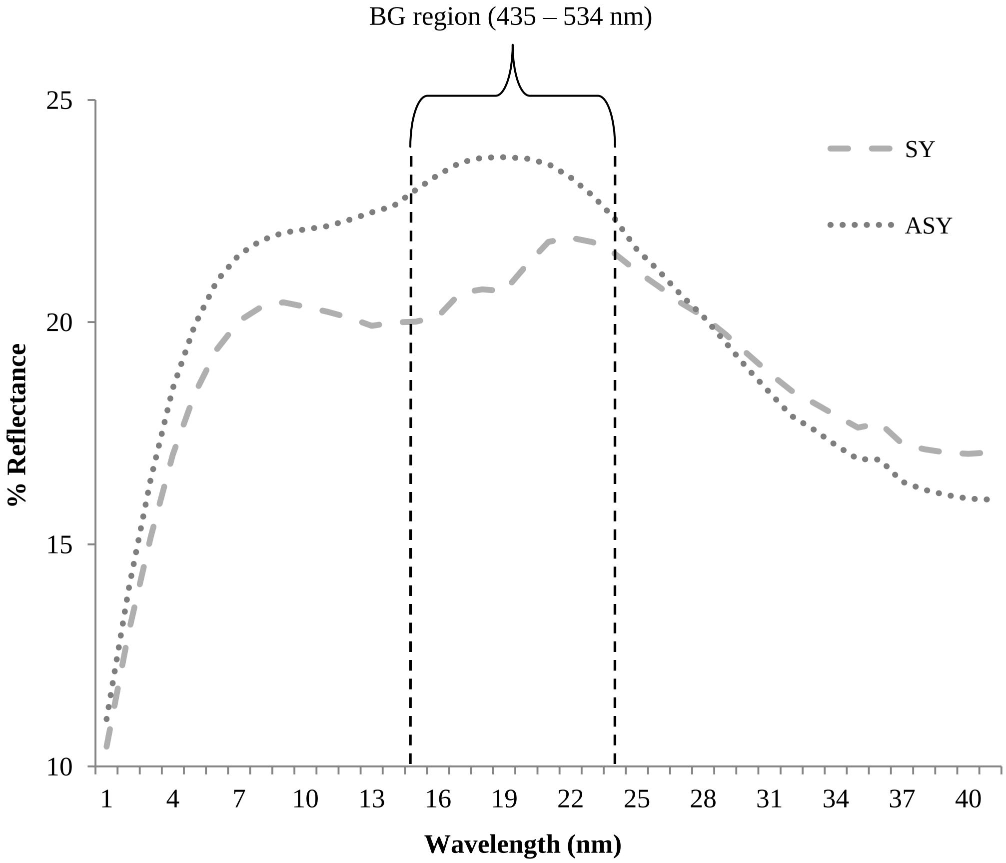

Figure 3.4. Rump reflectance spectrum from second-year (SY) and after-second-year (ASY) Cerulean Warblers captured in the Cumberland Mountains, TN, 2009–10. Blue-green (BG) region of spectrum used in analyses is highlighted.

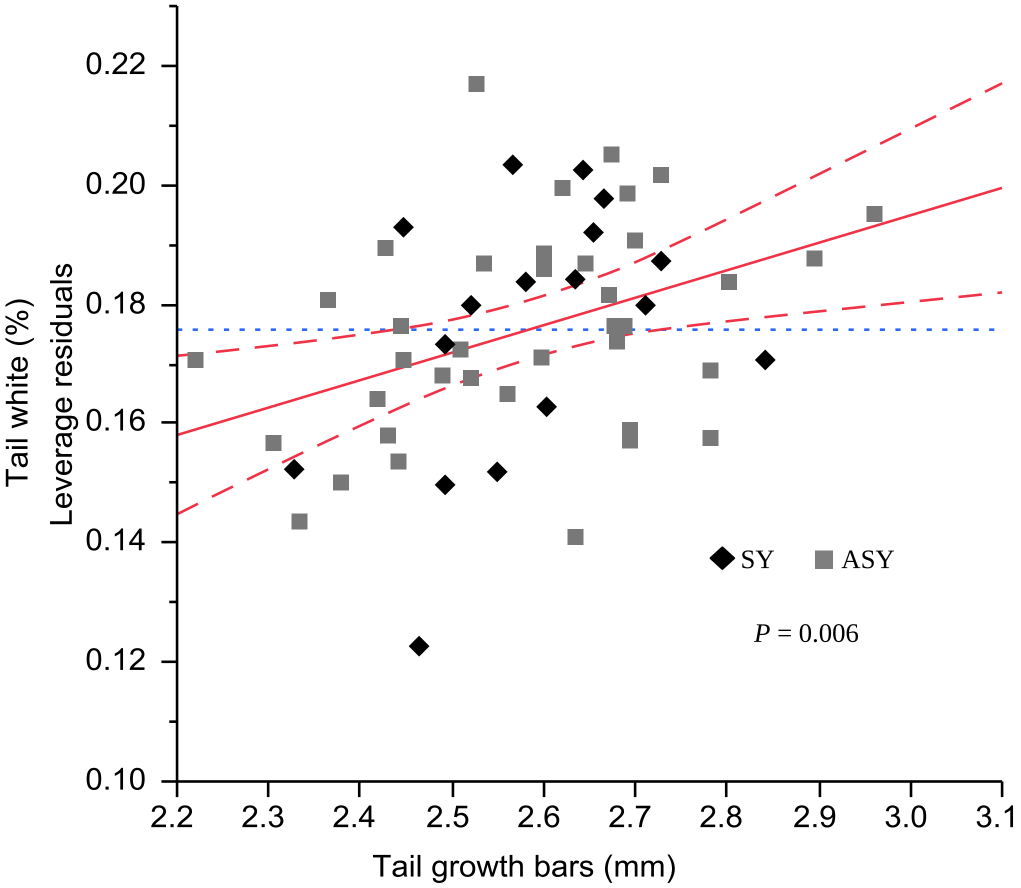

Figure 3.5a. Partial regression leverage plot indicating relationship between achromatic tail white and condition at molt (via tail growth bars) for male Cerulean Warblers after controlling for age and year. Solid red line depicts partial regression line, curved and dashed red lines represent 95% CI of partial regression line, and horizontal dotted blue line represents the null hypothesis of no relationship. CI lines cross horizontal line indicating partial regression slope is different than 0.

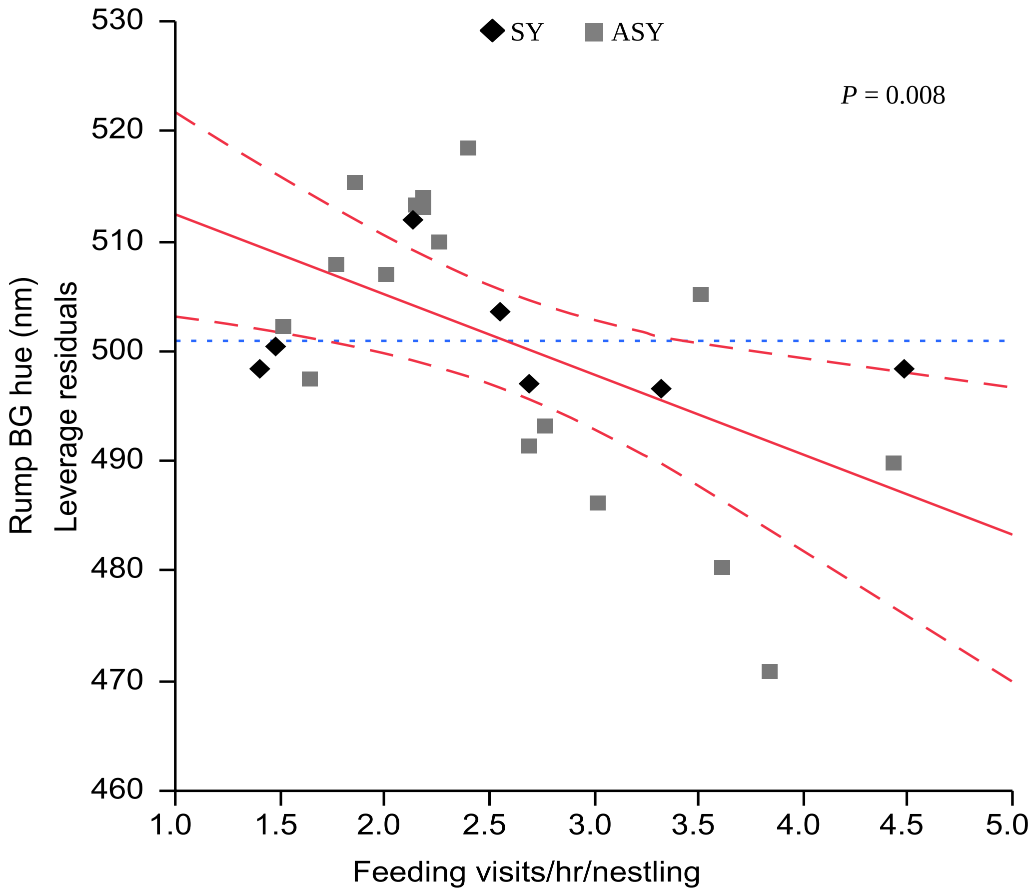

Figure 3.5b. Partial regression leverage plot indicating relationship between structural rump blue-green (BG; 435–534 nm) hue and provisioning rate for male Cerulean Warblers after controlling for age and year.

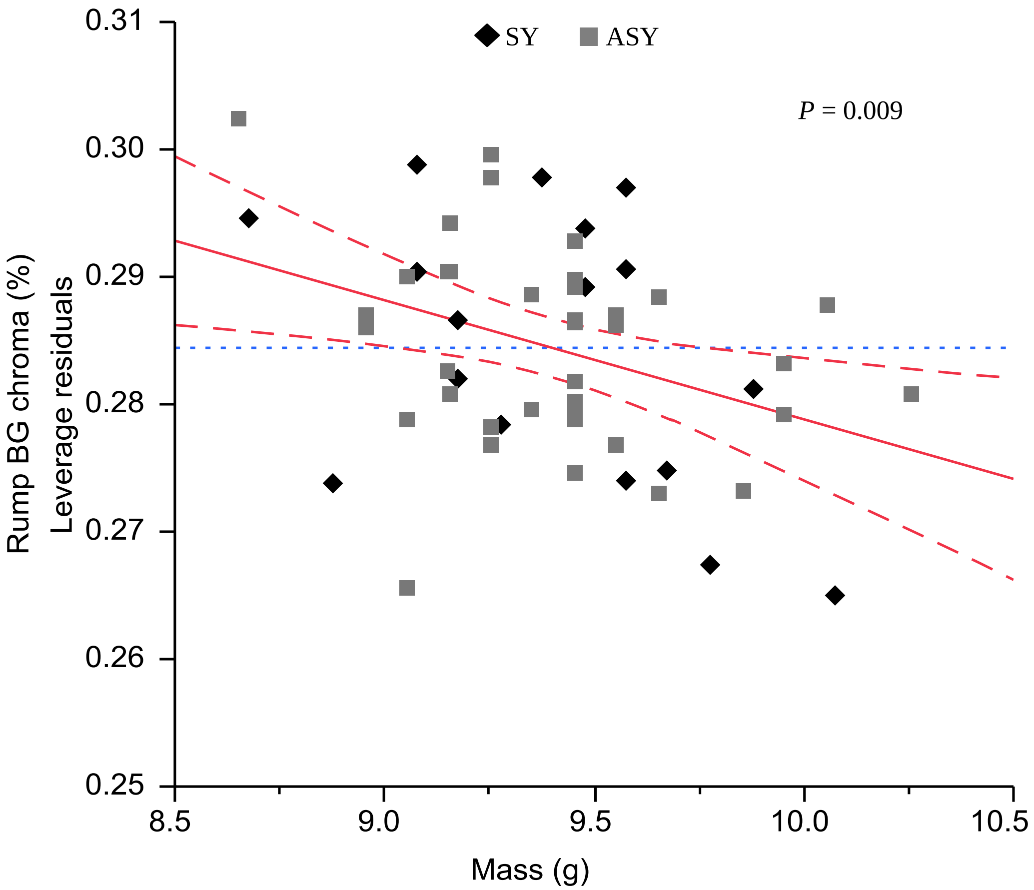

Figure 3.5c. Partial regression leverage plot indicating relationship between structural rump blue-green (BG; 435–534 nm) chroma and body mass for male Cerulean Warblers after controlling for age and year.

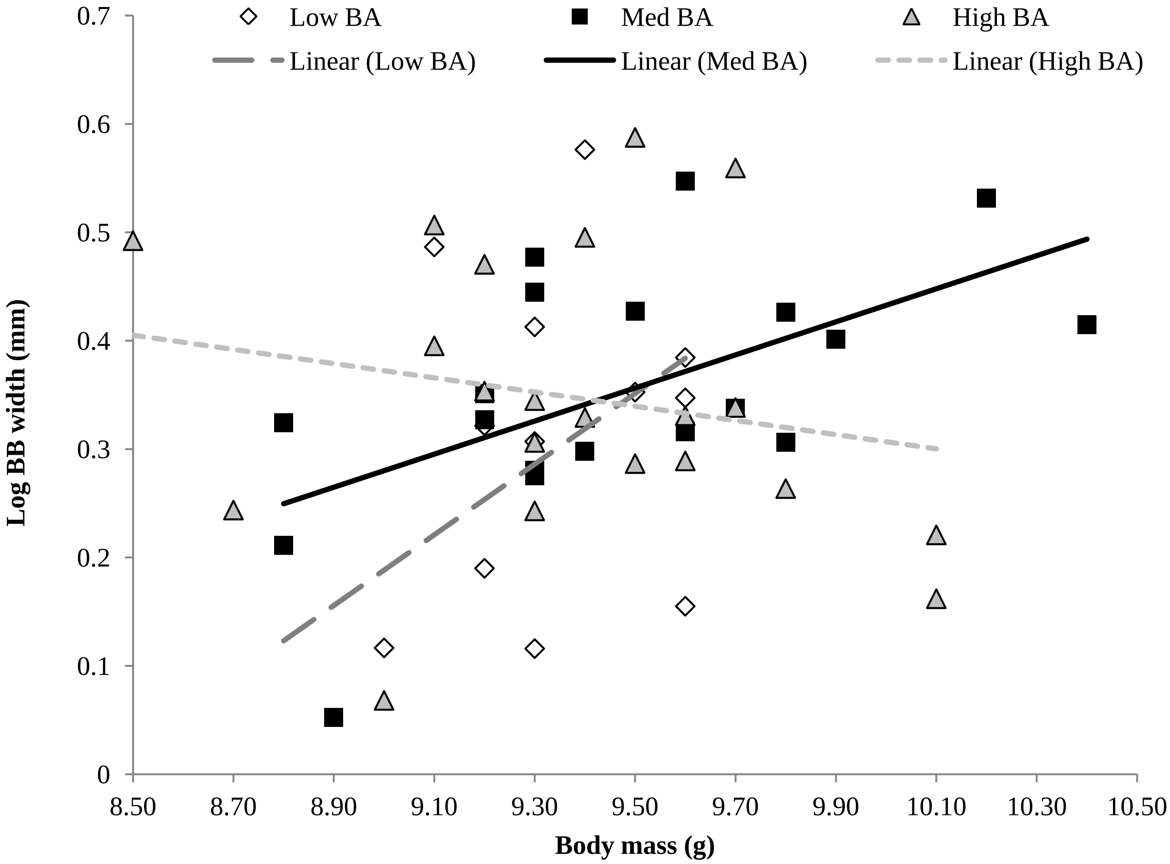

Figure 3.6. Relationships between melanin-based breast band (BB) width and body condition at time of capture (body mass) in different habitat conditions. We binned territory basal area (BA) measurements into three habitat groups: low (BA = 2.3–14 m^2/ha), medium (BA = 16–24 m^2/ha), and high BA (BA = 25–45 m^2/ha). We depict linear regression lines for each habitat group with age classes and years pooled. Low $R^2 = 0.22$, $P = 0.11$; Med $R^2 = 0.33$, $P = 0.009$; High $R^2 = 0.04$, $P = 0.43$.

Figure 3.7a.

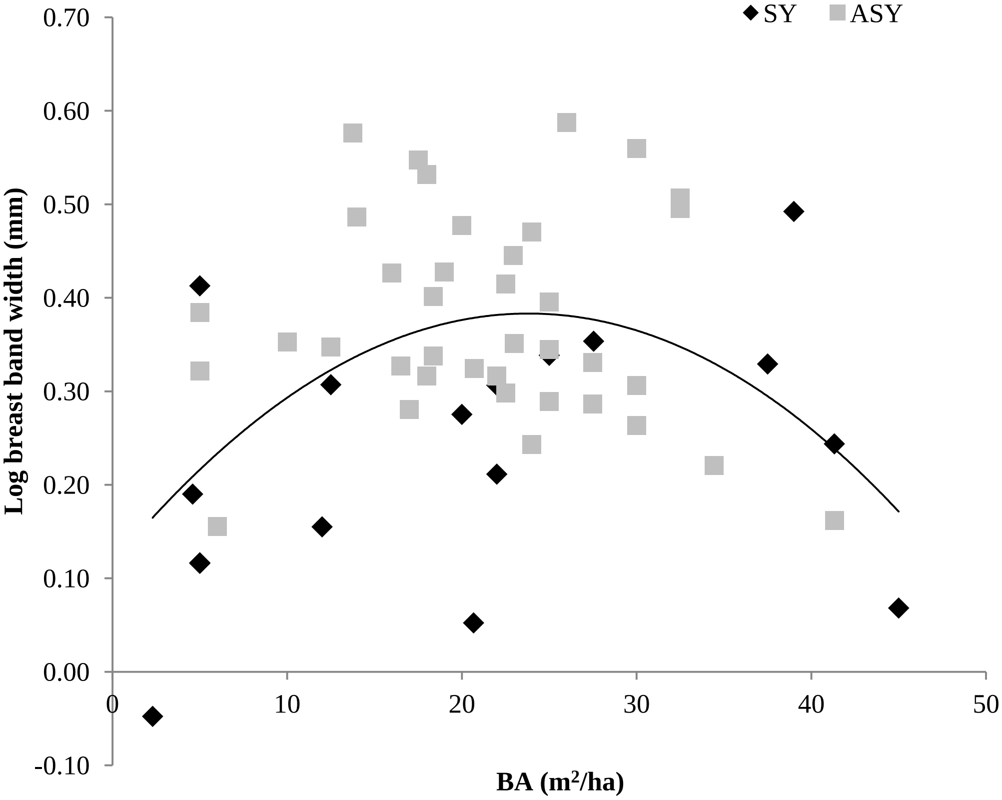

Figure 3.7a-b. Relationship between log breast band (a) and tail white (b) and forest openness (via basal area; BA). We depict quadratic regression line for age classes and years pooled. Breast band R^2 = 0.23, P = 0.0004; tail white R^2 = 0.17, P = 0.003.

Figure 3.7b.

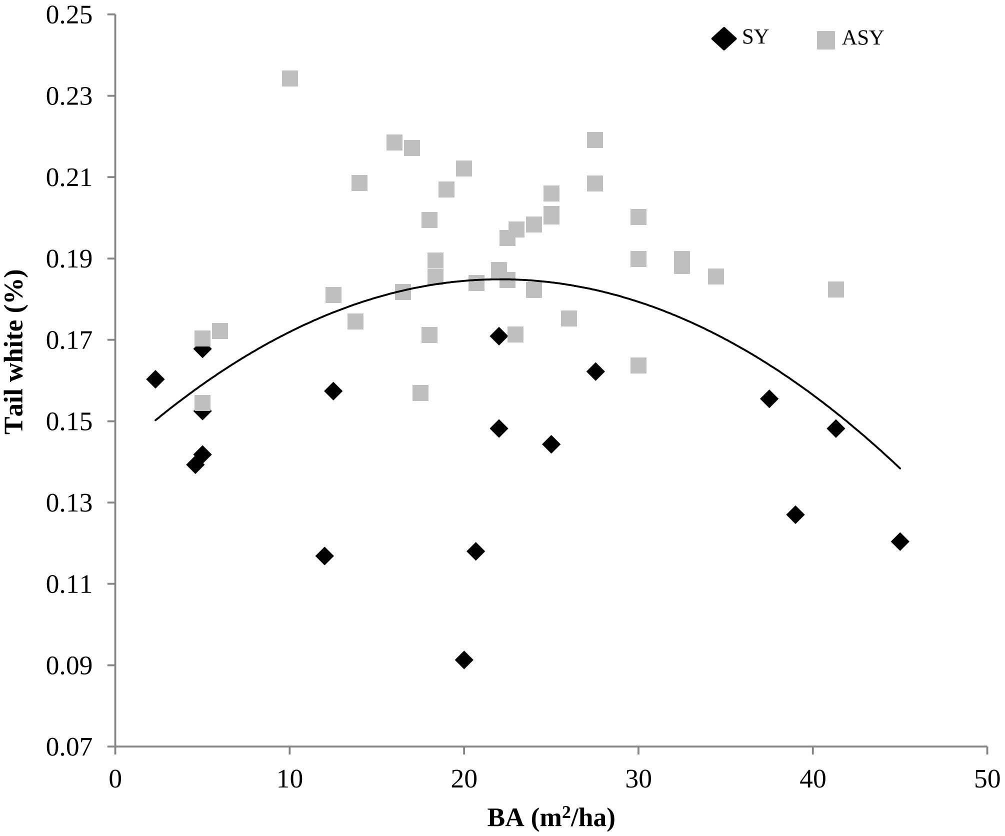

Figure 3.7a-b. Relationship between log breast band (a) and tail white (b) and forest openness (via basal area; BA). We depict quadratic regression line for age classes and years pooled. Breast band $R^2 = 0.23$, $P = 0.0004$; tail white $R^2 = 0.17$, $P = 0.003$.

Figure 3.8a.

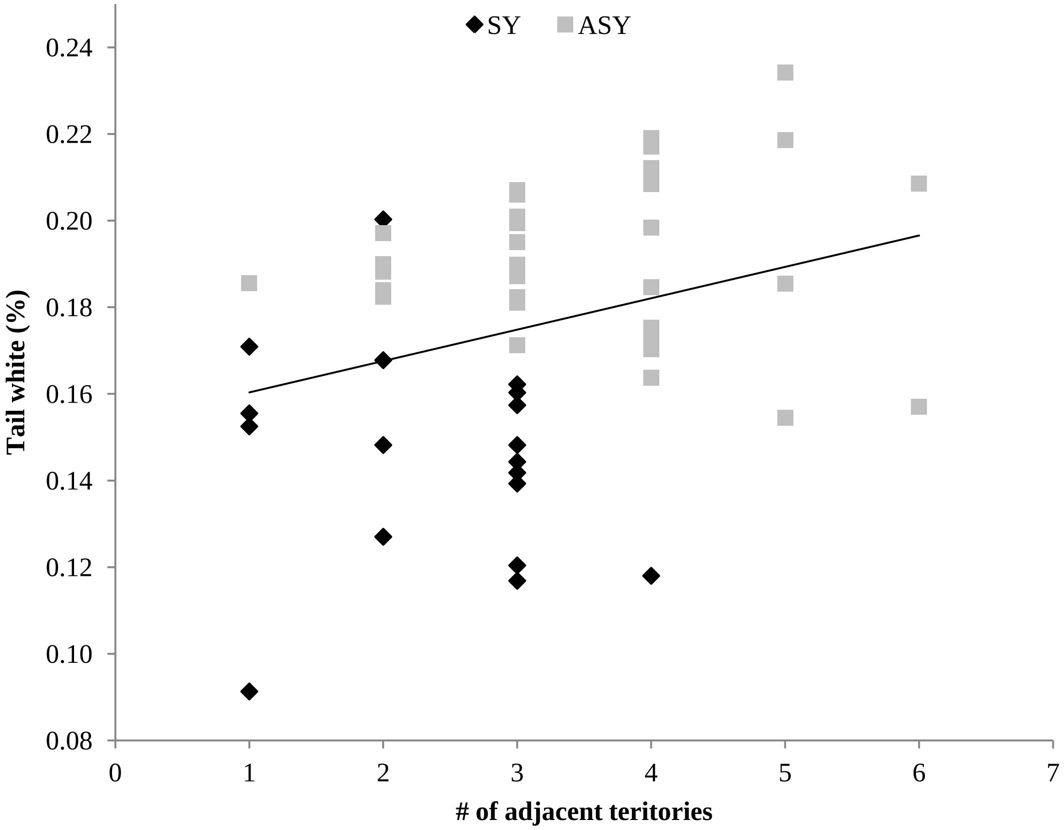

Figure 3.8a-b. Relationship between tail white (a) and breast band width (b) and density of competitors (# of adjacent territories). Tail white R^2 = 0.09, P = 0.03; breast band width R^2 = 0.11, P = 0.01.

Figure 3.8b.

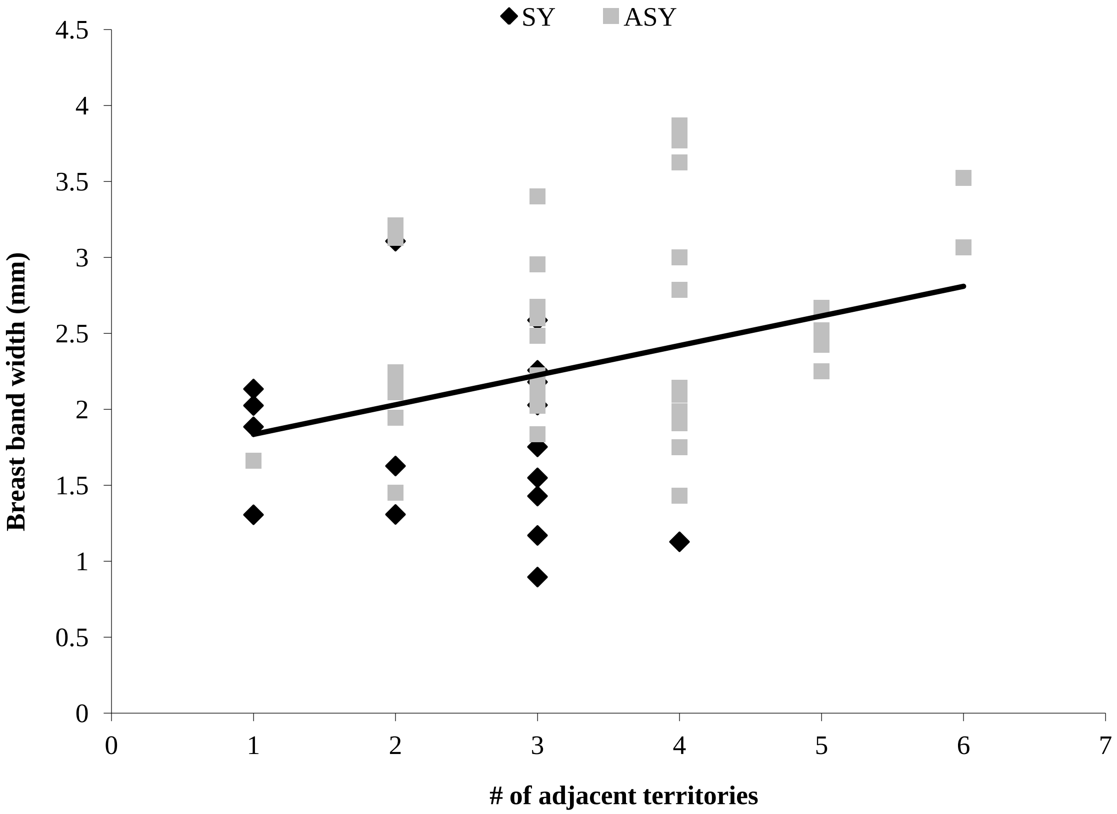

Figure 3.8a-b. Relationship between tail white (a) and breast band width (b) and density of competitors (# of adjacent territories). Tail white $R^2 = 0.09$, P = 0.03; breast band width $R^2 = 0.11$, $P = 0.01$.

CHAPTER 4: INFLUENCE OF HABITAT AND OTHER PROXIMATE FACTORS ON PARENTAL CARE BY CERULEAN WARBLERS

Abstract. Habitat disturbance may affect avian behavior by altering environmental factors such as vegetation structure, food availability, competition, predation, and micro-climate. One adaptive way in which individuals may respond to novel ecological conditions is to adjust parental behavior. In this study, we investigated the impact of habitat disturbance on parental behavior at nests across a range of experimentally disturbed forest conditions using the globally-vulnerable Cerulean Warbler (*Setophaga cerulea*) as a model species. We hypothesized that structural habitat variables that are positively related to habitat disturbance (increased understory cover and decreased basal area) would cause parents to adjust behavior adaptively to reflect increased predation risk previously observed in these habitats. Specifically, we predicted that parents would decrease feeding rates while increasing food loads and nest attendance as disturbance increased. To test these predictions, we used an information-theoretic framework to compare the influence of multiple factors, including habitat, temporal, abiotic, biotic, and individual-based variables, on feeding rates, food loads, and nest attendance at 56 successful nests from 2009–2010. As ceruleans engage in bi-parental care, we also compared influence of factors by sex. Contrary to our expectations, males fed at greater rates and brought decreased food loads as disturbance levels increased. Females showed similar patterns, but their behavior was affected by factors other than habitat structural variables, particularly nestling age. At least two alternative explanations for these contradictory results exist: 1) diurnal predation may not have been a major selective pressure at this stage of the nesting cycle in disturbed habitats and parents behaved in an adaptive manner, or 2) cerulean parents at nests in disturbed habitats were unable to accurately assess predation risk and thus behaved maladaptively and these nests survived for reasons unrelated to parental care at this stage in the nesting cycle. In addition, male and females responded similarly to all variables with the exception of year and male condition.

Male attendance time was positively related to their condition and they decreased feeding rates from 2009 to 2010; female attendance time was negatively influenced by their mate's condition and they increased feeding rates during that same time period.

INTRODUCTION

Habitat disturbance may affect avian species by altering environmental factors such as vegetation structure, food availability, competition, predation, and micro-climate (Brawn et al. 2001). While much information exists regarding population-level responses by avian species to the effects of habitat disturbance, information regarding more proximate individual responses which likely drive population response is often lacking (Sallabanks et al. 2000, Gerber 2006). Individuals may respond to environmental perturbations in many ways, behaviorally and physiologically (Lent and Capen 1995, Wasser et al. 1997). One adaptive way in which individuals may respond to novel environmental conditions brought about by disturbance is to adjust parental behavior to reflect altered ecological conditions.

Almost all avian species engage in some form of parental care, and parental behavior can have major consequences for the development and survival of offspring, thereby affecting individual fitness (Lack 1968, Clutton-Brock 1991) and, ultimately, population viability. Strategies of parental behavior in nesting birds often involve trade-offs between behaviors which address the competing pressures of food limitation and predation risk (Martin 1995). These competing ultimate factors are often directly opposed, and both can be influenced by habitat disturbance. To make adaptive decisions on parental care, birds must also be able to accurately assess both factors. Moreover, the balance between provisioning and predation may differ among habitats, and parents may need to adjust behaviors appropriately if they are to reproduce successfully in dynamic environments (Carlisle 1982, Lima 2009). For example, increasing provisioning rates in novel environments with greater food resources may lead to stronger, healthier nestlings, but may also alert predators to nest locations and increase the likelihood of depredation (Skutch 1949, Zanette et al. 2006). Therefore, natural selection should “reward” individuals breeding in areas of high predation that can accurately assess predation risk and decrease nest visitation rates while increasing average food load sizes (Martin et al. 2000, Eggers et al. 2005). Alternatively, birds occupying poor quality habitat (e.g., low food resources) may need to spend more time foraging and less time engaging in anti-predator activities (Rastogi et al. 2006).

In addition to the pressures of food limitation and predation risk, several other factors may tip the balance between costs and benefits of specific behaviors and influence parental care strategies (Drent and Daan 1980). Parental behavior may be influenced by temporal or climate-related variables (Conway and Martin 2000, Sperry et al. 2008), the number and age of nestlings (Curio 1987, Moreno 1987), the density of competitors (Qvarnström 1997), and individual quality or perceived quality of a mate (Pugesek and Diem 1983, Ardia and Clotfelter 2006). For example, older birds or birds in better condition may be able to provision more often than inexperienced individuals or those struggling to survive themselves (Tveraa et al. 1998). Or in nests with older nestlings, parents may bring larger food loads because the young are better able to consume larger items, and they may feed more often because they are not as concerned with predation risk (as the young will be better able to escape predation attempts).

Unlike most taxa, bi-parental care is very common in birds (Lack 1968). While both parents often contribute to the care of offspring, these contributions are often not equal (Olson et al. 2008). Differences in parental behavior between the sexes may reflect anatomical or physiological constraints such as brood patches in females and testosterone production in males

(Ketterson et al. 1992), differences in initial investment in offspring (typically greater for females, Trivers 1972), uncertainty of paternity for males (Westneat and Sherman 1993), or differences in perceived quality of their mate (Harris and Uller 2009). For example, while social monogamy is often the rule in passerines (Lack 1968), extra-pair paternity (EPP, Griffith et al. 2002) occurs in many species. As male assurance of paternity decreases, particularly in species where EPP is common, individual males may decrease the amount of energy they invest in a given brood. Alternatively, if a bird perceives their mate to be of high genetic quality, they may invest more energy in a brood as the offspring may be more valuable to their lifetime fitness (differential allocation hypothesis, Burley 1988).

In this study, we investigated parental behavior of Cerulean Warblers (*Setophaga cerulea*) at nests found across a range of manipulated forest conditions (created via partial timber harvests). Previous research on this population of ceruleans has shown that greatest breeding densities (i.e., preferred forest conditions) occur in areas where the upper canopy has been moderately disturbed and canopy openings exist (basal area = 10 – 20 m^2/ha), although individuals also occupy areas of greater and lesser canopy disturbance and stem density. Despite attraction to disturbed forest, reproductive success is decreased in these habitats (T.J. Boves, *unpublished data*), likely because of increased nest predation (Ricklefs 1969, Martin 1995, Boves and Buehler *In Revision*). Despite greater rates of nest failure, some broods are successfully raised to fledging in disturbed forest habitats. Therefore, we hypothesized that parents who raise broods successfully in disturbed habitats will adjust care strategies to match the prevailing ecological conditions. Specifically, we predicted that structural habitat variables positively related to habitat disturbance would cause parents to decrease feeding rates, increase food load sizes, and increase nest attendance, ultimately because of increased predation risk. Alternatively, we recognize that many other factors may impact parental care, so we evaluated the influence of a variety of other potentially important biotic, abiotic, and individual-based factors. Moreover, we evaluated parental behavior for both males and females separately to determine if, and how, habitat disturbance and other factors influence parental care differently by sex (e.g., competitor density may reduce male care more than female). In addition, because extra pair paternity may be common in the species (Barg et al. 2006) and males have been observed provisioning young at multiple nests (ca. 10% of males, Barg et al. 2006, Boves and Buehler *In Revision*), we tested the prediction that females contribute more to parental care, in terms of provisioning rates and attendance time, than males. While we were unable to address the ultimate causes of adjustments to parental behavior (e.g., food availability and predation), we were able to tease apart the importance of proximate factors (which may be more accurately measured in a canopy-dwelling avian species) that drive observed patterns of gender-specific parental behavior and then speculate on their ultimate cause.

METHODS

Study Area

We conducted this study in the North Cumberland Wildlife Management Area, Campbell County, TN, USA (36°12’ N, 84° 16’ W) in 2009–2010 on forest stands which were experimentally disturbed via partial timber harvest at a range of intensities during the fall of 2005 and spring of 2006. The manipulations provided a range of forest conditions in which ceruleans could nest, from heavily disturbed forest (>70% reduction in overstory canopy cover and basal area, hereafter BA) to undisturbed forest (closed canopy). We implemented disturbances on eight 10-ha forest plots, each separated by at least 500-m of undisturbed forest and located within a highly forested landscape (85% forested within 10-km radius). These disturbances potentially altered several ecological characteristics that could influence parental behavior. Structural vegetation features that were most distinctly altered were basal area (a highly repeatable measure and tightly correlated to upper canopy foliage area) and understory foliage cover (T.J. Boves, *unpublished data*). Breeding densities ranged from 0.3 pairs/ha in unharvested areas to >2 pairs/ha in moderately or heavily disturbed forest stands. Observed and likely nest predators in this area included Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), Sharp-shinned and Cooper's Hawks (*Accipiter striatus* and *cooperi*), Eastern Chipmunk (*Tamias striatus*), Southern Flying Squirrel (*Glaucomys volans*), Gray Squirrel (*Sciurus carolinensis*), Raccoon (*Procyon lotor*) and Black Rat Snake (*Elaphe obsoleta*).

Study species

Cerulean Warblers are small (9 g), territorial, socially monogamous, insectivorous mature forest songbirds that nest in the canopy of deciduous forests of the eastern United States (Hamel 2000). They are an ideal model organism to explore the relationship between forest disturbance and parental care because they are capable of occupying a wide-range of forest habitats, from heavily disturbed to closed canopy conditions. Cerulean behavior is also of interest because of their current conservation status. Cerulean Warblers are one of the fastest declining avian species in North America; populations declined 3.2%/yr from 1966 to 2003 and more recently (2003–2008) at -4.6%/yr (Ziolkowski et al.). Ceruleans are listed as a species of conservation concern by the U. S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2008) and considered 'vulnerable to extinction' by Birdlife International (BirdLife International 2010). Therefore, understanding how the species responds behaviorally to disturbance is of both ecological and conservation interest.

Two previous studies of Cerulean Warbler parental behavior have been conducted. One small study, focused on the partitioning of care between male and females at 4 nests in Indiana, reported that females provisioned young significantly more often than males (Allen and Islam 2004). A second study also studied gender partitioning and examined the impact of feeding and incubation frequency on nest survival in Ontario (Barg et al. 2006). This study found that both parents fed nestlings at the same rate, and pairs which fed nestlings more often had increased nest survival rates, but suggested that the overall low nest visitation rates (relative to congeners) may dampen the impact that increased provisioning may have on predator attraction. They reported that males and females combined made, on average, only 4.4 feeding trips/hr.

Field procedures

We intensively searched for and monitored Cerulean Warbler nests from late April to late June. We located the majority of nests by listening for female vocalizations and observing female behavioral cues during construction and incubation (and to a lesser extent, male vocalizations and behavior). Once located, we used spotting scopes equipped with 20–60X magnification eyepieces to monitor nests for 30–45 min every 1–2 d. During these observation periods, we determined the identity of the male associated with the nest (based on color-bands, see below), and counted nestlings present. Between nestling days 7–10, we video-recorded each nest for one 2-hr period (nestlings remain in the nest for 10.5 d, on average, before fledging, Boves and Buehler *In Revision*). We recorded nests with video-recorders equipped with 30X optical zoom lenses and began recordings between 7:30 and 9:00 AM on days with no precipitation and little or no wind. After the breeding season, we watched videos in their entirety and recorded the number of feeding visits, the amount of time spent at the nest (which included apparent nest guarding and nest maintenance; our measure of “nest attendance”), and the food load of each provisioning bout for both sexes. Nest attendance consisted mainly of what we considered "nest guarding", where parents would perch next to the nest, often responding vigilantly to any nearby sound or movement. As we could not measure the actual size of prey items, we used an index to quantify the food load. We considered food loads (combined size of all prey items brought to the nest) smaller than the bill to be of size "1", food loads as large as the bill, size "2", food loads larger than the bill, size "3", and food loads at least twice as large as the bill, size "4". We also recorded brooding time (female only) and nest maintenance behaviors such as fecal sac removal. On the morning of each video-tape date, we also recorded ambient temperature (in the shade) using a Kestrel handheld thermometer. We did not include nests from which any nestlings had already fledged before we began recording or nests that had uniparental care (3 nests).

To estimate intraspecific densities surrounding nests, we performed eight spot-mapping sessions from 15 May to 15 June across each forest plot following standard spot-mapping protocol (Bibby et al. 2000). Particularly important were records of counter-singing males, which allowed for determination of territorial boundaries. Color-banded males aided in determining where territorial boundaries existed. Once territories were delineated, we estimated the number of adjacent territories (a surrogate measure of intraspecific competition) by counting the number of territories in direct contact with each focal nest territory.

To capture individual male ceruleans, we erected mist nets within territories, broadcast territorial songs and call notes, and displayed a male cerulean decoy attached to a line that we agitated to produce movement. After capture, we aged birds as second-year (SY; first breeding season) or after-second-year (ASY; ≥ 2nd breeding season) by plumage and molt limits (particularly useful is that SY birds retain brownish juvenile alula and primary coverts, Pyle 1997). We measured right wing length to the nearest 0.5 mm (using a straight wing rule) and mass to the nearest 0.01 g (using a digital scale). We fit each bird with a unique combination of plastic colored leg bands to later identify individuals in the field without recapture. We were unable to capture a large enough sample of females to include in this study.

After the breeding season was completed, we collected vegetation data from points located on the ground directly under each nest. We measured two structural habitat variables that were highly related to disturbance: understory cover (%) and basal area (m^2/ha). We defined understory cover as the proportion of a 0.04-ha area (situated around point center) covered by woody vegetation and foliage (including *Vitis* and *Rubus* spp.) from 0.5–3 m in height. We measured basal area using a 2.5× factor metric prism.

Statistical procedures

To evaluate the influence of key predictors on three specific parental behaviors, we performed separate multiple linear regression analyses and used AIC_c model selection to compare models. Models included individual and additive combinations of variables related to structural habitat disturbance, temporal and climatic variation, intraspecific competition, and individual male traits (each sex analyzed separately). We chose all predictor variables *a priori* based on our understanding of the system and the species. Directly related to our predictions, measured response behaviors were feeding trips/hr, average nest attendance time, and average food load size. In addition, we evaluated the influence of predictors on the total food delivered/hr (feeding rate/hr * average food load size). Prior to regressions, we examined pairwise correlations of predictor variables to assess for potential multi-collinearity (Table 4.1). We found no evidence of multi-collinearity; all r were < 0.5. We also examined variance inflation factors (VIF) and leverage plots after model selection; all VIF were < 2 and we found no evidence for multi-collinearity in leverage plots. We examined distributions of response variables, bivariate plots, and partial residual vs. fitted values to evaluate parametric assumptions and assess linearity. We log-transformed average food load size and attendance time/visit for males and attendance time/visit for females to address issues of non-normality.

To limit the number of models evaluated, we performed AIC_c model selection hierarchically (Table 4.2). We first assessed the influence of three temporal and climate variables that could potentially influence parental care, but were not of primary interest (i.e., nuisance covariates). These included year (YEAR; 2009-10), Julian date of the nest (DATE, May 1 = day 1), and temperature at the time of recording (TEMP). We included year because substantial annual variation in predation and food availability exists in many habitats (Schmidt and Ostfeld 2003, White 2008). We included Julian date because time of year will likely impact food availability and predation risk (Sperry et al. 2008). We included ambient temperature because this will likely impact immediate nestling and parental thermoregulation and energy requirements (Tinbergen and Dietz 1994), insect activity (Taylor 1963), and predator activity (particularly of ectotherms such as snakes; Huey 1982). We modeled all individual and additive combinations of these variables and carried all models with $\Delta AIC_c < 2$ over to the next suite of models (Burnham and Anderson). The second suite included variables related to specific biotic factors that may influence parental care, but also not of our primary interest: nestlings and intraspecific competition. We included nestling age (N_AGE), number of nestlings (NO_N), and number of territories adjacent to the nest territory (DENS). We included nestling variables because both have been shown to impact feeding rates and other parental behaviors (Barg et al. 2006, Leckie et al. 2008) and included density because competition can decrease parental care (Qvarnström 1997). We again carried top candidate models over to the suite of variables representing our main interest: habitat structure. We included basal area (BA) and understory cover (UNDER). We used these two variables because they were the most affected by our habitat modifications and described much of the variation in habitat structure among forest stands after the harvests were implemented (T.J. Boves, *unpublished data*). We again included all individual and additive combinations of these variables and previously supported models. We considered final models to have strong support when $\Delta AIC_c < 2$.

We completed our analysis at this point for our complete set of nests (n = 56), however we added a fourth level of model selection for a reduced, subset of nests (n = 23) for which we had additional information regarding age and/or condition of the male provisioning the brood. In this case, we again carried over the top remaining candidate models to a final suite of predictors including male age (M_AGE) and body mass to assess how individual male traits affected parental behavior.

We compared all models to a null model which included only the intercept. We calculated Akaike weights for all competing models in the final set and we assessed the impact of specific factors by examining partial correlation coefficients (β estimate; derived from the top model containing that variable), 95% CI of β estimates, and leverage plots of the effects of those variables. For analyses assessing food loads, the full data set was slightly lower (n = 50) as we were unable to estimate size of prey items for 6 nests.

To compare differential parental contributions by gender, we used paired t-tests. We first examined differences for normality; the differences of the matched pairs for nest attendance time did not follow a normal distribution, so we used the non-parametric Wilcoxon signed-rank test to analyze this data. Tests were two-tailed and we considered an alpha level of 0.05 to indicate a significant difference and 0.10 for a marginal difference. We performed all statistical analyses in JMP (v.9.02, SAS Institute, Cary, NC).

RESULTS

Gender differences in behavior

Males and females both fed nestlings nearly 8 times/hr (male = 7.70 ± 0.37, female = 7.93 ± 0.44 feeding trips/hr, Table 4.3) and total food delivered index was identical between parents (Male = 15.32 ± 6.20, female = 15.32 ± 6.50). Nest attendance time (not including brooding) was 93% greater in females (28.19 ± 3.00 s) than males (14.60 ± 0.67 s, $t_{55} = 4.69$, $P < 0.0001$). Males (2.04 ± 0.05) brought marginally larger average food loads than females (1.95 ± 0.04, $t_{49} = 1.83$, $P = 0.07$) and both genders removed fecal sacs at the same rate (male = 1.62 ± 0.11 sacs removed/hr, female = 1.65 ± 0.15, $t_{55} = 0.49$, $P = 0.63$). Only females brooded the young during our observations (261.39 ± 47.50 s/hr).

Factors influencing feeding rates

The highest ranked model explaining variation in male feeding rate was an additive model including understory cover, number of nestlings, and year (Table 4.4a). Other competing models with support included combinations of these three variables along with intraspecific density. In regards to habitat structure, after controlling for number of nestlings and year, feeding rate was positively related with understory cover (Figure 4.1, all β-estimates summarized in Table 4.5). Male feeding rate was also strongly positively related with the number of nestlings and weakly to year and intraspecific competition, as 95% CIs for these two covariates overlapped 0.

The highest ranked model explaining variation in female feeding rate was an additive model of nestling age and year (Table 4.4b). Other models with support included combinations of these two variables along with basal area and number of nestlings. In regards to habitat structure, after controlling for year, feeding rate was weakly negatively related to basal area (Figure 4.2). Feeding rates were also strongly negatively related to year and weakly positively related to age of nestlings. Incorporating male age and body mass in the reduced data set did not alter the models described above which best explained male or female feeding rates.

Factors influencing nest attendance time

The highest ranked model explaining variation in nest attendance time (log-transformed) by males only included temperature at the time of recording, while several other additive models also drew support (Table 4.6a). These included combinations of basal area, age of nestlings, and interspecific density. In regards to habitat structure, after controlling for temperature, nest attendance time was weakly positively associated with basal area. Nest attendance time was strongly negatively associated with temperature and weakly negatively associated with age of nestlings and intraspecific density. When including male age and body mass (reduced data set), the best model became an additive combination of male age, temperature, and Julian date (Table 4.7a). Body mass was also found in models with support. Nest attendance time was weakly negatively associated with male age and it was strongly positively associated with male body mass.

The highest ranked model explaining variation in nest attendance time (log-transformed) by females included age of nestlings alone, while several other additive models also had support (Table 4.6b). All supported models included age of nestlings in combination with basal area, intraspecific competition, temperature, Julian date, and year. In regards to habitat, after controlling for age of nestlings, nest attendance time was weakly positively associated with basal area. Attendance time was also strongly negatively associated with age of nestlings, and weakly negatively associated with intraspecific density, temperature, and Julian date. When including male age and body mass (reduced data set), the best model retained age of nestlings alone, but also with support was an additive combination of age of nestlings and male body mass (Table 4.7b).

Factors influencing food load sizes

The highest ranked model explaining variation in food load sizes (log-transformed) brought by males was an additive combination of understory cover, intraspecific density, temperature, and year (Table 4.8a). The only other model with support included the same first three variables, but date rather than year. In regards to habitat, after controlling for intraspecific density, temperature, and year, food load size was strongly negatively associated with understory cover (Figure 4.3). Food loads were also strongly positively associated with Julian date and year and strongly negatively associated with intraspecific density.

The highest ranked model explaining variation in food load sizes brought by females included an additive model including basal area, intraspecific density, temperature, date, and year (Table 4.8b). All other supported models included various combinations of these same variables as well as understory cover. In regards to habitat, after controlling for intraspecific density, temperature, date, and year, food load sizes were weakly positively associated with basal area (Figure 4.4) and weakly negatively associated with understory cover. Food loads were strongly negatively associated with temperature and intraspecific density and weakly positively associated with Julian date and year. Incorporating male age and body mass in the reduced data set did not alter the models which best explained male or female feeding rates.

Factors influencing total food delivered

The highest ranked model explaining variation in total food delivered by males was an additive model of year and number of nestlings (Table 4.9a). Other competing models with support included combinations of these two variables and understory cover and temperature. In regards to habitat, after controlling for year and number of nestlings, total food delivered was positively associated with understory cover, albeit weakly. Total food delivered was strongly positively associated with year and number of nestlings and weakly negatively associated with temperature.

The highest ranked model explaining variation in total food delivered by females included only the number of nestlings (Table 4.9b). Other competing models with support included additive combinations of this variable, age of nestlings, year, and basal area. In regards to habitat, after controlling for the number of nestlings, total food delivered was weakly negatively associated with basal area. Total food delivered was strongly positively associated with the number of nestlings, weakly positively associated with age of nestlings, and weakly negatively associated with year. Incorporating male age and body mass in the reduced data set did not alter the models which best explained total food delivery for males or females.

DISCUSSION

We observed plasticity of several parental behaviors with respect to structural habitat variables that were altered by forest disturbance. This was particularly true for male Cerulean Warblers. Males increased feeding rates markedly, but brought smaller food loads to nests located in habitats that had greater understory cover, a vegetative feature highly related to disturbance in this system. Males also spent less time attending nests in habitats with lower basal area (although this was a weaker association). Females showed similar patterns, however mothers altered behavior more in response to variation in basal area (which is related to overstory canopy foliage area) than understory cover, and their behavior was often influenced more heavily by factors other than habitat structure (e.g., nestling age and annual variability). Females increased feeding rates, decreased nest attendance, and brought smaller food loads as basal area decreased (i.e., as disturbance increased).

Adaptiveness of parental behavior

These results were contradictory to our predictions as we expected parents at nests in disturbed habitat (increased understory cover and decreased basal area) to engage in behavior aimed at reducing predation risk (i.e., decrease feeding visits and increase average food loads and nest attendance time). At least two exclusive explanations for these contradictory results exist: 1) diurnal predation is not a major selective pressure (at this stage of the nesting cycle) in disturbed habitats and parents behaved in a neutral or adaptive manner, or 2) parents at nests in disturbed habitats were unable to accurately assess predation risk and thus behaved maladaptively (and these nests survived for reasons unrelated to parental care at this stage in the nesting cycle).

Despite >1000 h of direct diurnal nest observation and video-recording (across the entire nesting cycle), we observed predators at only 3 of 93 (3.2%) failed nests (Boves and Buehler *In Revision*). Therefore, we propose that nocturnal predation may be largely responsible for nest failures (we inferred predation at another 13 nests). If this is the case, diurnal parental behavior may have little impact on nest survival, and increased feeding rates may simply reflect a greater abundance of small insects available in disturbed habitats. These diurnal behaviors could then potentially be adaptive if it improved the condition of nestlings and increased post-fledgling survival (Naef-Daenzer et al. 2001). Total food delivered/hr was positively related to disturbance for both males and females (weakly), so increased nest visits may have resulted in greater biomass provided to nestlings. However, it is difficult to explain how reducing food loads would be an adaptive behavioral response under most ecological circumstances. We were not able to quantify the number of food items brought to nests in all cases, but we were able to estimate this at some nests and it ranged from 1–5 insects per food load (T.J Boves, *unpublished data*). Therefore, parents were physically capable of adjusting food loads, but those with nests in disturbed habitats did not do so as readily as parents nesting in more undisturbed forest. Thus, because nest failure increased in disturbed conditions and was most commonly caused by predation (as is the case for most passerines), these parental behaviors could also be maladaptive, despite the fact that all the nests that we recorded were successful (produced ≥1 nestling). Alternative factors which could have aided in the success of these nests include variation in micro-habitat characteristics or concealment (Martin and Roper 1988), active parental defense strategies (such as injury-feigning, Brunton 1990), alternate parental behavior during more vulnerable times of the nesting cycle (e.g., earlier in the nestling period), or these nests may have merely been "lucky" and benefited from the semi-stochastic nature of predation.

The difference in behavior among parents in various forest conditions may in fact help explain why nest failure was greater in disturbed habitats. If parents are unable to accurately assess predation risk in specific habitats, they may act in maladaptive ways that attract predators (Fontaine and Martin 2006). As contemporary fragmentation and land use patterns have been altered by humans, associated edge and disturbance-related predators may have increased (Chalfoun et al. 2002). This, along with the extirpation of top predators, has likely increased populations of many mesopredators, which are among the main predators responsible for nest depredation of passerines (Crooks and Soulé 1999). Therefore, contemporary predation pressures in disturbed habitats may not be well-recognized by ceruleans and may explain the behavioral patterns that we observed. At a minimum, our data suggest that nests which succeeded in disturbed habitats did so because of factors other than adjustments to parental care (at this stage of the nesting cycle). Twenty-four hour monitoring of nests throughout the entire nesting cycle will be an important next step to better understand what predators are responsible for nest failure, and will help clarify the question of (mal)adaptiveness of these parental behaviors.

Other factors influencing parental behavior

We found that several factors other than habitat structure also strongly influenced parental behavior. In males, feeding rate was positively associated with brood size, nest attendance time was negatively related with temperature and positively related to male condition, and food load fluctuated annually and was negatively related to ambient temperature and intraspecific competition. In females, feeding rate varied annually, nest attendance was negatively related to nestling age, and female food loads were negatively related to ambient temperature and intraspecific density.

Of the three behaviors, nest attendance was the least strongly influenced by habitat variables. Instead, for males, attendance was influenced by, more than any other behavior, male age and condition (as well as ambient temperature). Interestingly, younger males spent more time attending the nest. A potential explanation for this is that SY birds were less likely to be polygynous or garner extra-pair copulations (von Haartman 1951, Bouwman et al. 2007) and therefore had more time available for nest defense. More expectedly, males in better condition spent markedly more time attending nests, possibly because they were more efficient foragers. In females, nest attendance was best explained simply by the age of nestlings. Females spent less time at the nest as the nestlings aged, which is contradictory to nest defense patterns in many other species (Montgomerie and Weatherhead 1988). However, this response seems to be adaptive in ceruleans at this point in the nesting cycle. Anecdotally, we found that as nestlings aged from 7–10 d, the likelihood of predation declined so that the need to guard the nest intensively during the last few days was not as crucial. We estimated that only 3 (of 93 failed nests) nests failed after day 8 of the nestling period, and we observed two cases of forced-fledging by predators on days 8 and 9 (by Blue Jay and Eastern Chipmunk, T.J. Boves, *unpublished data*). These observations, along with the nest attendance patterns of females, suggest that once nestlings were able to escape predation, females relaxed their vigilance and spent more time on other parental and self-maintenance activities.

Gender differences

Males and females fed nestlings at nearly the same rate, which was contrary to our expectations. Because provisioning duties were divided nearly equally, we would hypothesize that males should be fairly certain of the paternity of their offspring; if large amounts of uncertainty existed, we would expect them to contribute less than females (Dixon et al. 1994, Møller and Thornhill 1998). Unfortunately, very little information regarding EPP exists for ceruleans and EPP differs greatly among species (Griffith et al. 2002). Barg et al. (2006) referred to two cerulean nests where 4/7 total young were sired by extra-pair partners in Ontario, and we made anecdotal observations of likely extra-pair copulations on our sites, but as access to cerulean nestlings is exceedingly difficult, little information exists in this regard.

In most cases, the direction of influence for specific ecological correlates on behavior was similar for both parents. However, there were two notable exceptions: feeding rates in relation to annual variability and nest attendance in relation to male body condition. Females increased feeding rates from 2009 to 2010, while males decreased their feeding rate over that same period, suggesting that females altered their behavior based on their mate’s level of parental care. In addition, males increased feeding rates more so in response to increased understory cover while females responded more to decreased basal area. These gender-specific responses may reflect alternate foraging strategies combined with oscillations of insect composition and abundance between years and forest strata (Myers 1988). Males provisioned nestlings with marginally larger food loads than females, often consisting of large lepidopteran larvae (T.J. Boves, *unpublished data*). While we did not identify these prey items to species, they may represent taxa whose populations fluctuate and peaked in 2009, or were relatively depressed in 2010. In relation to male condition, male nest attendance increased strongly as body mass increased, while female nest attendance decreased in response to male body mass (although weakly). These patterns are both congruent with the reproductive compensation hypothesis of parental investment (Harris and Uller 2009) and suggest that females adjust the time and effort they invest in broods, contingent on contributions by the father.

Geographic variation

We documented much greater feeding rates than those reported in both Ontario and Indiana. In Ontario, Barg et al. (2006) found that both males and females provisioned nestlings 2.2 ± 0.2 times/hr, with the maximum number of feeding visits for females being 6 trips/hr and 8 trips/hr for males. Thus, the maximum feeding rate recorded in Ontario was below the mean feeding rate for females, and approximately equal to the mean feeding rate for males in this study. These differences may be related to specific ecological factors that allow ceruleans to feed at higher rates, such as decreased predation risk or increased insect availability. However, we believe these differences may at least partially be explained by sampling methods (direct observation vs. video recording). Barg et al. implied that cerulean nest behavior was not influenced by human presence; however our experiences did not support this assertion. Despite the extreme heights of cerulean nests (>18 m on average, T.J. Boves, *unpublished data*), we often observed parents, females in particular, refuse to approach nests while we were monitored them from the ground below. In some cases, parents would approach their nest only after we concealed our presence using a blind. Therefore, we believe that these previous studies of cerulean nest behavior may be influenced by the effect of human presence and should not necessarily be considered valid measures of behavior under natural conditions.

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APPENDIX

	DATE	TEMP	NO_N	AGE_N	DENS	BA	COVER	MASS
DATE	1							
TEMP	0.45	1						
NO_N	-0.46	-0.18	1.00					
N_AGE	0.07	0.14	0.08	1				
DENS	-0.09	-0.07	-0.07	0.22	1			
BA	-0.24	-0.11	0.08	-0.09	-0.34	1		
COVER	-0.01	0.08	-0.12	-0.05	0.31	-0.39	1	
MASS	-0.48	-0.34	0.10	-0.11	-0.03	0.36	0.30	1

Table 4.1. Pairwise correlations (estimated using REML method) for 8 continuous predictor variables of measures of parental care by Cerulean Warblers. We also included binary variables of year (YEAR) and male age (M_AGE).

Suite	**Variables**
I. Abiotic: Temporal and climate	Year (YEAR)
	Julian date (DATE)
	Temp at recording (TEMP)
II. Biotic: Nestling and competition	Age of nestlings (N_AGE)
	Number of nestlings (NO_N)
	Number of adjacent territories (DENS)
III. Habitat structure/disturbance	Basal area (BA)
	Understory cover (UNDER)
IV. Individual characteristics (Reduced dataset)	Male body mass (MASS)
	Male age (M_AGE)

Table 4.2. Environmental and ecological factors included in model selection process, listed hierarchically in the order we performed the analyses.

		Males		**Females**					
Behavior	**n**	$\bar{x}$	**Range**	$\bar{x}$	**Range**	**Mean Dif**	**SE**	***t/S***	***P***
Feeding visits/hr	56	7.93	1.50–14	7.70	2–18.5	0.23	0.59	0.38	0.70
Nest attendance/visit (s)	56	14.60	5.29–31.79	28.19	7.69–120	13.59	2.90	624.5	**>0.0001**
Average food load (index)	50	2.05	1.43–2.90	1.94	1–2.58	0.11	0.048	1.83	**0.07**
Total food delivered/hr (index)	50	15.32	3–31	15.32	5–32	0.00	1.33	0.00	1.00
Fecal sacks removed/hr	57	1.60	0–4	1.69	0–5	0.09	0.37	0.49	0.63
Brooding/hr (s) (female only)	60	0	-	261.39	0–1430	261.39	-	-	-

Table 4.3. Summary of gender-specific parental care behaviors. Results of statistical tests are included; paired t-tests were used for all statistical comparisons except nest attendance time (Wilcoxon signed-rank). Marginal and significant results are in **bold**.

Table 4.4a. Males

Model	**AIC$_c$**	**ΔAIC$_c$**	**K**	***w***	**R^2**
UNDER + NO_N + YEAR	272.16	0	4	0.17	0.17
UNDER + DENS + NO_N + YEAR	272.38	0.22	5	0.15	0.20
DENS + NO_N + YEAR	272.70	0.53	4	0.13	0.16
UNDER + DENS + NO_N	273.00	0.84	4	0.11	0.16
DENS + NO_N	273.84	1.68	3	0.07	0.11
UNDER	273.99	1.83	2	0.07	0.07
INTERCEPT ONLY (NULL)	275.68	3.52	1	0.03	0.00

Table 4.4b. Females

Model	**AIC$_c$**	**ΔAIC$_c$**	**K**	***w***	**R^2**
AGE_N + YEAR	292.23	0	3	0.20	0.12
YEAR	292.46	0.23	2	0.17	0.07
BA + YEAR	293.68	1.45	3	0.09	0.09
BA + AGE_N + YEAR	293.77	1.54	4	0.08	0.13
NO_N + YEAR	293.80	1.57	3	0.08	0.09
AGE_N + NO_N + YEAR	293.84	1.61	4	0.08	0.13
AGE_N	294.12	1.89	2	0.07	0.05
INTERCEPT ONLY (NULL)	294.57	2.33	1	0.04	0.00

Table 4.4a-b. Final models (and null) using full nest set (*n* = 56) with strong support explaining variation in feeding rates for (a) males and (b) females. ΔAIC$_c$ = AIC$_{c\,i}$ - AIC$_{c\,min}$ and *w* is the Akaike weight reflecting the probability that the model is the best among all competing models. Habitat variables included are in **bold**.

Feeding rate

		Female			**Male**		
Factor suite	**Variable**	**β**	**Lower 95% CI**	**Upper 95% CI**	**β**	**Lower 95% CI**	**Upper 95% CI**
Temporal	**TEMP**	-	-	-	-	-	-
	DATE	-	-	-	-	-	-
	YEAR	**-0.86**	**-1.71**	**-0.01**	0.56	-0.15	1.27
Biotic	**NO_N**	0.64	-0.69	1.96	**1.20**	**0.11**	**2.28**
	N_AGE	0.80	-0.22	1.82	-	-	-
	DENS	-	-	-	0.40	-0.15	0.94
Habitat	**BA**	-0.04	-0.12	0.04	-	-	-
	UNDER	-	-	-	**3.02**	**0.21**	**5.83**
Individual	**M_AGE**	-	-	-	-	-	-
	MASS	-	-	-	-	-	-

Nest attendance

		Female			**Male**		
Factor suite	**Variable**	**β**	**Lower 95% CI**	**Upper 95% CI**	**β**	**Lower 95% CI**	**Upper 95% CI**
Temporal	**TEMP**	-0.04	-0.10	0.02	**-0.04**	**-0.07**	**-0.01**
	DATE	-0.01	-0.02	0.01	-	-	-
	YEAR	0.08	-0.08	0.23	-	-	-
Biotic	**NO_N**	-	-	-	-	-	-
	N_AGE	**-0.22**	**-0.41**	**-0.04**	-0.06	-0.16	0.04
	DENS	-0.09	-0.20	0.03	-0.04	-0.10	0.03
Habitat	**BA**	0.01	-0.01	0.02	0.004	-0.004	0.01
	UNDER	-	-	-	-	-	-
Individual	**M_AGE**	-	-	-	-0.09	-0.19	0.02
	MASS	-0.25	-0.74	0.25	**0.31**	**0.05**	**0.57**

Table 4.5. Summary of partial regression coefficients (β estimates) and 95% CI for key predictor variables included in final models that garnered strong support. Estimates were derived from the top model that included the respective variable. For nest attendance, individual male traits improved models and we therefore show estimates from reduced data set for those behavior, while β estimates for all other behaviors come from using full data set**.** Variables where 95% CI of β did not overlap 0 are in highlighted in **bold.**

Table 4.5 (cont'd).

Food load size

		Female			**Male**		
Factor suite	**Variable**	**β**	**Lower 95% CI**	**Upper 95% CI**	**β**	**Lower 95% CI**	**Upper 95% CI**
Temporal	**TEMP**	**-0.05**	**-0.09**	**-0.01**	**-0.02**	**-0.04**	**-0.004**
	DATE	0.01	-0.001	0.02	**0.004**	**0.0002**	**0.01**
	YEAR	0.08	-0.01	0.16	**0.05**	**0.01**	**0.09**
Biotic	**NO_N**	-	-	-	-	-	-
	N_AGE	-	-	-	-	-	-
	DENS	**-0.07**	**-0.13**	**-0.01**	**-0.03**	**-0.06**	**-0.01**
Habitat	**BA**	0.01	-0.001	0.01	-	-	-
	UNDER	-0.22	-0.53	0.10	**-0.22**	**-0.37**	**-0.07**
Individual	**M_AGE**	-	-	-	-	-	-
	MASS	-	-	-	-	-	-

Total food delivered

		Female			**Male**		
Suite	**Variable**	**β**	**Lower 95% CI**	**Upper 95% CI**	**β**	**Lower 95% CI**	**Upper 95% CI**
Temporal	**TEMP**	-	-	-	-0.48	-1.23	0.28
	DATE	-	-	-	-	-	-
	YEAR	-0.67	-2.48	1.15	**2.46**	**0.86**	**4.05**
Biotic	**NO_N**	**2.77**	**0.04**	**5.50**	**2.79**	**0.37**	**5.22**
	N_AGE	1.29	-1.04	3.72	-	-	-
	DENS	-	-	-	-	-	-
Habitat	**BA**	-0.06	-0.23	0.11	-	-	-
	UNDER	-	-	-	3.05	-3.48	9.59
Individual	**M_AGE**	-	-	-	-	-	-
	MASS	-	-	-	-	-	-

Table 4.5. Summary of partial regression coefficients (β estimates) and 95% CI for key predictor variables included in final models that garnered strong support. Estimates were derived from the top model that included the respective variable. For nest attendance, individual male traits improved models and we therefore show estimates from reduced data set for those behavior, while β estimates for all other behaviors come from using full data set. Variables where 95% CI of β did not overlap 0 are in highlighted in **bold.**

Table 4.6a. Males

Model	**AIC$_c$**	**ΔAIC$_c$**	**k**	***w***	**R^2**
TEMP	33.53	0	2	0.17	0.09
AGE_N + TEMP	34.48	0.95	3	0.11	0.11
DENS + TEMP	34.55	1.02	3	0.11	0.11
BA + TEMP	34.72	1.18	3	0.10	0.11
INTERCEPT ONLY (NULL)	36.64	3.11	1	0.04	0.00

Table 4.6b. Females

Model	**AIC$_c$**	**ΔAIC$_c$**	**k**	***w***	**R^2**
AGE_N	101.65	0.00	2	0.14	0.10
DENS + AGE_N	101.77	0.12	3	0.13	0.13
DENS + AGE_N + TEMP	102.37	0.72	4	0.11	0.16
AGE_N + TEMP	102.65	1.00	3	0.08	0.12
BA + AGE_N	102.76	1.11	2	0.08	0.12
DENS + AGE_N + DATE	102.77	1.12	4	0.08	0.15
AGE_N + DATE	102.98	1.33	3	0.07	0.11
AGE_N + YEAR	103.07	1.42	3	0.07	0.11
DENS + AGE_N + YEAR	103.33	1.68	4	0.06	0.14
DENS + TEMP	103.42	1.77	3	0.05	0.11
INTERCEPT ONLY (NULL)	105.10	3.45	1	0.02	0.00

Table 4.6a-b. Final models (and null) using full nest set (*n* = 56) with strong support explaining variation in nest attendance time (log-transformed) for (a) males and (b) females. ΔAIC$_c$ = AIC$_{c\ i}$ - AIC$_{c\ min}$ and *w* is the Akaike weight reflecting the probability that the model is the best among all competing models. Habitat variables are in **bold**.

Table 4.7a. Males

Model	**AIC_c**	**ΔAIC_c**	**k**	***w***	**R^2**
M_AGE + TEMP + DATE	-2.61	0.00	4	0.40	0.44
MASS + MALE_AGE	-1.17	1.44	3	0.17	0.30
MASS + MALE_AGE + TEMP + DATE	-0.89	1.72	5	0.15	0.49
INTERCEPT ONLY (NULL)	0.99	3.60	1	0.05	0.00

Table 4.7b. Females

Model	**AIC_c**	**ΔAIC_c**	**k**	***w***	**R^2**
AGE_N	25.36	0.00	2	0.62	0.27
AGE_N + MASS	27.16	1.80	3	0.22	0.31
INTERCEPT ONLY (NULL)	29.64	4.28	1	0.05	0.00

Table 4.7a-b. Final models (and null) using reduced data set (*n* = 22) and including data on male characteristics (age and mass) as predictors, with most support explaining variation nest attendance time (log-transformed) for (a) males and (b) females. $\Delta AIC_c = AIC_{c\,i} - AIC_{c\,min}$ and *w* is the Akaike weight reflecting the probability that the model is the best among all competing models.

Table 4.8a. Males

Model	**AIC_c**	**ΔAIC_c**	**k**	***w***	**R^2**
UNDER + DENS + TEMP + YEAR	-57.31	0.00	5	0.59	0.47
UNDER + DENS + TEMP + DATE	-55.94	1.37	5	0.31	0.45
INTERCEPT ONLY (NULL)	-35.51	21.80	1	0.00	0.00

Table 4.8b. Females

Model	**AIC_c**	**ΔAIC_c**	**k**	***w***	**R^2**
BA + DENS + TEMP + DATE + YEAR	14.12	0.00	6	0.15	0.43
DENS + TEMP + YEAR	14.31	0.19	4	0.13	0.37
BA + DENS + TEMP + DATE	14.64	0.51	5	0.11	0.39
BA + DENS + TEMP + YEAR	14.75	0.63	5	0.10	0.39
UNDER + DENS + TEMP + YEAR	14.80	0.67	5	0.10	0.39
DENS + TEMP + DATE + YEAR	15.16	1.04	5	0.08	0.39
UNDER + DENS + YEAR	15.36	1.23	4	0.07	0.35
UNDER + DENS + TEMP + DATE + YEAR	15.94	1.81	6	0.05	0.41
DENS + YEAR	15.95	1.83	3	0.05	0.31
DENS + TEMP + DATE	16.07	1.94	4	0.05	0.34
INTERCEPT ONLY (NULL)	30.01	15.88	1	0.00	0.00

Table 4.8a-b. Final models (and null) using full nest set (*n* = 50) with most support explaining variation in average food load size for (a) males (log-transformed) and (b) females. $\Delta AIC_c = AIC_{c\,i} - AIC_{c\,min}$ and *w* is the Akaike weight reflecting the probability that the model is the best among all competing models. Habitat variables are in **bold**.

Table 4.9a. Males

Model	**AICc**	**ΔAICc**	**k**	***w***	**R^2**
NO_N + YEAR	319.34	0	3	0.38	0.23
NO_N + TEMP + YEAR	320.07	0.73	**4**	0.27	0.25
UNDER + NO_N + YEAR	320.86	1.52	4	0.18	0.24
TEMP + YEAR	321.00	1.66	3	0.17	0.20
INTERCEPT ONLY (NULL)	327.48	8.14	1	0.01	

Table 4.9b. Females

Model	**AICc**	**ΔAICc**	**k**	***W***	**R^2**
NO_N	330.49	0.00	2	0.36	0.08
NO_N + AGE_N	331.56	1.07	3	0.21	0.10
NO_N + YEAR	332.28	1.79	3	0.15	0.09
INTERCEPT ONLY (NULL)	332.38	1.89	1	0.14	
BA + NO_N	332.40	1.90	3	0.14	0.09

Table 4.9a-b. Final models (and null) using full nest set (n = 50) with most support explaining variation in total food delivered/hr (feeding rate/hr * average food load size) for (a) males and (b) females. $\Delta AIC_c = AIC_{c\,i} - AIC_{c\,min}$ and *w* is the Akaike weight reflecting the probability that the model is the best among all competing models. Habitat variables are in **bold**.

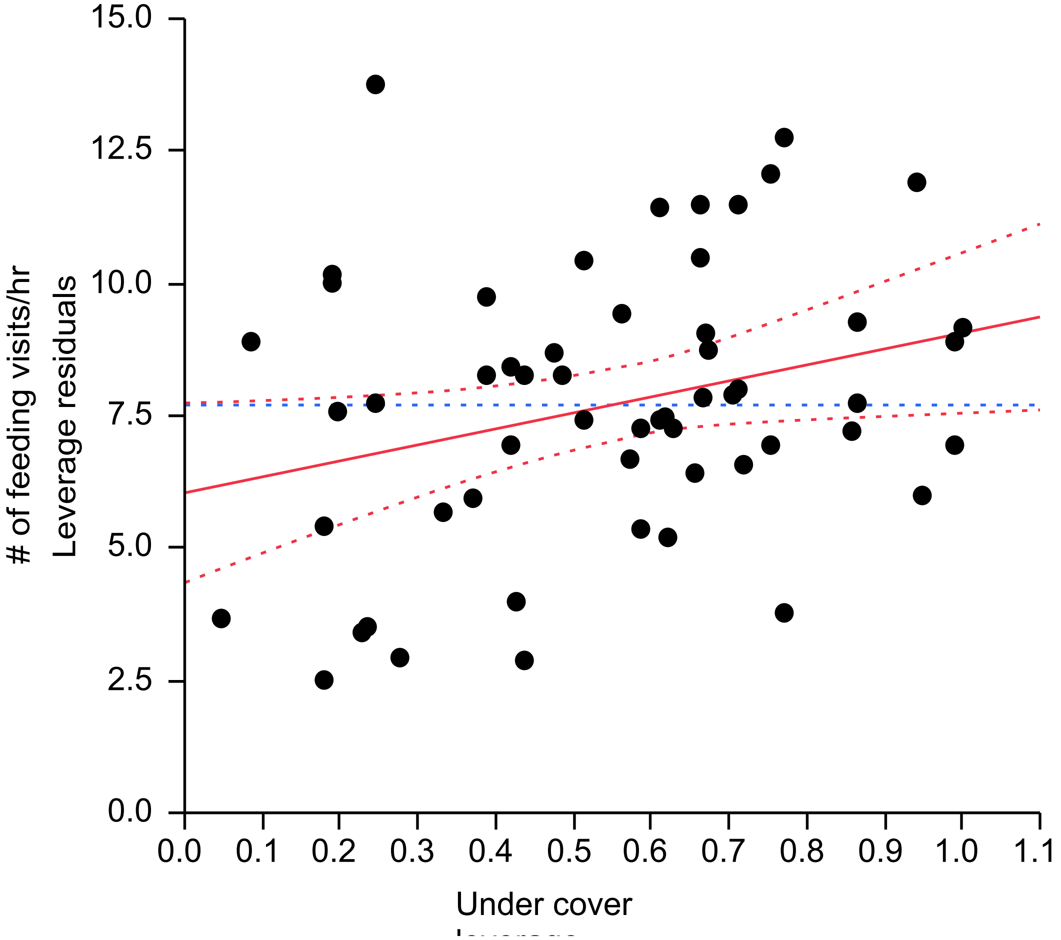

Figure 4.1. Leverage plot indicating the strength of understory cover influence on feeding rates of male Cerulean Warblers (after controlling for year and number of nestlings).

Solid red line depicts partial regression line, curved and dotted red lines represent 95% CI of partial regression line, and horizontal dotted blue line represents null hypothesis of no influence of understory cover. CI lines cross horizontal line indicating partial regression slope is different than 0.

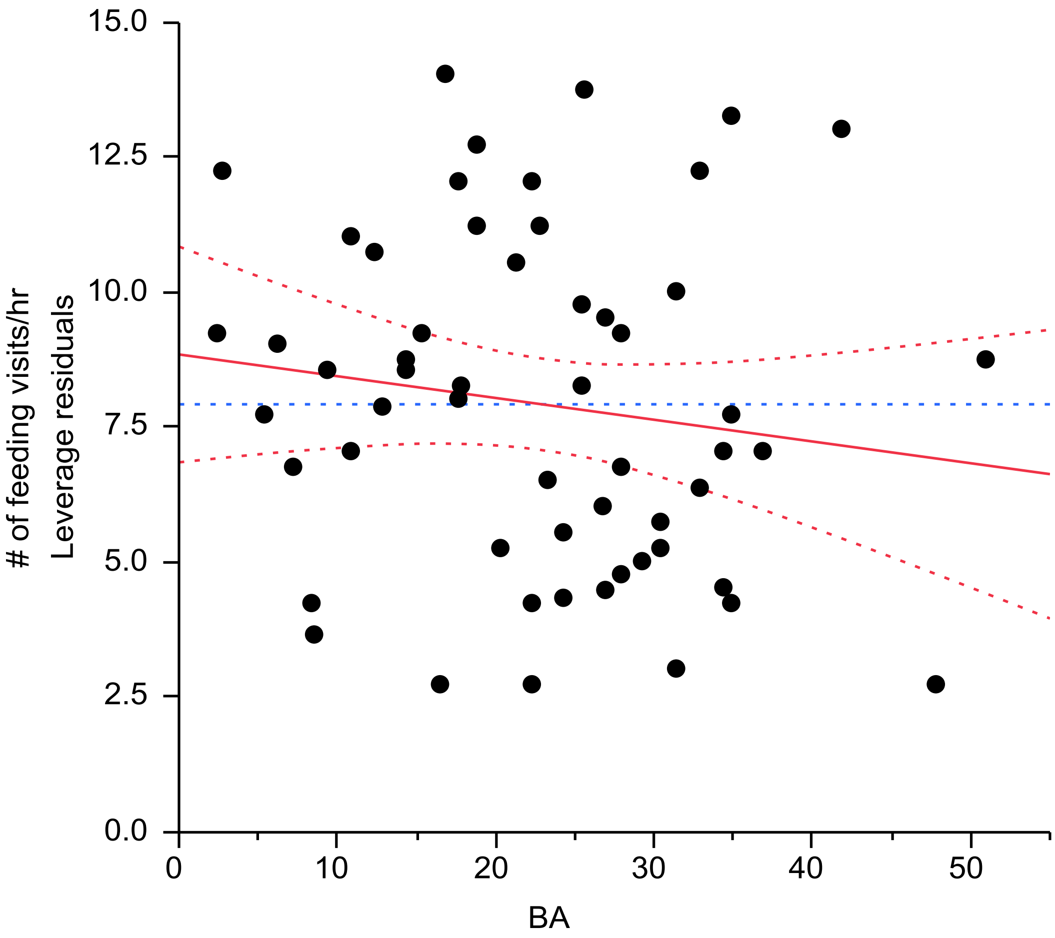

Figure 4.2. Leverage plot indicating the strength of basal area (BA) influence on feeding rates of female Cerulean Warblers (after controlling for year).

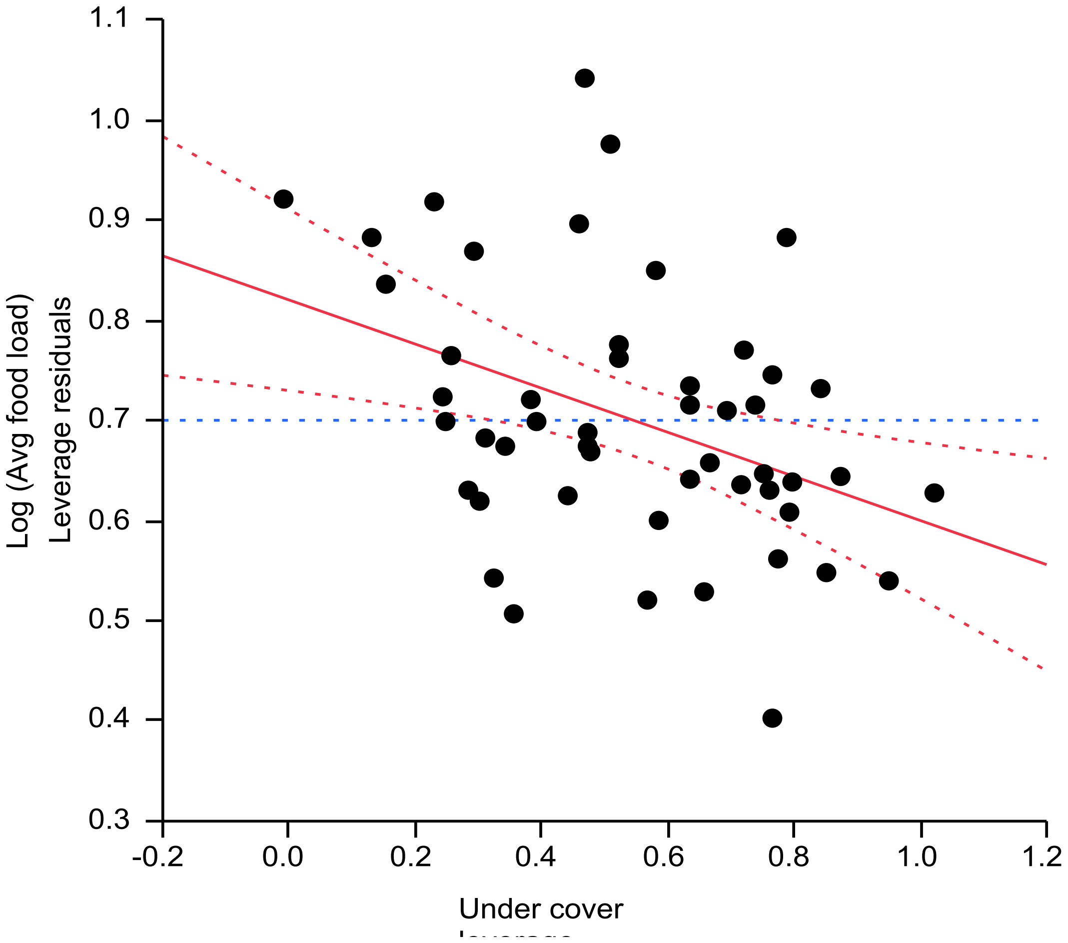

Figure 4.3. Leverage plot indicating the strength of understory cover (proportion) as an influence on average food loads (log-transformed) brought to nests by male Cerulean Warblers (after controlling for density of competitors, ambient temperature, and year).

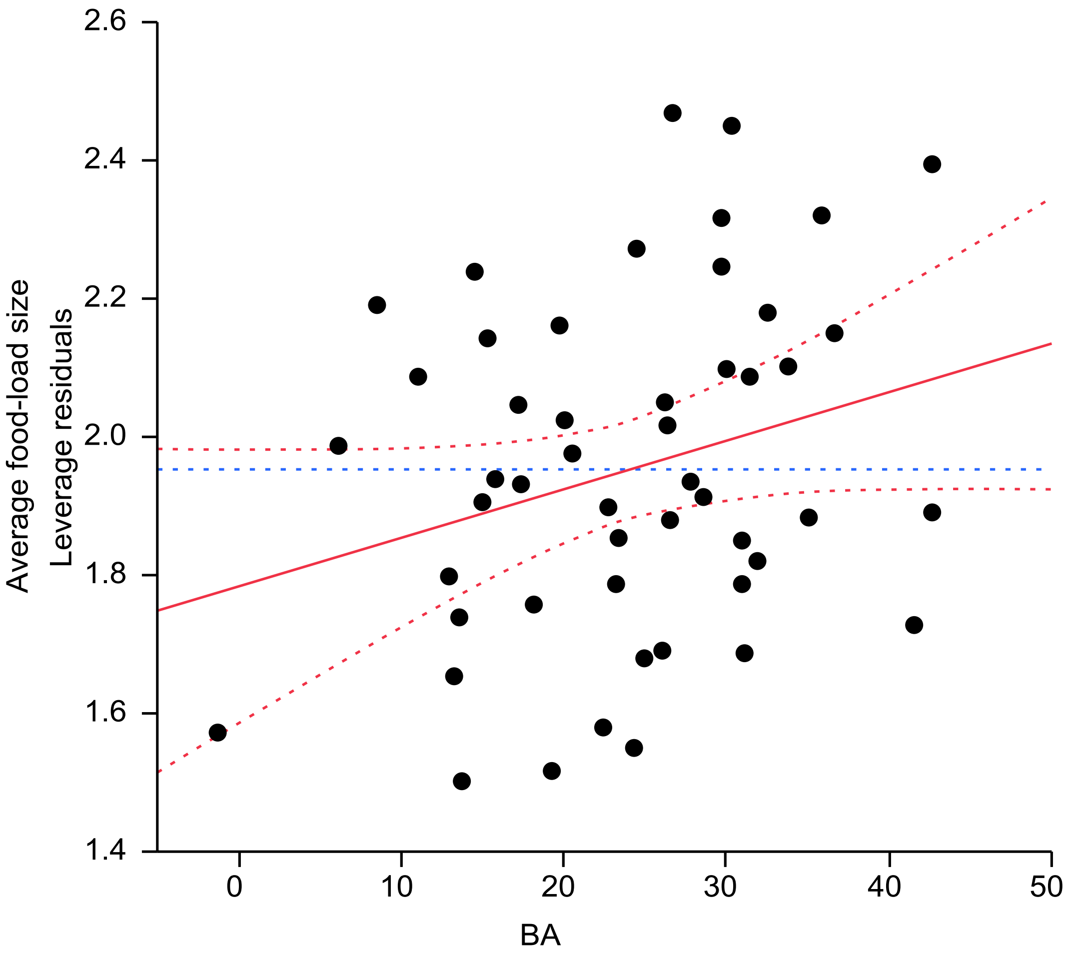

Figure 4.4. Leverage plot indicating the strength of basal area (BA) as an influence on average food loads brought to nests by female Cerulean Warblers (after controlling for ambient temperature, intraspecific density, Julian date, and year).

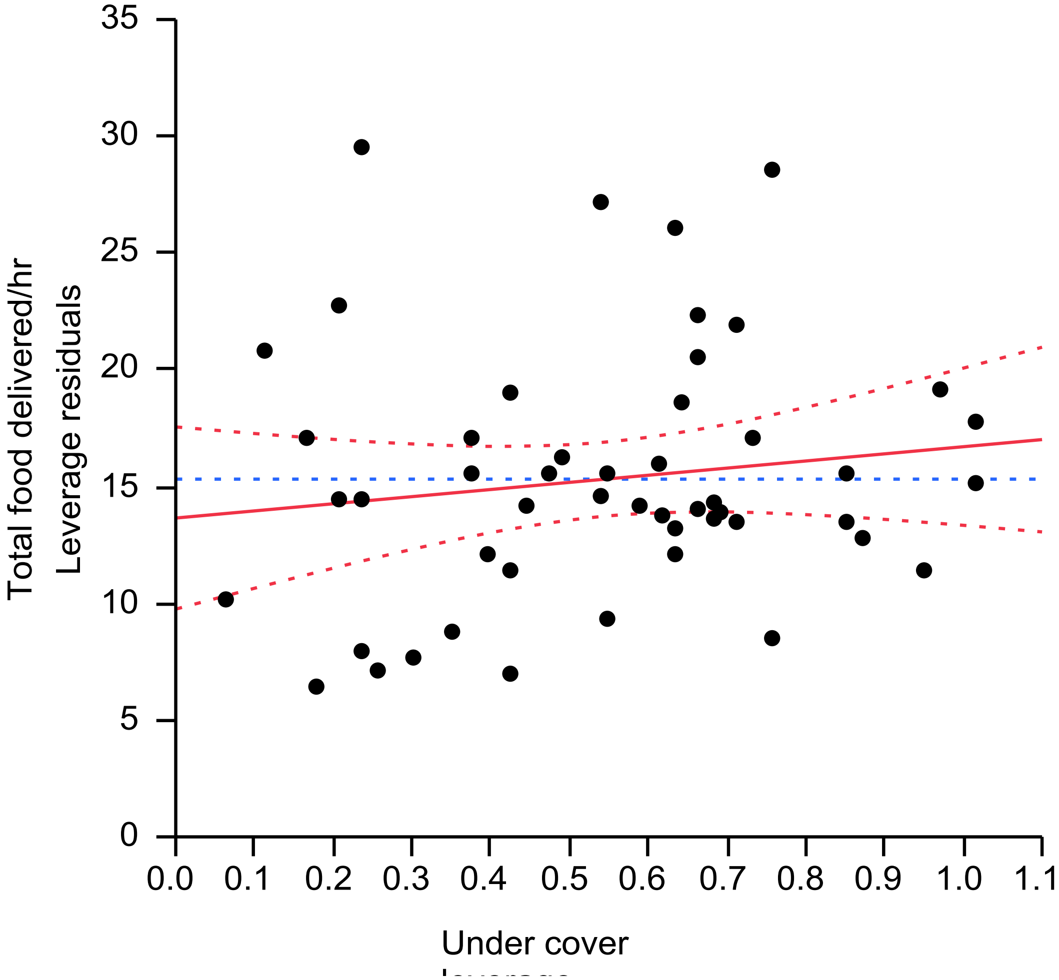

Figure 4.5. Leverage plot indicating the strength of understory cover (proportion) as an influence on total food delivered/hr (average food load size * feeding rate/hr) to nests by male Cerulean Warblers (after controlling for year and number of nestlings).

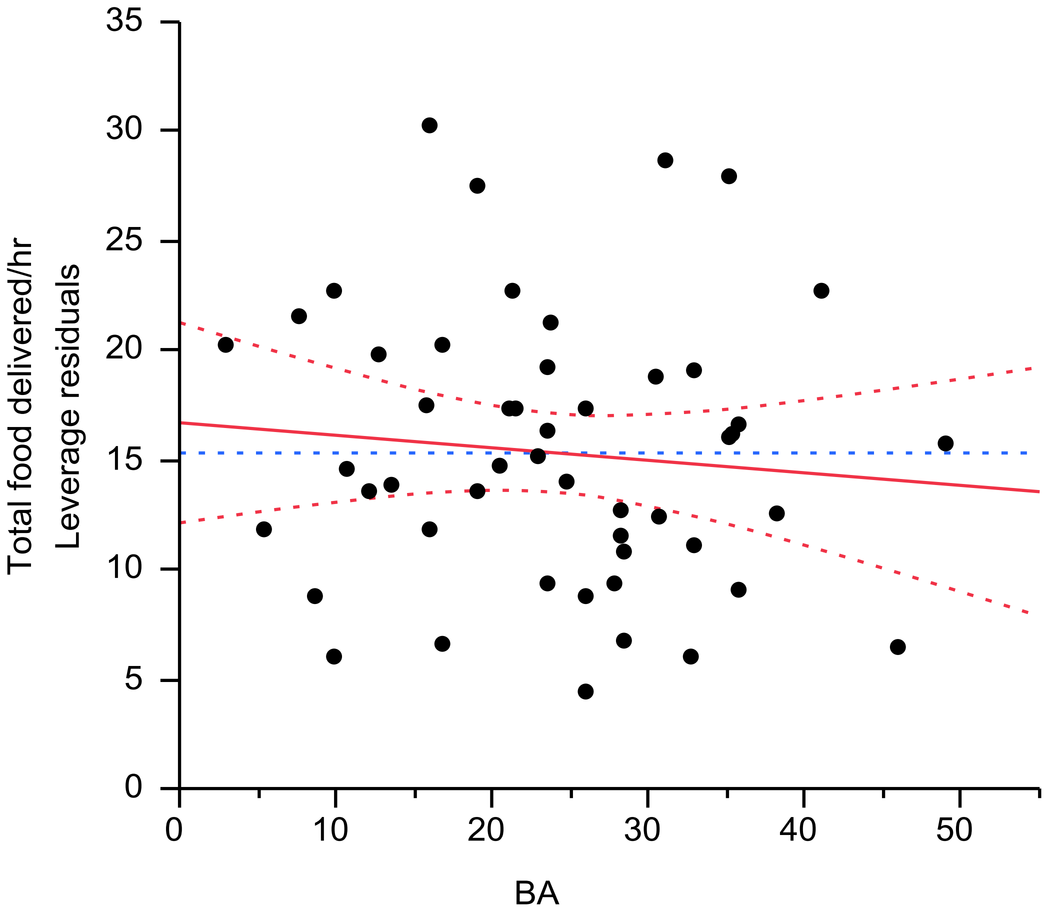

Figure 4.6. Leverage plot indicating the strength of basal area (BA) as an influence on total food delivered/hr (average food load size * feeding rate/hr) to nests by female Cerulean Warblers (after controlling for number of nestlings).

CONCLUSIONS

The goal of this dissertation research was to evaluate multiple responses by the vulnerable Cerulean Warbler to experimental forest disturbance in the Appalachian Mountains. To meet this goal, we replicated disturbances of various intensities on forest stands at seven widely-spaced study areas across the core of the Cerulean Warbler's range. We then assessed the consequences of these manipulations in terms of territory density, reproduction, source-sink dynamics, age structure, body condition, habitat selection, parental care, and sexual signaling. From these efforts, we made the following conclusions:

- Male Cerulean Warblers consistently selected territories located relatively close to canopy gaps, resulting in increased breeding densities in disturbed habitats (particularly on intermediate disturbances)
- Nest success was significantly depressed on all disturbances (relative to controls) in the southern region, and on the light treatment and buffers in the northern region
- Attraction to disturbances, combined with decreases in fecundity, produced local ecological traps at study areas in the southern region, but the global effect of these traps is still in question
- Given documented measures of adult survival, only areas in the southern region (Cumberland Mountains) could potentially function as source populations
- Spatial variation in selection for some territory features existed, with males selecting for opposing conditions among some study areas
- Female ceruleans consistently placed nests in patches characterized by habitat features associated with disturbed conditions (increased understory cover, decreased midstory cover, decreased basal area)

- White oaks, cucumber magnolias, and sugar maples were preferred as nest trees; red oaks and red maples were avoided
- Male Cerulean Warblers appear well-suited to foraging in disturbed canopies as body condition and provisioning rates increased in these conditions
- Age structure was not affected greatly by disturbances
- Parents (particularly males) adjusted their nest behavior in disturbed habitats in a manner opposite of predicted, potentially indicating maladaptive parental behavior
- Intermediate disturbances attracted males with larger breast bands and greater tail white and mediated the covariation between plumage and current body condition
- Additionally and unrelated to disturbance, male ceruleans displayed several plumage ornaments that signaled age (crown and rump blue-green chroma and hue, tail white, and breast band width), as well as ornaments that signaled long-term condition (tail white) and parental ability (rump blue-green hue)

In light of these findings, we currently recommend the following forest management strategies for Cerulean Warblers in highly forested areas (>80% forested within 10-km) in the Appalachian Mountains.

1) On stands with >5 Cerulean Warbler territories/10 ha, no harvesting should occur. Mature forest that has sufficient structural heterogeneity and in which ceruleans are already occupying at above average densities provides important breeding habitat for ceruleans. Anthropogenic disturbances on these sites could cause a decline in reproductive success that would reduce the overall sustainability of the population.

2) On stands with <5 territories/10 ha, intermediate disturbances have the potential to increase Cerulean Warbler densities, without harming reproduction to a high degree, on 10-ha forest stands. The characteristics of these disturbances should include:
    - Reduce basal area to 13 – 18 m^2/ha
    - Basal area reduction should initially be focused on midstory removal. Subsequently, the smallest diameter overstory trees should be removed first in an effort to retain as many large overstory trees (>40 cm dbh) as possible
    - Retain the following species, if present, as residual canopy trees: white oak, cucumber magnolia, and sugar maple

To determine cerulean density, stands to be harvested in the coming year should be surveyed for ceruleans between May 10–20 based on two visits to the stand during good survey conditions (no rain, light winds), systematically walking across the stand and recording the number of different singing males. All harvesting should occur outside the dates of 15 April – 30 July.

VITA

Than James Boves was born and raised in Downers Grove, IL, a southwest suburb of Chicago. As a teenager, he became interested in nature and the outdoors, and he was particularly fascinated by the only living organisms with feathers, birds. From 1994 to 1996, Than attended Kalamazoo College and then transferred to the University of Illinois at Urbana-Champaign, where he earned a bachelor's of science degree in biology in 1998. As an undergraduate, Than worked as field assistant on avian ecology and conservation research projects in the tropical forests of Belize and in restored oak savannahs in the Chicagoland area. For several years after graduating, Than worked two biologically-relevant jobs: as an environmental consultant and as a product specialist for a medical diagnostics company. In 2000, he returned to school at North Central College in Naperville, IL and received a secondary teaching certificate in biology. With that certification, Than taught high school biology at Proviso East High School in Maywood, IL for two years. In 2004, Than returned to school once again at Boise State University in the raptor biology program. Under the direction of James R. Belthoff, he conducted research on roadway mortality and sexual ornamentation of Barn Owls in Idaho and received his master's of science degree in 2007. After he completed his M.S. degree, Than took a job with Pacificorp Energy as a ecological consultant in Klamath Falls, OR. However, he soon returned to school again, this time at the University of Tennessee, Knoxville to conduct his doctoral research on the response of Cerulean Warblers to experimental forest disturbance, under the direction of David A. Buehler. Than earned his doctorate in natural resources, with an emphasis on wildlife ecology, in December, 2011. Beginning in January 2012, Than will return to his alma mater (University of Illinois) as a post-doctoral researcher, where he will study Black-capped Vireos (and Brown-headed Cowbirds).