DEMOGRAPHY AND HABITAT USE OF CERULEAN WARBLERS ON

BREEDING AND WINTERING GROUNDS

A Dissertation

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By

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ABSTRACT

Because their annual movements span continents, Nearctic-Neotropical migratory birds represent one of the most challenging groups for which effective conservation strategies can be developed. Knowledge of the ecology and management of migratory bird communities comes primarily from studies conducted on the breeding grounds. However, recent work demonstrates that events that occur throughout the annual cycle may also contribute to population declines. The Cerulean Warbler (*Dendroica cerulea*), a Neotropical migrant exhibiting precipitous population declines, is an excellent example of a species that may be impacted by events on both the breeding and nonbreeding grounds. My dissertation research examined habitat use and population demography of Cerulean Warblers on breeding (southern Ohio) and wintering (Venezuelan Andes) grounds to evaluate potential factors that contribute to declines in Cerulean Warblers.

During the breeding season, we surveyed Cerulean Warblers across 12 mature forest sites in southeast Ohio, 2004-2006. Research on the breeding grounds identified 1) how clearcutting impacted spatial distribution, density, and nesting success of Cerulean Warblers at multiple spatial scales (i.e., from local/edge to landscape), and 2) specific microhabitat and nest-patch characteristics selected by Cerulean Warblers. At each site, Ceruleans were intensively spot-mapped 8 times each year from May to July, adult behavior was used to locate and monitor nesting attempts, and nest, local, and

ii

landscape habitat characteristics were quantified. Results suggest that the presence of regenerating clearcuts did not influence density or nesting success of Cerulean Warblers in adjacent mature forest. Instead, local habitat features explained variation in warbler density and daily nest survival better than landscape-scale characteristics. Density and nesting success were positively associated with features typical of heterogeneous steady-state phase forests. In particular, nest plots had 14%, 24%, and 94% greater canopy openness, understory stems, and number of grapevines, respectively.

On the nonbreeding grounds, my research examined 1) the suitability of shade coffee plantations and 2) foraging and habitat use by wintering migrant birds, with emphasis on Cerulean Warblers. This portion of the study was conducted in 3 primary forest sites and 3 shade coffee plantations on the western slope of the Cordillera de Mérida of the Andes Mountains. At each site, migrants were surveyed using distance-based line transects, mist-netted and banded, and observed to characterize habitat use and flocking behavior during November – February 2005/06 and 2006/07. During these two seasons, 29 individual Cerulean Warblers were color-banded and resighted to estimate apparent monthly survival, annual return rates, and apparent annual survival. Densities of migrants were 3-14x higher in shade coffee plantations than primary forest sites, even after accounting for differences in detectability. Apparent monthly survival of Cerulean Warblers was estimated at 97% and overwinter persistence was similarly high. Banding data also suggest that migrants using shade coffee improve their body condition over the winter. Adult Cerulean Warblers had 62% higher apparent annual survival than juvenile birds (0.73 versus 0.45). Apparent monthly migration survival for adults (0.97) was similar to values throughout the remainder of the annual cycle, though juveniles

experienced up to 6x higher mortality during migratory periods. Abundance of Neotropical migrants in shade coffee plantations was significantly related to both structural and floristic characteristics where upper canopy foragers and lower canopy/ground foragers were positively associated with 1) number of large trees (>38 cm dbh), tree height, and understory vegetation density, and 2) numbers of small (8 – 23 cm dbh) and medium (23 – 38 cm dbh) trees and increased canopy cover, respectively.

Most species of Neotropical migratory birds have been well-studied on their breeding grounds in North America, while considerably less is known about the wintering and migratory ecology of these same species. My research efforts stand out as a relatively unique body of research given that I simultaneously examined population ecology during two phases of the annual cycle. Collectively, my research efforts have allowed me to generate specific management recommendations on both the breeding and nonbreeding grounds that can benefit Cerulean Warblers.

ACKNOWLEDGMENTS

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FIELDS OF STUDY

Major Field: Natural Resources

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Introduction

Nearctic-Neotropical migratory birds are truly "birds of two worlds", as they breed in the temperate zones of North America and spend winters in tropical locations in Latin America. Romantic as the notion of living in these two worlds is, the life history strategies of these migratory birds make them vulnerable to habitat loss, fragmentation, and degradation across the entire western hemisphere. Neotropical migrants are often highly sensitive to anthropogenic impacts and represent one of the most challenging groups for which effective conservation strategies can be developed. Perhaps there is no better species to illustrate both the complexity of and urgent need for Neotropical migratory bird conservation than the Cerulean Warbler (*Dendroica cerulea*). My doctoral research sought to (1) use Cerulean Warbler as a model species for demonstrating how biologists can better identify which stages of the annual cycle most limit populations of declining species, and (2) facilitate effective conservation of Cerulean Warblers by estimating key demographic parameters and examining population responses to anthropogenic disturbances on breeding and nonbreeding grounds. This is one of the few studies to systematically evaluate breeding and wintering ground factors that contribute to population declines and the conservation plight of a Neotropical migrant.

Cerulean Warbler is a Neotropical migrant that breeds in large tracts of mature deciduous forest concentrated in the mid-Atlantic regions and winters in sub-montane forests of the Andes Mountains in northern South America (Hamel 2000). Since 1966, Cerulean Warblers have experienced precipitous declines throughout their breeding range (-4.0% per year, Sauer 2003). Consequently, Cerulean Warblers have an extremely high priority ranking from Partners in Flight (PIF) Watchlist and were recently petitioned for federal protection. Currently there is great debate over the extent to which breeding or wintering ground events contribute to Cerulean Warbler population declines. Still, strong evidence is lacking, and management plans on the breeding and wintering grounds are hampered by poor knowledge of geographical distributions, habitat affinities, area requirements, demographic responses to different land management practices, or other threats (Rosenberg et al. 2000).

The goal of my dissertation was to examine habitat use and population demography of Cerulean Warblers on breeding (southern Ohio) and wintering (Venezuelan Andes) grounds to evaluate potential factors that contribute to declines in Cerulean Warblers. Reasons for declines of some migratory songbird populations, including Cerulean Warblers, remain unclear and the debate over breeding versus non-breeding limitations continues (Latta and Baltz 1997, Rappole and McDonald 1998). The objectives proposed in this study represent some of the highest priority research needs that were identified by the Cerulean Warbler Technical Group (CWTG) during their December 2002 "Summit" in Shepherdstown, West Virginia, USA. The CWTG has recognized that basic ecological data are lacking, and this may seriously constrain conservation efforts. In particular, demographic information is virtually nonexistent for

both the breeding and especially the wintering grounds for Cerulean Warblers (Robbins et al. 1992). These information needs are essential to properly evaluate causes of population declines and threats to Cerulean Warbler populations.

This study took place on the breeding grounds in southeast Ohio (ca. 4 months per year in 2004-2006), complemented with a winter study on the western slopes of the Andes in Venezuela (2-3 months per year in 2005-06 and 2006-07). Both the Ohio Hills and the Venezuelan Andes (Rosenberg and Dettmers 2004, Rosenberg et al. 2000) represent core breeding and wintering ranges of Cerulean Warblers. Thus, both portions of this project lie in important breeding and wintering areas, and play a central role in future conservation of the species.

Dissertation Layout

Each chapter is written as a separate manuscript that will be submitted for publication. In addition to providing an organizational overview of the dissertation, the main body of this chapter is intended to be a popular article or extension fact sheet. Chapter 2 examines Cerulean Warbler response to forest management and structure on the breeding grounds and is formatted for *Ecological Applications*. In this chapter, I apply a multiscale approach to examine 1) how clearcutting impacted density, spatial distribution, and nesting success, and 2) microhabitat and nest-patch characteristics selected by breeding Cerulean Warblers. Chapter 3 focuses on the nonbreeding grounds in the Andes Mountains of South America and examines the suitability of shade coffee plantations for wintering Neotropical migratory birds. Because this chapter is appropriate for a wider audience that focuses on conservation-related issues, it is formatted for

submission to the journal *Conservation Biology*. Chapter 4, also focused on the wintering grounds, identifies specific habitat features in shade coffee plantations used by migrant birds – something that is important for the implementation of management strategies that can enhance the overwinter survival of migratory birds. This manuscript is formatted for publication in *The Auk*, a top ornithological journal. Chapter 5 uses data on within-season and annual survival rates to answer the question of which stage during the annual cycle contributes most to annual mortality in Cerulean Warbler populations. This chapter is formatted for submission to *Journal of Animal Ecology*.

Extension Article: Cerulean Warbler – singing the blues

When I was young, I spent countless afternoons walking through the woods observing nature. Among my favorite pastimes was quietly watching birds go about their daily activities. My family even kept a yard list to keep track of each bird species we had seen in the area. Unfortunately, many of the same bird species that frequented my childhood home have experienced population declines. Some species of eastern forests, like the Ivory-billed Woodpecker (*Campephilus principalis*) or Bachman's Warbler (*Vermivora bachmanii*), may already be extinct or have their fate sealed. But for other species that are struggling right now there still may be hope to recover populations.

The Cerulean Warbler (*Dendroica cerulea*), is a small, sky-blue Neotropical migratory bird that is experiencing alarming population declines (Appendix A). In fact, their declines are so steep that since the mid-1960s, about 70% of the global population of Cerulean Warblers is estimated to have been lost. Because the Cerulean Warbler is an intercontinental traveler, flying up to 4000 km on migration each way, the underlying

4

causes of population declines are not yet identified. Fortunately, recent studies

examining Cerulean Warblers on both the breeding and wintering grounds provide new

information about what we can do right here in the U.S. that will help Cerulean Warblers

year-round.

Life Up North: Breeding Ecology

<u>Breeding Range</u>

Cerulean Warblers breed in large tracts of mature deciduous forest concentrated

in the mid-Atlantic regions (Appendix B). Their breeding range extends northward from

Arkansas to Ontario and westward from New York to Minnesota. The highest breeding

concentrations of Ceruleans occur in the Ohio Hills region, which is the area by the Ohio

River through Pennsylvania, West Virginia, Ohio, and Kentucky. In fact, the Ohio Hills

region accommodates nearly 50% of the global population of Cerulean Warblers during

the breeding season.

Birds typically arrive on Ohio breeding grounds from late April to early May.

Onset of fall migration can start as early as late July and last through August. Both

spring and fall migration patterns are thought to follow the Mississippi and Ohio River

Valleys with a nonstop flight over the Gulf of Mexico. Spring migration typically lasts

approximately 2 months but fall migration can last up to 4 months.

On the breeding grounds, Cerulean Warblers are insectivorous and spend most of

their time foraging and nesting in the upper canopy. Despite this simple description,

Ceruleans, like all birds, have a complex suite of ecological requirements necessary for

successful breeding and survival. By studying the specific factors that influence mating

success, clutch size, nesting success, within- and between-season survival, and age structure biologists ultimately can learn about the underlying causes of population change and, hopefully, identify effective conservation strategies.

Habitat Associations

Because Cerulean Warblers nest and forage high in the canopy of mature forests, most knowledge of breeding biology comes from coarse habitat associations. Cerulean Warblers are considered area-sensitive, which means that birds prefer to settle and nest in large forest patches. Habitat area requirements, however, vary widely across the breeding range, probably due to the surrounding land use. In highly forested landscapes, Cerulean Warblers are more likely to settle in small patches of forest compared to areas with very little forest cover where they nest only in large forest patches. In these highly forested landscapes Cerulean Warblers seem to be more sensitive to the characteristics within the forest stand than the amount of forest in the region. Consistent with this, studies have not found that density or nesting success of Cerulean Warblers are affected by presence of regenerating clearcuts in highly forested regions.

Cerulean Warblers are most likely to breed in forests with a broken canopy, such as riparian (or streamside) and ridgetop forests. Ceruleans select different characteristics for nesting than locations throughout the forest. Some forest characteristics that Cerulean Warblers select include canopy gaps, large trees (averaging 17 inches diameter at breast height), grapevines, and thick understory vegetation. Cerulean Warblers seem to be selecting habitat features that mimic older or steady-state forests. This type of forest has

a mix of old trees dying with young trees regenerating, creating a complex layering of vegetation and structure.

Reproductive Biology

Until recently, relatively little was known about the breeding biology of Cerulean Warblers, due in part to the fact that the species is notoriously difficult to study. Cerulean Warbler nests are located on a lateral limb, around 5m from the trunk of the tree, in the mid- to overstory of the canopy and usually above an open space. Average nest height across the breeding range varies from 11 – 20 m. Differences in nest height among localities may be reflective of different tree species and/or forest age across the breeding range. Nests are constructed with materials like grapevines, spider webs, and lichens. In the core of their breeding range, Ceruleans most often nest in large, tall trees such as white oaks (60% of nests), tulip-poplars (7%), hickories (4%), and sycamores (4%). White oak trees may be especially important because they support a high diversity and abundance of insects. Along ridges, the majority of nests are placed on southeast-facing slopes. Researchers think they may be selecting this slope because it offers high insect abundance as a food supply.

Once the eggs in the nest hatch, both male and female Cerulean Warblers will feed nestlings. Females are often seen in the understory vegetation foraging between incubation periods. Nest success fluctuates greatly between years with studies documenting very low levels of nest success ($< 20\%$) across several years. A suite of predators, like Blue Jays, flying squirrels, gray squirrels, and snakes, are likely responsible for most of the failed nests. Certain habitat features may reduce the risk of

predation, though. For example, nesting success of Cerulean Warblers increased with increasing amounts of understory vegetation and grapevines surrounding the nest.

Life Down South: Nonbreeding Ecology

<u>Wintering Range</u>

Once breeding activity ceases, Cerulean Warblers begin a journey south to wintering grounds (Appendix C). Cerulean Warblers spend the winter months in a narrow elevational band (~1650 – 5000 feet) in montane forests of the northern Andes Mountains of South America, primarily in Venezuela, Colombia, and Ecuador. Currently, there is a large-scale study in the northern Andes that aims to define current range and identify important areas for Ceruleans given that much of the forest habitat in this elevation has been cleared for agriculture and human settlement.

<u>Habitat Associations</u>

Nonbreeding studies in the past have provided little information regarding the range of habitats used by Cerulean Warblers with most information from scattered and anecdotal sightings. At one time, biologists thought that Cerulean Warblers relied upon mature forest on the wintering grounds, but recent studies have documented Cerulean Warblers in different types of habitats, including shade coffee plantations. Several other species of Neotropical migratory birds also are known to heavily use shade coffee plantations on the wintering grounds.

Shade coffee is a form of agriculture where coffee plants grow under a canopy of shade trees. Other crops, such as banana, citrus, avocado, and cacao, often are grown in

these plantations as well. Shade coffee plantations are typically small in size (~8 acres) and generate a nominal income for farmers. Shade coffee is recognized as one of the most sustainable agroforestry practices in Latin America because it provides a variety of forest products (e.g., coffee, fruits, firewood, lumber, and medicines), while at the same time maintaining forest cover and reducing erosion, insecticide use, and chemical runoff compared to other intensive agricultural systems such as sun coffee, pasture, and sugar cane. Complex layering of vegetation and structure in shade plantations mimics an open forest system for wildlife.

Wintering Ecology

Cerulean Warblers wintering in shade coffee plantations have been found in higher densities than in primary forest. Ceruleans may prefer shade coffee plantations because they mimic a type of natural forest that is no longer common on the landscape. Cerulean Warblers often exhibit two types of behavior – either territorial or members of mixed-species foraging flocks. Territorial birds defend a small area from other birds, especially other Cerulean Warblers. Territorial behavior is beneficial because the bird has a familiarity with the surroundings and can monopolize a local food supply. Mixed-species foraging flocks, on the other hand, are a mix of resident and migrant bird species that travel together through habitats. Flocking behavior can be advantageous in finding food and detecting predators. At times, large numbers of Cerulean Warblers, up to 9 individuals, participate in mixed-species flocks.

Although some species segregate habitat by sex and age on the wintering grounds, this does not seem to be the case for Cerulean Warblers. Just like on the breeding

grounds, Cerulean Warblers are insectivorous on the wintering grounds. Cerulean Warblers use a wide variety of trees and shrubs for foraging, including *Inga, Erythrina*, and *Acnistus*, all known as important sources of food for wildlife. Interestingly, Cerulean Warblers show similar habitat preferences as Blackburnian Warblers, a closely related species. It has been suggested that these two species may compete for resources. If Blackburnian Warblers are dominant, this competition may restrict Ceruleans to a narrow elevational range, where numbers of Blackburnian Warblers are lower.

However, presence of birds alone does not provide evidence that shade coffee plantations are suitable habitats. Migrants could be pushed into these habitats by dominant resident birds and suffer from suboptimal conditions. Recent research, though, has documented high survival and energetic condition, all measures of high quality habitat, of Cerulean Warblers throughout the winter. In addition, Cerulean Warblers exhibit high between-season fidelity, where a large proportion of birds return to the same coffee plantations the following year.

Unfortunately, recent changes in this industry have led to the development of new varieties of coffee that are tolerant to the sun. These sun coffee plantations, which leave no overstory canopy, are replacing traditional plantations at an alarming rate and may have serious economic and environmental consequences. Not only do sun coffee plantations reduce forest cover, but they also increase erosion, insecticide use, and chemical runoff. Furthermore, sun coffee offers little to no conservation value for Neotropical migrants and biodiversity. Sun coffee plantations, then, may be poor quality habitat for migrants.

Conservation Measures-

What can we do to help Cerulean Warblers on the both ends of their range?

Breeding grounds:

Engage in landscape-scale planning:

- *Provide large blocks of forest* – Cerulean Warblers are area-sensitive and require large patches of contiguous forest for suitable breeding habitat, especially in fragmented or low forest cover landscapes.

- *Minimize edge* – Patches of forest should possess as little edge habitat as possible. In other words, a patch should be shaped like a square or circle rather than an irregular or long, thin rectangle.

- *Reduce contrast along edges* – Soft edges are a gradual transition between habitat types and exhibit fewer edge effects (e.g., increased nest depredation) than hard edges where there is an abrupt change between habitats. An example of a soft edge is when forest management (e.g., partial timber cutting) blends into surrounding forest. A hard edge, however, may occur when mining or agriculture abuts a mature forest. Harsh edges may be reduced by preserving understory vegetation and scattered trees along edges.

Manage for increased structural complexity of forests:

- *Create vertical stratification of vegetation within forests* – A complex layering of vegetation from the understory to midstory to canopy provides abundant food resources and potential nest site locations for wildlife.

- *Promote old forest characteristics* - We can use silvicultural practices to create structural characteristics associated with old or steady-state forests. In particular,

we can create canopy gaps, and promote standing snags (dead trees) and grapevines.

- *Retain large trees* – Large, well-spaced trees that are emergent canopy trees >40 cm dbh are important to retain for nesting locations and singing posts for Cerulean Warblers.

Institute longer rotation periods in forest management:

- *Extend rotation periods of forest clearing* – Rotation periods (~80 years) in forest management often do not allow enough time for the formation of steady-state forest conditions.

- *Retain forest patches >100 years of age* – Forests >100 years of age often have higher densities of Cerulean Warblers than younger stands of forest.

Restore forest composition:

- *Restore disturbance regimes* - Changes in disturbance regimes and loss of key tree species may carry unknown repercussions in the wildlife community. Even-aged forests that lack disturbance promote the growth of shade tolerant tree species, like maples, and discourage shade intolerant species, like oaks and poplars.

- *Promote white oak regeneration* – In southeast Ohio, Cerulean Warblers prefer to nest and feed in white oak trees. Periodic controlled fire might be the best strategy in reducing maple growth and favor oak regeneration. Oak trees have been shown to provide abundant food resources (insects and acorns) to a wide variety of wildlife.

Wintering grounds

Engage in landscape-scale planning:

- *Preserve primary forest* – Primary, montane forests are among the most intensively logged and cultivated regions in the Neotropics. Preservation of primary forests should be of top priority in tropical conservation.

- *Provide forest patches near agroforestry habitats* – Areas of land which are not suitable for growing crops, like rocky, swampy or steep slopes or along streams, are the perfect spots to retain patches of native forest. Migratory birds may depend on these patches of forest as roosting sites

Promote diverse shade agroforestry systems:

- *Provide vertical stratification of vegetation* – Shade plantations should avoid just canopy and understory vegetation and have a mix of layering of vegetation throughout the vertical strata. The more layers of vegetation available, the greater habitat and food resources will be available to wildlife species.

- *Promote diversity in canopy tree and shrub species* – A mix of tree species will provide a wide variety of food resources for wildlife. Insects, seeds, nectar, and fruit are common sources of food for wildlife using shade plantations. Some shrub species, like *Acnistus arborescen*, may be just as important to wildlife as canopy trees like *Inga* spp. or *Erythrina* spp. In order to promote diversity of tree species, *Inga* spp. should consist of < 70% of the total canopy trees.

- *Provide adequate canopy cover* – Crops growing in the understory need some light to transmit through the canopy, but too little canopy cover will not provide

habitat for wildlife. Plantations should provide a minimum of 40% canopy
cover.

- *Promote tall, large trees* – Plantations should provide large trees with an average
  canopy height of > 15 m. Height of trees in the canopy is especially important to
  those species, like Cerulean Warblers, which forage high in the canopy.

- *Retain secondary plant structures* – Many secondary plant structures, like vines
  and epiphytes, are important components of tropical ecosystems.

- *Retain dead trees* – Dead trees, or snags, can provide food resources for wildlife
  and critical nesting cavities for resident bird species, like parrots and parrotlets.

Please consult the Smithsonian Migratory Bird Center for further criteria for shade
management for "Bird Friendly®" coffee.

Support shade agroforestry systems by being a responsible consumer:

- *Use socio-economic incentives* – Prices paid to growers of crops (e.g., banana,
  coffee) in the tropics have declined steadily over the past decades. Consumers
  can support small-scale farmers in the tropics by purchasing socially-responsible
  products. Look for these labels on products: *Fair trade* – Fair Trade aims to
  improve the livelihoods and well-being of small producers by providing a fair
  wage; *Organic* – Organic certification promotes natural soil activity and prohibits
  synthetic agrochemicals; and *Eco-friendly/ shade-grown* – This certification
  guarantees traditionally farming practices under a diverse canopy of trees.
  Currently, Rainforest Alliance and Smithsonian Migratory Bird Center ("Bird
  Friendly®" coffee) offer criteria for shade-grown management.

- *Support sustainable forestry* – Buy wood products that come from sustainable forests (see Sustainable Forestry Initiative, Rainforest Alliance).

Support organizations engaged in international conservation efforts:

- *Conservation-related organizations* - Examples include The Nature Conservancy, National Audubon Society, Smithsonian Migratory Bird Center, American Bird Conservancy, Conservation International, and others that support research and conservation of birds, wildlife, and their habitats.

- *Agricultural education programs* – Many organizations promote the education of local farmers and promote the use of agroforestry practices in agriculture. Examples of these organizations include The Tropics Foundation, Tropical Agricultural Research and Higher Education Center, Sustainable Harvest International, Fairtrade Foundation, and CENICAFE.

- *Support ecotourism* – Ecotourism focuses on reducing the impact of travel while promoting the floral, faunal, and cultural attractions of the destination. An important aspect of ecotourism is providing economic opportunities and incentives for local communities in preservation of natural resources.

As with most Neotropical migratory birds, there remain substantial gaps in our understanding of the ecology of Cerulean Warblers. Research conducted at Ohio State University's School of Environment and Natural Resources along with a diverse group of collaborators (e.g., The Nature Conservancy, U.S. Fish and Wildlife Service, Ohio Department of Natural Resources, Division of Wildlife, U.S.D.A. Forest Service, El Grupo Cerúleo) is beginning to elucidate factors that contribute to population declines and steps we can take to aid this and other migrant birds species.

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CHAPTER 2

THINK GLOBALLY, MANAGE LOCALLY: THE IMPORTANCE OF STEADY-STATE FOREST FEATURES FOR A DECLINING SONGBIRD

Running head: Steady-state forest features for a declining songbird

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Abstract. Changes in historical forest composition and structure may have cascading effects throughout the forest community. The Cerulean Warbler (*Dendroica cerulea*), a mature-forest breeding Neotropical migrant, is one excellent example of a species that may be tied to subtle features of eastern forests. Although Cerulean Warbler populations have declined precipitously over the last 40 years, exhibiting one of the steepest declines of any North American bird, ecologists have a poor understanding of the ecological factors influencing their distribution and demography. In our study, we identified 1) the extent to which clearcutting affected density, spatial distribution, and nesting success of Cerulean Warblers in adjacent uncut forest and 2) local and nest-patch habitat characteristics selected by breeding Cerulean Warblers across 12 sites in southeast Ohio, 2004-2006. Results suggest that the presence of regenerating clearcuts did not influence density or nesting success of Cerulean Warblers in adjacent mature forest. Instead, local habitat features explained variation in warbler density and daily nest survival better than landscape-scale characteristics. Density and nesting success were positively associated with canopy openness, numbers of large-diameter trees, and number of grapevines – all of which are typical of heterogeneous steady-state phase forests. Consequently, our study provides evidence that improved management for Cerulean Warblers may require creating features (e.g., large canopy gaps) that mimic old-growth forests.

Key words: Cerulean Warbler, daily nest survival, *Dendroica cerulea*, density, forest, regenerating clearcut, steady-state forest

INTRODUCTION

Land cover in the eastern United States has undergone remarkable transformation since European settlement. Despite the near-complete clearing of forests for agriculture and logging by the early 20th century (Whitney 1994) and widespread disease (Ellison et al. 2005), many eastern landscapes have returned to forested conditions. Nevertheless, today's forests carry a legacy from their past and they now lack many of the structural and floristic features that characterized presettlement forests (Steyaert and Knox 2008). Research shows that regenerated forests typically have lower floristic diversity and structural complexity than pre-Euro-American forests (Schulte et al. 2007). Some of these changes result from altered disturbance regimes, particularly gap phase dynamics that operate within older forests (Bormann and Likens 1979). Older or steady-state forest may be important for wildlife due to its structural and floristic complexity including standing dead trees, widely-spaced large trees, treefall gaps, continuous vertical foliage, rich leaf litter, undisturbed soils, thick herbaceous layer, and downed trees (Davis 1996, Oliver and Larson 1996).

The absence of gap dynamics within forests may explain, in part, the apparent paradox of certain declining mature forest birds in the face of decades-long increases in forest cover in the East. One species in particular, the Cerulean Warbler (*Dendroica cerulea*), was once a common breeding bird of eastern forests, but populations are estimated to have declined approximately 70% since 1966 (Sauer et al. 2003). In fact, Cerulean Warblers are experiencing the greatest declines of any North American warbler (Sauer et al. 2003) and are one of the top priority species for conservation action.

Anthropogenic land use changes on breeding and wintering grounds have been implicated as the most likely cause of population declines for Cerulean Warblers. At landscape scales, fragmentation of mature, deciduous forest on breeding grounds is frequently cited as an important contributing factor, particularly given that Cerulean Warblers are usually considered area-sensitive (Hamel 2000). At smaller spatial scales, changes in forest structure as a consequence of even-aged forest management and loss of key tree species also may, in part, drive population declines (Hamel 2000). Unfortunately, a paucity of specific information on the responses of Cerulean Warblers to habitat alteration and management at local and landscape scales seriously constrains conservation efforts. In an effort to fill some of these gaps in knowledge, we examined multiscale impacts of clearcutting on the density, spatial distribution, and nesting success of Cerulean Warblers and identified microhabitat and nest-patch characteristics selected by breeding Cerulean Warblers in mature forest. These objectives represent among the highest priority research needs identified by the Cerulean Warbler Technical Group (Hamel 2000).

METHODS

Study system

Our study area was located in southern Ohio within the Ohio Hills Physiographic Province, which represents the core breeding range of Cerulean Warblers and supports nearly 50% of the global population during the breeding season (Rosenberg and Dettmers 2004, Appendix B). Land uses within the ecoregion are diverse, but are primarily in agriculture, silviculture, and exurban development. Common tree species in mature

forests included white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), and hickory (*Carya* sp.). Regenerating clearcuts were dominated by shrub communities of woody plants generally < 5 m tall (Hunter et al. 2001) and were comprised of tree saplings (see above), *Rubus* sp., greenbrier (*Smilax* sp.), and sumac (*Rhus* sp.). Twelve mature forest sites (80–120 years in age), at least 16 ha each, were selected from Perry, Athens, Vinton and Jackson Counties in southeast Ohio (Table 2.1). Study sites were selected such that six sites were adjacent to a regenerating clearcut stand (<10 years old, treatment = harvest) and six were completely surrounded by mature forest (treatment = unharvested).

Sampling of Cerulean Warblers

In order to estimate density of Cerulean Warblers and to examine territory placement relative to regenerating clearcut edges, an intensive spot-mapping approach was used on the 12 sites. Spot-mapping allows estimation of the density of birds within a specified area, and is based on the territorial behavior of birds (Ralph et al. 1993). By marking locations of birds on a detailed map of the study area, we were able to count the number of territories in an area (i.e., density). At each site, a 16 – 20 ha grid was marked with flagging at 50-m intervals to determine bird locations. We spot-mapped territorial Cerulean Warblers 8 times during May to July 2004 – 2006 at each study site. On each compiled spot map, we estimated the center of each territory (the intersection of the 2 longest axes bisecting the territory polygon, Weakland and Wood 2005) to calculate a distance of the territory center to the nearest harvest edge. For the 6 sites adjacent to

harvests, we split each site's spot-map in half to represent distance categories (i.e., edge versus interior) from the clearcut edge. Territory centers located in the 'interior' were >200 m from the regenerating clearcut edge; a distance where most edge effects are no longer detected in forested landscapes (Patton 1994, Flaspohler et al. 2001). Because number of territories did not significantly differ among years ($P > 0.50$), we first averaged number of territories across years in each distance category and then examined if number of territories was related to distance category.

An information-theoretic approach was used to evaluate and rank 6 *a priori* models explaining variation in Cerulean Warbler density among sites. The following hypotheses were constructed: 1) canopy structure – Cerulean Warblers respond primarily to the structure of the forest canopy and prefer tall canopies with gaps (canopy height + canopy openness), 2) tree size – Cerulean Warblers are positively associated with the numbers of large trees (number of large trees), 3) light gap – Cerulean Warblers respond positively to canopy openness and associated understory characteristics in gaps (number of understory stems + canopy openness), 4) forest structure – Ceruleans respond to a wide suite of forest structural features (understory stems + large trees + canopy openness + canopy height), 5) landscape context – Cerulean Warblers respond more strongly to characteristics of the surrounding landscape than to local forest structure, and 6) the full model (all variables) based on previous studies of Cerulean Warbler habitat associations (Oliarnyk and Robertson 1996, Weakland and Wood 2005, Jones and Robertson 2001, Roth and Islam 2007). We used a generalized linear model with a negative binomial distribution (Schabenberger and Pierce 2002) to calculated log-likelihood estimates for each model (SAS Institute 1990) and then calculated Akaike's Information Criterion

corrected (AIC$_c$) for bias because of small sample size. The best model has the lowest

AIC$_c$ value, and subsequent models were assessed by their difference in AIC$_c$ values

(ΔAIC$_c$) and weight of evidence (ω_i). Models with ΔAIC$_c$ < 2 are considered plausible

given the data (Burnham and Anderson 2002). We assessed goodness-of-fit for the

global model by calculating a variance inflation factor ($\hat{c}$), where a $\hat{c}$ close to one is

considered a relatively good model fit (Burnham and Anderson 2002).

Measurement of Habitat Characteristics

Local habitat characteristics were measured in twenty 0.04-ha circular plots at

each site (modified from James and Shugart 1970, Martin et al. 1997). Plots were located

at 100-m intervals to collect data at increasing distances from the harvest edge (0–400

m). At each plot, numbers and sizes of trees by species, numbers of fallen logs, stumps,

and standing dead trees were recorded. Vertical foliage density (woody shrubs and

saplings from 0-3 m) was measured at 2-m intervals along two 20-m perpendicular

transects established through the plot center. Hemispherical photographs were taken at

20 locations throughout each site using a Nikon Coolpix 4500 camera and FC-E8 fisheye

lens. Photos were taken skyward with a 180° (fisheye) camera lens at a height of 2.5 m

to avoid understory shading. Gap Light Analyzer (GLA) imaging software was used to

extract gap light transmission indices (i.e., percent canopy openness) from true-color

hemispherical photographs. Correlations among habitat variables were also tested using

Spearman's correlation coefficients. Forest cover within a 1-km radius of each study site

was calculated from digitized maps from the Ohio Division of Wildlife and ARC/VIEW

3.2 (Environmental Systems Research Institute). Because sites adjacent to clearcuts had

significantly less forest cover (>45 years old) than sites surrounded by more mature forest ($F_{1,10} = 14.07$, $P = 0.004$), we used treatment as a landscape variable.

<div align="center">*Measurement of nest placement and nest-patch vegetation*</div>

Nest-searching and monitoring followed Breeding Biology Research and Monitoring Database protocol (Martin et al. 1997). Nests were monitored from April through July, and all located nests were checked every 2 – 4 days. Numbers of eggs and nestlings were not counted given the height of most Cerulean Warbler nests (>10m). Instead, each nest was determined to be successful (at least 1 young fledged) or failed, based on length of nestling stage, careful observation of behavioral cues of parents (e.g., feeding), destruction of nest, and detection of fledglings (Martin et al. 1997).

After nest activity ceased, nest placement and vegetation characteristics surrounding each nest were measured in a 0.04-ha circular plot centered on the nest (Martin et al. 1997, Rodewald and Yahner 2001). For each nest, we recorded nest height, species, dbh (diameter breast height), and height of the nest substrate, and distance from nest to central axis of substrate. In addition, we measured canopy openness by averaging values from 5 hemispherical photographs (1 under the nest and four at 25m from the nest in each cardinal direction) associated with each nest. The same vegetation and photo data were collected in unused but available habitat (i.e., within the territory) that were randomly-located within 50m of each nest (hereafter called available plots). We identified nest-patch characteristics selected by Cerulean Warblers by comparing variables in available and nest-patches with a multivariate analysis of variance.

Vegetation variables that were not normally distributed were square root transformed for analyses.

Daily nest survival

Similar to the density analysis, we used an information-theoretic approach to model nest daily survival rate (DSR). We ran two sets of models to examine the relationship of 1) temporal and 2) nest-patch habitat characteristics on DSR. Candidate models for the first set contained year, time of season, trend, and combinations. Habitat candidate models consisted of the same hypotheses indicated in our modeling of density of Cerulean Warblers plus the variables nest height, grapevine density, and aspect because these were thought to play an influence in nest success (Tarvin and Smith 1995, Weakland and Wood 2005, Newell and Kcstalos 2007). We used the nest survival model in program MARK (White and Burnham 1999) to rank candidate models given the data and generate DSR estimates. We incorporated covariates in models using the logit-link function (Dinsmore et al. 2002).

RESULTS

Density

We detected Cerulean Warblers breeding at 11 of the 12 study sites (Table 2.2). Because densities did not significantly differ among years ($F_{2,31} = 0.05$, $P = 0.952$) we averaged across years for each site (Table 2.2). Mean density ranged from 0 to 7.5 males per 10 ha. Based on our spot-mapping data, mean density of Cerulean Warblers in forest stands adjacent to regenerating clearcuts (1.31 birds/ha ± 0.59 SE) did not significantly

differ from those in more forested landscapes (2.62 ± 1.25 SE; $F_{1,10} = 0.91$, P = 0.364).

Similarly, the number of territories near harvest edges compared to the interior of sites

were not significantly different ($F_{1,10} = 0.507$, P = 0.493).

Habitat associations

Among-site variation in habitat structure was largely associated with differences

in density of understory stems (Table 2.2). In contrast, there was no evidence of

differences in local habitat features between sites surrounded by mature forest and those

adjacent to clearcuts (Wilks' Lambda $F_{4,7} = 2.02$, P = 0.837).

Variation in density of Cerulean Warblers among sites was best explained by the

"forest structure hypothesis", which contained several variables reflecting forest and

canopy structure ($\Delta AIC_c = 0.00$, $w_i = 0.55$, Table 2.3). Based on Akaike weights, this

model was ranked 1.5x better than the next model and 4.6x better than all remaining

models combined (global model fit, ĉ = 1.15). Densities were positively associated with

both canopy openness and understory stem density (Fig. 2.1a and 2.1b). Surprisingly,

densities of Ceruleans were negatively associated with numbers of large trees (Fig. 2.1c)

in the forest stand as a whole, which may be related to the negative correlation between

canopy openness and numbers of large trees at a site (correlation coefficient r = -0.36,

Table 2.4).

Vegetation characteristics differed significantly between nest and available plots

(Wilks' Lambda $F_{11,198} = 6.44$, P < 0.001, Appendix D). Examination of vegetation

revealed that nest plots had 14% greater amount of canopy openness (F = 14.60, P <

0.001), 94% of grapevines (F = 10.97, P = 0.001), 24% of understory stems (0-5m, F =

8.67, P = 0.004; Fig. 2.2), and 32% larger nest tree dbh (F = 24.84, P < 0.001; Table 2.5) than in systematically-located habitat plots.

Daily nest survival

Over three years we monitored the fate of 113 nests of Cerulean Warblers. For sites that had > 5 nests, average daily survival for Cerulean Warblers ranged from 0.936 to 0.985 and averaged 0.951 ± 0.006 SE across all sites, which corresponds to 19 - 69% nesting success based on a 25-day nesting period (Buehler et al. 2008). Using Program Mark, the best temporal model explaining daily survival rate included the variable year ($\Delta AIC_c = 0$, $\omega_i = 0.56$). Daily nest survival fluctuated greatly among years for Cerulean Warblers, where 2004 and 2006 had lower survival rates (0.915 and 0.936, respectively) than 2005 (0.972, Fig. 2.3).

Several vegetation features explained variation in daily nest survival (Table 2.6). In particular, both the number of grapevines and understory stems (0-5 m) were positively associated with daily nest survival (Fig. 2.4a and 2.4b, Appendix E). In fact, the collective weight of these variables and their combination (i.e., Light gap hypothesis) explained nearly 45% of all variation in the data, which provides strong evidence that these are important factors in Cerulean Warbler nest success. We have no evidence that daily survival rate was affected by the presence of regenerating clearcuts within the surrounding landscape ($\omega_i = 0.07$). For nests in sites adjacent to clearcuts (n = 56), the distance to the edge was not related to nest fate ($\chi^2 = 0.152$, P = 0.697).

DISCUSSION

For many declining mature forest species, fragmentation and declining forest cover are the usual suspects as drivers of population declines. However, our work in the forested landscape of southern Ohio suggests that Cerulean Warblers respond strongly to local forest structural characteristics. In particular, Cerulean Warblers seem to select and be positively affected by structural characteristics normally associated with steady-state forests that are subject to gap phase dynamics. These forests typically have more features, such as canopy gaps, grapevines, and large trees that were positively associated with density, nest placement, and nesting success of Cerulean Warblers. This finding is consistent with other descriptions of habitat selection by Cerulean Warblers, most of which stress the importance of uneven-aged forests containing canopy gaps (Oliarnyk and Robertson 1996, Jones and Robertson 2001, Weakland and Wood 2005, Wood et al. 2006, Roth and Islam 2008).

Our study is the first to show that habitat features typically associated with these old steady-state/gap phase forests are positively related to nesting success. Although no vegetation measures predicted nesting success for birds studied by Jones and Robertson (2001), Oliarnyk (1996) found that unsuccessful nests were associated with a dense understory. In contrast, daily survival rate in this study was positively associated with understory vegetation density and canopy openness. A thick understory shrub layer may be a consequence of increased light penetration at gaps in the canopy. A thick shrub layer may be used by Cerulean Warblers for several reasons. First, females frequently drop to the understory for intensive foraging bouts during incubation (M. Bakermans, *personal observation*). The high vegetation volume in the shrub and sapling layer may

28

improve foraging efficiency for females at this period of time. Second, a thick shrub layer may provide important post-fledging habitat for Cerulean Warblers (M. Bakermans, personal observation). Mature-forest breeding songbirds are known to move into areas with dense understory vegetation during the post-fledging period (Vitz and Rodewald 2006, Vitz and Rodewald 2007). Birds may move into these thick areas to either avoid predators or for easy access to food resources (e.g., fruits). In fact, movement into thick habitat promotes survival of post-fledging mature-forest birds (Vitz and Rodewald, in review).

Placement of Cerulean Warbler nests in southern Ohio was generally similar to that described in other studies, particularly regarding placement on a lateral limb in the mid to overstory canopy (see Hamel 2000). Mean nest height (~20 m) in our region was higher than those found in Ontario (Oliarnyk and Robertson 1996) but similar to nests in Michigan (Rogers 2006) and Indiana (Roth and Islam 2008). Differences in nest height among localities may be reflective of different tree species and/or forest age across the breeding range. Tree species composition has been shown to play an important role in habitat selection for some bird species (Rice et al. 1984). For example, Cerulean Warblers were the second most selective forager in a Cache River floodplain forest where they showed a strong preference for kingnut hickory (*Carya laciniosa*) and avoided red maple (*Acer rubrum*, Gabbe et al. 2002). In our study region, Cerulean Warblers showed a preference for white oaks and an avoidance of red oaks for nesting. Cerulean Warblers may select white oaks due to their high levels of leaf-chewing insect communities (Jeffries et al. 2006).

One of the distinguishing aspects of this study is that we documented highly variable reproductive success among years, with two years having extremely low levels of nest success (i.e., <20%). Because Cerulean Warblers nest high in the canopy and nests are difficult to locate, few studies have published nest survival data. In a study in Ontario, daily nest survival rate was reported to average 0.986 from 1994 – 1997 but plummeted to 0.911 after an ice storm wiped out much of the forest canopy. The fluctuations observed in our study system may be tied to changes in predator abundance, which also varied tremendously across years (M. Bakermans, personal observation). Observations of nest depredation events and adult behavior, indicate that eastern gray squirrels (*Sciurus carolinensis*), Southern flying squirrels (*Glacomys volans*), and Blue Jays (*Cyanocitta cristata*) are common nest predators of canopy-nesting songbirds in the region. Fluctuations in nest survival rates of songbirds may be related to overwinter survival of nest predators based on the previous year's mast crop (Schmidt & Ostfeld 2003, Clotfelter et al. 2007).

Regenerating clearcuts in our southern Ohio study system were not significantly associated with edge-related nest predation of Cerulean Warbler nests. An important caveat to this finding is that our study areas were highly forested (>70% forest cover), which has been shown to mediate the presence and severity of edge effects. In particular, high levels of fragmentation tend to magnify edge-related nest predation, whereas forested landscapes will seldom show them (e.g., Andrén 1995, Donovan et al. 1997, Hartley and Hunter 1998). One explanation for the absence of edge effects in forested landscapes is that populations of generalist predators often associated with increased predation near edges do not substantially increase until the landscape has become quite

fragmented (Chalfoun et al. 2002). Thus, in our study area, regenerating clearcuts may not have been associated with edge effects because they occurred within heavily forested landscapes. If the landscapes were to become more fragmented, we might see an increase in edge-related nest predation.

We failed to find evidence of sensitivity of Ceruleans to intensive timber harvesting in the immediate landscape surrounding mature-forest sites. A tolerance to silvicultural activity is also suggested by recent work in West Virginia showing that abundance of Cerulean Warblers in mature forest adjacent to clearcuts and two-aged harvests was comparable to that in unharvested control stands (Wood et al. 2005). Cerulean Warblers also were more likely to occur in forested landscapes disturbed by silviculture than forested landscapes disturbed by agriculture (Rodewald and Yahner 2001). Our results differ from Weakland and Wood (2005) who found landscape-level variables had greater explanatory power than microhabitat. This disparity may be a result of mountain-top removal having greater effects (i.e., edge, predator, etc.) in the landscape than regenerating clearcuts.

Variation in density of Cerulean Warblers among forest stands was best explained by variation in forest structure. We found that Ceruleans selected forests with similar features as documented in previous studies (Hamel 2000). Cerulean Warblers often are associated with well-spaced, large trees with high canopies (Jones and Robertson 2001, Roth and Islam 2008). In our study, densities were positively related to canopy openness and numbers of understory stems, which both indicate heterogeneous canopies with light gaps. Ceruleans also use edges of timber harvests, roads, and ridgetops within heavily forested areas (Rodewald and Yahner 2000, Weakland and Wood 2005, Wood et al.

2006). The unexpected negative association between Cerulean Warbler density and numbers of large trees may reflect the fact that sites with large numbers of trees tend to have more closed canopies. Due to their apparent preference for tall, uneven forest canopies, shorter rotation periods and even-aged silvicultural methods may negatively affect Cerulean Warblers because fewer stands reach maturity (Hamel 2000).

CONCLUSIONS

Our work highlights the important role that local forest management can play in the conservation of some declining mature forest species, like the Cerulean Warbler. Although many forests of the East have regenerated, they still lack structural characteristics typical of the once-common presettlement steady-state forests (Steyaert and Knox 2008). Anticipated changes in floristic composition with a shift from oak to maple forests (Copenheaver et al. 2006) are likely to further reduce the abundance of features preferred by Cerulean Warblers. Ultimately, the structural and floristic conditions of current forests can have cascading effects on biodiversity and functional ecology (Schulte et al. 2007). Forest management that mimics characteristics associated with steady-state and gap-phase forests may be necessary to restore and enhance function and habitat that is required by some species. For example, insect, mammal, and bird community density and richness were found to be greatest in old-growth forests (Davis 1996, Haney and Schaadt 1996, Jeffries et al. 2006). As a whole, our study suggests that in highly forested landscapes forest quality, rather than quantity alone, may be an important contributor to population declines for specialist species, like the Cerulean Warbler.

ACKNOWLEDGMENTS

Site	Latitude	Longitude	Ownership	Adjacent to Clearcut?
Wildcat	39N 35'	82W 02'	Wayne National Forest	N
Burr Oak	39N 33'	82W 04'	Wayne National Forest	N
Waterloo	39N 20'	82W 16'	Ohio Division of Wildlife	N
King Hollow	39N 20'	82W 19'	Ohio Division of Forestry	N
Lake Hope	39N 20'	82W 21'	Lake Hope State Park	N
Webb Hollow	39N 18'	82W 24'	Ohio Division of Forestry	Y
CCC	39N 17'	82W 20'	Ohio Division of Forestry	Y
Will Tract	39N 15'	82W 24'	Ohio Division of Forestry	Y
Kickgate	39N 13'	82W 23'	Mead Westvaco*	Y
Rema 2	39N 11'	82W 22'	Mead Westvaco*	N
Rema 1	39N 09'	82W 23'	Mead Westvaco*	Y
Cemetery	39N 04'	82W 36'	Mead Westvaco*	Y

* Mead Westvaco lands have been sold to a private real estate company, and final ownership status is still TBA due to multi-organization/agency efforts to purchase property.

Table 2.1. Study sites in the Ohio Hills Physiographic Province in southeast Ohio in Vinton, Athens, Jackson, and Perry counties.

Site	Density (per 10 ha)	% Canopy openness	Canopy height (m)	Trees 8-23 cm dbh	Trees 23-38 cm dbh	Trees >38 cm dbh	Stem hits (0.5-3.0 m)	% Forest cover
Burr Oak	0.30 (0.30)	8.8 (0.37)	26.0 (0.8)	8.0 (0.9)	3.5 (0.4)	2.2 (0.3)	13.7 (2.9)	89.1
CCC	1.28 (0.37)	9.2 (0.61)	31.2 (1.4)	9.5 (0.9)	2.0 (0.2)	2.4 (0.3)	9.6 (1.4)	96.7
Cemetery	0.30 (0.30)	8.4 (0.32)	31.0 (0.9)	7.9 (0.8)	3.7 (0.4)	2.8 (0.4)	10.8 (2.5)	82.7
Kickgate	2.55 (0.50)	9.0 (0.44)	30.4 (1.4)	6.2 (0.7)	2.2 (0.4)	3.0 (0.4)	24.8 (2.6)	85.0
King Hollow	1.28 (0.02)	7.6 (0.37)	34.7 (1.1)	7.8 (0.8)	2.9 (0.4)	3.5 (0.4)	17.1 (2.9)	99.4
Lake Hope	0.20 (0.20)	8.6 (0.38)	29.0 (1.0)	11.0 (1.3)	3.3 (0.6)	3.0 (0.4)	4.3 (0.7)	100.0
Rema 1	3.53 (0.26)	10.5 (0.82)	30.3 (1.2)	8.8 (1.4)	3.0 (0.5)	3.1 (0.3)	25.2 (3.7)	82.1
Rema 2	7.47 (0.52)	9.9 (0.44)	33.2 (1.4)	6.9 (0.7)	2.4 (0.3)	2.3 (0.4)	16.6 (2.7)	98.5
Waterloo	1.08 (0.23)	7.8 (0.35)	33.2 (0.9)	9.7 (1.0)	2.2 (0.3)	3.1 (0.3)	10.8 (1.9)	98.1
Webb Hollow	0.20 (0.20)	7.4 (0.33)	38.5 (0.8)	9.5 (0.7)	2.1 (0.6)	3.1 (0.4)	14.6 (2.0)	83.9
Wildcat	5.41 (0.20)	8.7 (0.63)	29.3 (1.1)	7.7 (0.6)	2.8 (0.4)	1.9 (0.4)	17.7 (2.6)	100.0
Will Tract	0.00 (0.00)	8.9 (0.42)	22.8 (1.4)	12.2 (1.4)	2.6 (0.3)	3.0 (0.4)	9.7 (1.2)	72.1

Table 2.2. Mean (SE) density of Cerulean Warblers and habitat measurements at study sites. Density estimates are averaged over 3 years (2004–2006). Vegetation measurements were averaged over 20 0.04-ha plots per site.

35

Model[a]	K[b]	AIC$_c$[c]	delta AIC$_c$ (Δ_i)[d]	Akaike weights (ω_i)[e]
Forest structure	5	4.20	0.00	0.55
Full	6	5.23	1.03	0.33
Canopy structure	3	9.33	5.13	0.04
Light gap	2	9.64	5.44	0.04
Tree size	3	10.06	5.85	0.03
Landscape	2	11.69	7.49	0.01

[a] Potential factors affecting mean density of Cerulean Warblers at the site level: Canopy structure = canopy height + canopy openness; Tree size = number of large trees; light gap = number of understory stems + canopy openness; Forest structure = understory stems + large trees + canopy openness + canopy height; Landscape = treatment; Full model includes all explanatory variables

[b] Number of parameters in model includes the intercept.

[c] Corrected Akaike's information criterion adjusted for small sample size relative to number of parameters.

[d] Delta AIC$_c$ indicating difference in AIC$_c$ value from that of the best model.

[e] Akaike weight indicating relative support for the model.

Table 2.3. Models explaining variation in Cerulean Warbler density among sites in southeast Ohio, 2004-2006. Models are ranked according to AIC$_c$ and ΔAIC$_c$ values, where the best supported models have smaller values.

Habitat variable	Cerulean Warbler density	Canopy height	Trees >38 cm dbh	Stems (0-3m)
Canopy height	0.14			
Trees >38 cm dbh	-0.49	0.31		
Stems (0-3m)	0.53	0.18	0.08	
% Canopy openness	0.56	-0.41	-0.36	0.46

Table 2.4. Spearman's correlation coefficients of factors hypothesized to affect Cerulean Warbler density across 12 study sites in southeast Ohio, 2004-2006. Values were averaged over 20 systematically located plots throughout each site.

Variable	Nest Mean	SE	Available Mean	SE	F	P
Canopy height	29.60	0.46	29.31	0.47	0.01	0.999
Canopy openness	11.81	0.39	10.36	0.28	**14.60**	**<0.001**
'Nest' tree dbh	44.45	1.46	33.74	1.42	**24.84**	**<0.001**
Trees 8-23 cm dbh	8.22	0.40	8.60	0.43	0.12	0.726
Trees 23-38 cm dbh	3.32	0.21	3.21	0.20	0.03	0.869
Trees >38 cm dbh	3.65	0.25	3.01	0.19	0.08	0.779
Number of grapevines	3.48	0.46	1.84	0.45	**10.97**	**0.001**
Understory stems[a]	26.56	1.63	21.39	1.31	**8.67**	**0.004**
Midstory stems[b]	19.81	1.01	19.99	1.26	0.01	0.950
Canopy stems[c]	24.16	1.27	23.58	1.19	0.08	0.775
Aspect	160.34	7.78	171.95	8.02	0.20	0.659

[a]Understory stems = vegetation hits 0–5m; [b] Midstory stems = vegetation hits 5.1 – 10m; [c] Canopy stems = vegetation hits 10.1–15 m.

Table 2.5. Comparison of habitat characteristics at nest and available plots in southeast Ohio, 2004-2006. Vegetation characteristics differed significantly between nest and available plots (Wilks' Lambda $F_{11,198}$ = 6.44, P < 0.001). Bold text indicates individual habitat characteristics that differed significantly (P < 0.05) in post-hoc univariate tests.

Model	Parameters	AICc	Delta AICc	AICc Weights
S Grapevine	2	360.38	0.00	0.25
S Light gap hypothesis	3	360.97	0.59	0.19
S constant	1	361.05	0.67	0.18
S Tree size hypothesis	2	362.11	1.73	0.10
S Nest height	2	362.88	2.50	0.07
S Landscape hypothesis	2	363.03	2.65	0.07
S Aspect	2	363.05	2.67	0.07
S Canopy structure hypothesis	3	363.92	3.54	0.04
S Forest structure hypothesis	5	364.08	3.70	0.04

Table 2.6. Ranked models for daily nest survival rate that incorporate vegetation characteristics surrounding Cerulean Warbler nests in southeast Ohio, 2004-2006. See Table 2.3 for description of factors included in each hypothesis.

a)

b)
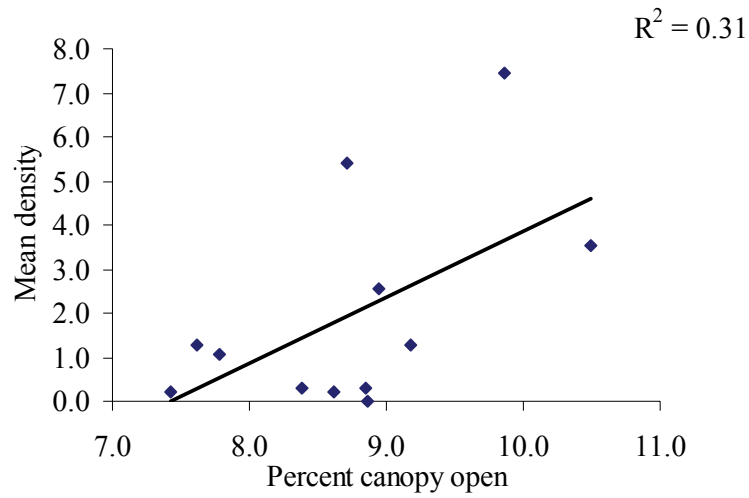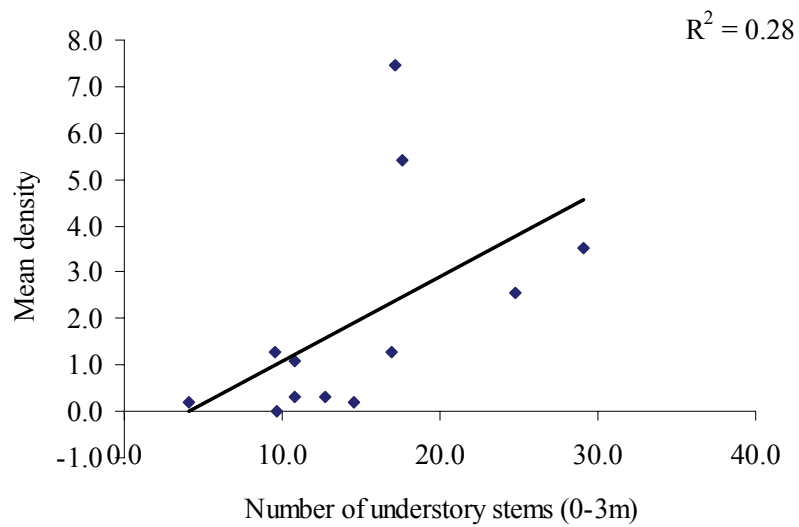
Figure 2.1. Relationship between density of Cerulean Warblers at a site and a) percent canopy openness, b) number of understory stem hits <3 m high, and c) number of trees >38cm dbh at 12 sites in southeastern Ohio, 2004-2006.

Figure 2.1 (continued)

c)

Figure shows a scatter plot with regression line. Y-axis labeled "Mean density" ranging from 0.0 to 8.0. X-axis labeled "Number of trees >38 cm dbh" ranging from 1.5 to 3.5. $R^2 = 0.24$
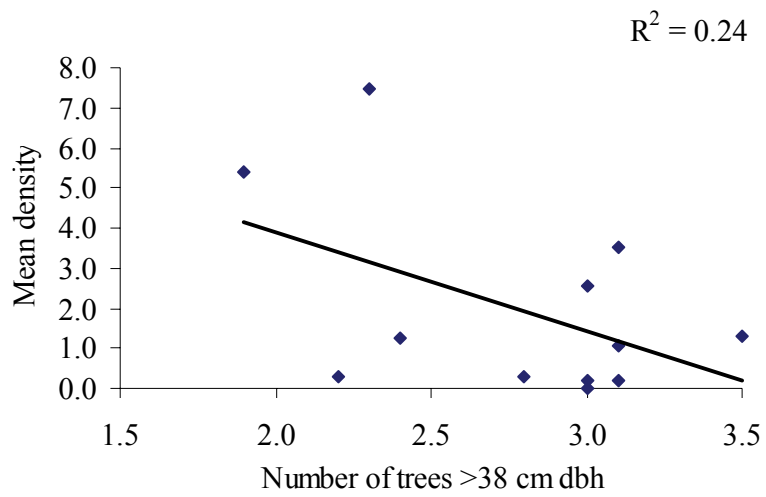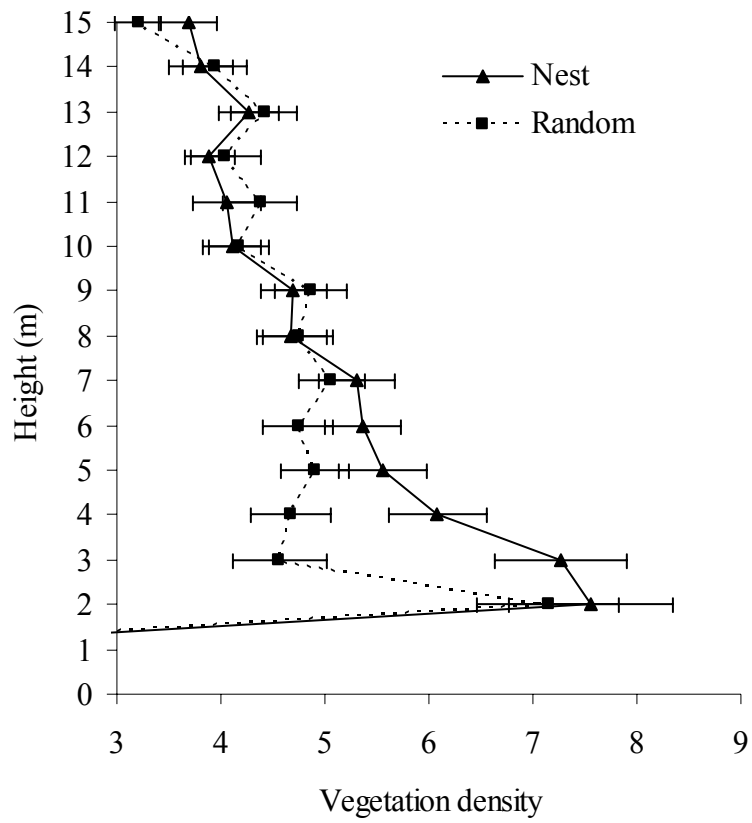
Figure 2.2. Vertical vegetation density profiles at 113 paired nest and random plots located in 10 sites in southeastern Ohio, 2004-2006.
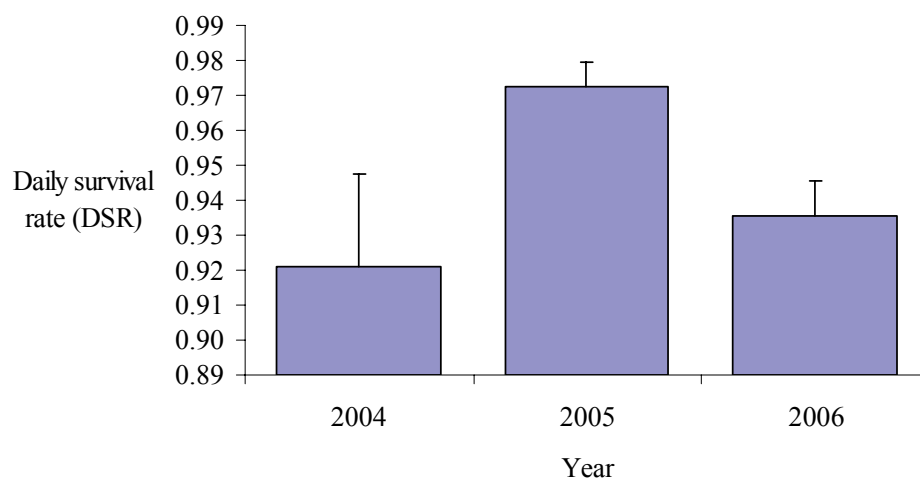
Figure 2.3. Daily survival rate of Cerulean Warblers nests for 2004 (n = 15), 2005 (38),

and 2006 (58) in southeast Ohio.

a)
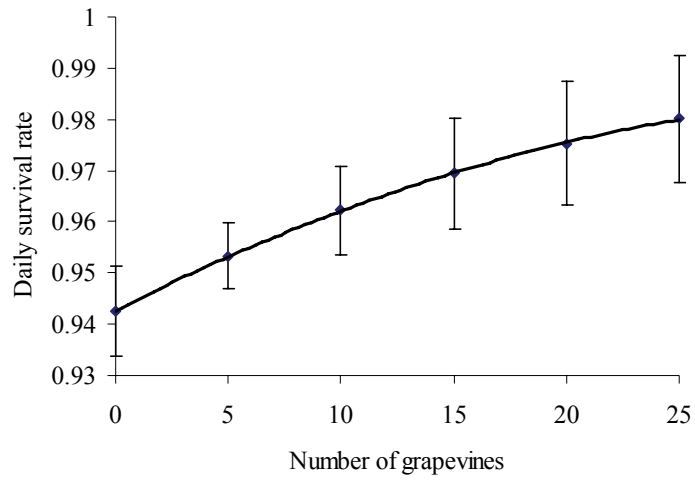
b)
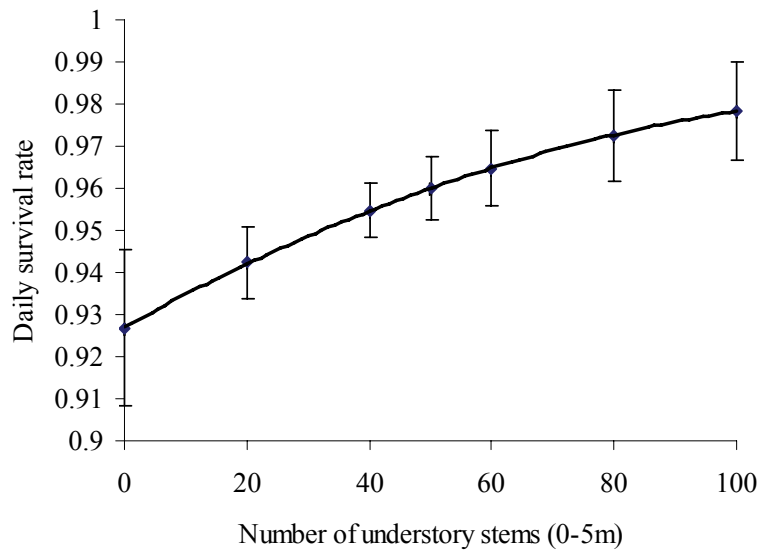
Figure 2.4. The relationship between daily survival rate for Cerulean Warbler nests and

a) number of grapevines and b) understory vegetation density (0-5m) in southeast Ohio,

2004-2006.

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CHAPTER 3

BEANS AND BIRDS: SHADE COFFEE'S ROLE IN BIRD CONSERVATION

Running head: Shade coffee as wintering habitat for migrants

Keywords: shade coffee, habitat quality, Cerulean Warbler, wintering grounds

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Abstract: Although previous studies have demonstrated high use of shade coffee plantations by Neotropical migratory birds, we still have a poor understanding of the suitability of shade coffee plantations as habitat on the wintering grounds. We compared density, body condition, and survivorship of Neotropical migrants, with emphasis on Cerulean Warbler (*Dendroica cerulea*), between primary forest and shade coffee plantations in Venezuela. We worked in three primary forest sites and three shade coffee plantations on the western slope of the Cordillera de Mérida of the Andes Mountains. At each site, we surveyed migrants using distance-based line transects, mist-netted and banded migrants, and documented flocking behavior during November – February 2005/06 and 2006/07. During these two seasons, we also color-banded and resighted 29 individual Cerulean Warblers to estimate apparent monthly survival. Densities of migrants were 3-14x higher in shade coffee plantations than primary forest sites, even after accounting for differences in detectability. Apparent monthly survival of Cerulean Warblers was estimated at 97% and overwinter persistence was similarly high. In addition, Cerulean Warblers demonstrated high between-season fidelity, with 65% of the birds banded the first year being resighted during the second year. Interestingly, immature birds returned at nearly half the rate as did adults. Banding data also suggest that migrants using shade coffee improve their body condition over the winter. Condition increased significantly as the season progressed for Cerulean Warblers, Tennessee Warblers (*Vermivora peregrina*), and American Redstarts (*Setophaga ruticilla*). Combined, these data provide evidence that shade coffee plantations offer high quality wintering habitat for Neotropical migrants, including Cerulean Warblers.

Introduction

Population declines of numerous Neotropical migratory birds in recent decades have fueled ongoing debates of where or when bird populations are most limited (i.e., breeding versus wintering grounds). Although most research on bird populations occurs on the breeding grounds, this debate has stimulated studies examining the possibility that deteriorating quality of wintering ground habitat is a potential cause of declines. In addition to continued efforts to protect unharvested forest, non-governmental organizations and agencies are increasingly recognizing that certain agroforestry practices (e.g., shaded cacao, allspice, or coffee) also may contribute positively to biodiversity conservation, particularly in terms of their ability to provide habitat for wintering Neotropical migratory birds (Greenberg et al. 2000; Reitsma et al. 2001; King et al. 2007).

One form of agroforestry, shade-grown coffee, seems especially well-suited to simultaneously provide a variety of economic, social, and ecological benefits. Coffee is the highest grossing agricultural commodity in the world, generating approximately $55 billion globally each year (Wild 2004). According to the International Coffee Organization, or ICO, more than 45 countries cultivate and export coffee to around 141 countries around the world. Because small-scale farms (i.e., < 10 ha) produce 70% of the world's coffee (Rice 2003), over 23 million people worldwide are estimated to be employed or reliant upon the coffee industry for their livelihood (O'Brien & Kinnaird 2003). In Latin America, shade coffee stands out as one of the most sustainable agroforestry practices because it provides a variety of forest products (e.g., coffee, fruits, firewood, lumber, and medicines; McNeely 2004), while at the same time maintains

forest cover and reduces erosion, insecticide use, and chemical runoff compared to other intensive agricultural systems such as sun coffee, pasture, and sugar cane. At the same time, shade coffee plantations support impressive biodiversity across taxa ranging from arthropods to birds to mammals (Estrada et al. 1993; Mas & Dietsch 2004; Johnson 2000). Not surprisingly, floristic and structural diversity can determine the conservation value of a shade coffee system (Perfecto & Snelling 1995; Rice & Ward 1996; Greenberg et al. 1997*a*; Calvo & Blake 1998; Perfecto & Vandermeer 2002).

Contrasting sharply with shade coffee in terms of biodiversity is sun coffee (Wunderle & Latta 1996; Greenberg et al. 1997*a*), which was originally cultivated to avoid a fungal disease and is grown under full sunlight as a monoculture. Despite its incompatibility with conservation, sun coffee has been rapidly replacing shade coffee throughout regions of the Latin America. For example, approximately 40 – 50% of all shade coffee plantations in Latin America were converted to sun coffee by the 1990s (Perfecto et al. 1996; Rice & Ward 1996). Some regions show disproportionate amounts of conversion to sun coffee. Colombia, for example, has converted about 70% of its coffee production from shade to sun coffee management (Rice & Ward 1996). Likewise, Venezuela lost approximately 38% of its shade coffee plantations between 1950 and 1990 (Roseberry 1983), often to other forms of intensive agriculture unsuitable for biodiversity protection, such as cattle pastures. These trends in conversion of shade coffee to agricultural habitats with limited support of biodiversity demonstrate the need to better evaluate the quality of shade coffee for biodiversity.

Research has documented high use of shade coffee plantations by Neotropical migratory birds, and shade coffee plantations support higher abundances and diversity of

migrant species than any other agricultural habitat (Petit et al. 1999; Wunderle & Latta 1996; Tejeda-Cruz & Sutherland 2004) and up to 6 times greater abundances than some forest habitats (Greenberg et al. 1997*c*; Petit et al. 1999; Johnson & Sherry 2001; Tejeda-Cruz & Sutherland 2004). However, this previous work is limited in two key respects. First, nearly all prior studies did not account for detection probability, which means that higher documented abundance in shade coffee may simply have been an artifact of the more open habitat and increased likelihood of detecting birds in shade coffee (Komar 2006). Second, habitat quality is likely better reflected by sex and age ratio, body condition, return rates, overwinter and annual survival (Johnson et al. 2006) and delayed migration to breeding grounds (Marra et al. 1998) than by abundance alone. In particular, body condition, a factor that is known to be highly correlated with annual survival (Johnson et al. 2006), has not been thoroughly examined in shade coffee habitats.

In this study, we evaluated the suitability of shade coffee plantations in the Venezuelan Andes by (1) comparing density, sex and age ratios, and flock membership in shade coffee and primary forests, (2) examining seasonal variation in body condition within shade coffee plantations, and (3) estimating overwinter apparent monthly survival and return rates for banded Cerulean Warblers in shade coffee plantations. We focused on the northern Andes Mountains because they are considered an urgent conservation priority for biodiversity conservation (Stattersfield et al. 1998; Stotz et al. 1996). Unfortunately, these forests are among the most highly harvested and cultivated regions in the Neotropics (Robbins et al. 1992). In addition to providing wintering habitat for several species of Neotropical migrants (e.g., Olive-sided Flycatcher, *Contopus cooperi*;

Western Wood-pewee, *Contopus sordidulus*; Scarlet Tanager, *Piranga olivacea*; Canada Warbler, *Wilsonia canadensis*), the entire range of the Cerulean Warbler, a globally vulnerable species (BirdLife International 2004), is found between 500-1500 m (Hamel 2000) within forests of the northern Andes.

Study Sites

We studied Neotropical migratory birds in shade coffee plantations and primary forest during two winters (2005-2006 and 2006-2007) in the Venezuelan Andes Mountains (Appendix C). The study was conducted on the western slopes of the Cordillera de Mérida facing the Maracaibo basin. Three study sites were selected in shade coffee plantations and 3 sites in 'undisturbed', primary forest habitat (n = 6 sites in total). Study areas were located in the state of Mérida near the town of La Azulita. The locations and elevation of each site are listed as follows: Cafétal-1 (8˚ 42'N, 71˚ 25'W; 1094 m), Cafétal-2 (8˚ 42'N, 71˚ 25'W; 1050 m), Cafétal-3 (8˚ 41'N, 71˚ 27'W; 1213 m), Bosque-1 (8˚ 45'N, 71˚ 29'W; 1251 m), Bosque-2 (8˚ 46'N, 71˚ 28'W; 1142), and Bosque-3 (8˚ 42'N, 71˚ 25'W; 947 m). Land use within 10 km of the center of the study region was visually estimated with vegetation maps generated and facilitated by the Venezuelan NGO Programa Andes Tropicales-InfoGeo. Land uses are diverse and include forest with little to no human intervention (20%), forest with moderate to heavy human intervention (15%), coffee production (20%; mostly shade grown), and agriculture (e.g., pasture) and human settlement (45%). A portion of a Venezuelan National Park, Parque National Sierra de la Culata (200,000 ha), is located in the region.

Individual shade coffee plantations were approximately 3-5 hectares in size and several plantations were usually connected together to form a band of similar habitat in the immediate landscape. Shade coffee plantations had 38 – 63% canopy cover comprised of a mixture of cultivated trees such as coffee (*Coffea arabica*), cacao (*Theobroma cacao*), avocado (*Persea americana*), and citrus (*Citrus* sp.) as well as shade trees such as *Inga* sp., *Erythrina glauca*, *Cedrela mexicana*, and *Heliocarpus americanus*. Shade coffee plantations were seasonally cleared of all weedy vegetation by manual labor using machetes. All primary forest sites were located in habitats classified as little to no human intervention according to vegetation maps produced by Programa Andes Tropicales. Tree species commonly found in primary forests often overlapped with species remaining as shade trees in coffee plantations. Other species found in primary forest included *Tabebuia rosea*, *Cyathea* sp., and *Ceiba pentandra*. Primary forest had a diverse and thick vertical vegetation structure and a range of 50 – 88% canopy cover.

Methods

Density

Distance-based line transects were used to estimate density of wintering birds within each habitat type. Because primary forest and shade coffee plantations are structurally very different, the probability of detecting birds in each habitat was expected to differ. In particular, the open canopy and midstory structure of shade coffee plantations might make it easier to detect birds compared to vegetatively-dense primary forests. Distance-based methods explicitly estimate the probability of detection, which is then used to adjust estimates of bird densities (Buckland et al. 2001).

Ten 80 m-long line transects were established in each habitat type ($n = 20$

transects in total). Each transect was visited 7 times per season (i.e., approximately once

per week) from early-December to early-February. All Neotropical migrants were

recorded over a 20-minute time period. We recorded bird age and sex as well as distance

and angle (with a rangefinder and compass) from the line transect. Because program

DISTANCE 5.0 (Thomas et al. 2006) ideally requires 40-60 detections to estimate

density, estimates were generated for the 4 species with the greatest number of

detections: American Redstart, and Cerulean, Blackburnian, and Tennessee Warblers (see

Appendix F for scientific names). Detections were pooled over years because numbers of

detections for each species did not differ between years in shade coffee plantations ($F_{1,26}$

$= 0.14$, $P = 0.709$) or primary forest ($F_{1,20} = 0.05$, $P = 0.829$). We right-truncated the

largest 5% of distances of both Cerulean Warbler and American Redstart shade coffee

data because each had several detections at far distances (e.g., >32 m) which added little

to the detection probability function (Buckland et al. 2001). Confidence intervals (95%)

for detection probability estimates for American Redstart, and Cerulean, Blackburnian,

and Tennessee Warblers in shade coffee plantations were $0.52 – 0.64$, $0.50 – 0.71$, $0.62 –$

0.88, and $0.54 – 0.84$, respectively. Because we had fewer detections in primary forest,

we combined detections for American Redstart with Cerulean, Blackburnian, and

Tennessee Warblers given that these species display similar foraging locations and

strategies and had similar detection functions in shade coffee plantations (i.e., 95%

confidence intervals overlapped). Consequently, we calculated a global detection

function to use in generating species-specific densities in primary forest.

Banding & Body Condition

We mist-netted from late November–early February in the winters of 2005–2006 and 2006–2007 and banded all Neotropical migrants captured. Due to extremely low capture rates (i.e., 0.74 captures per 100 net hours) in primary forest, we concentrated mist-netting efforts in shade coffee plantations to support the demographic objectives of the study. Most of our efforts involved passively capturing birds using 10-18 nets (12-m long, 3-m high, 30 mm mesh) deployed at each site. Note that our intent was to maximize number of Cerulean captures rather than use mist-nets to sample understory bird communities. Consequently, net locations were not randomly selected because we purposefully chose locations that were used frequently by mixed-species foraging flocks or individual Cerulean Warblers. In addition to passive banding, we opportunistically broadcast songs and chip notes of Cerulean Warblers near net locations because we found that Cerulean Warblers were occasionally responsive to playback and were lured into the net. As a sidenote, no Cerulean Warblers were recaptured using song playback. At time of capture, we banded all Nearctic-Neotropical migrants with USGS aluminum bands, determined their mass with a Pesola scale (0.2 g accuracy), and measured their wing chord with a wing rule (0.5 mm accuracy) and tarsus and exposed culmen with calipers (0.1 mm accuracy). Birds were aged (immature or adult) and sexed according to Pyle (1997). Cerulean Warblers were color-banded to facilitate later identification in the field.

We examined change in body condition for the top 5 species captured (Tennessee, Mourning, and Cerulean Warblers, Northern Waterthrush and American Redstart; see Appendix F for scientific names) throughout the 2 seasons. Our body condition metric accounted for body frame (structural) size by first performing a principal components

analysis (PCA) on morphometric variables (wing chord and tarsus length). Mass was
then regressed against the body size principal component and the residuals were used as a
condition index. The extent to which the predicted values deviated from expected mass
given a certain body size (i.e., residuals) indicated whether the bird was in good (i.e.,
residual above the regression line) or poor (i.e., residual below) body condition (Strong &
Sherry 2001; Wunderle & Latta 2000). Data were pooled over original and recapture
events.

Apparent Monthly Survival

Apparent monthly survival was estimated from the early portion of the season
(late November) to the late portion of the season (early February). Because Cerulean
Warblers are difficult to capture on the wintering grounds, we were not able to catch all
birds in the beginning of the winter season. We assumed that birds captured late in the
season were present at the site in the beginning of the season and included these birds in
the analysis. In fact, 8 out of 12 birds captured late in the first season were resighted or
recaptured early in the second season. During all visits to each study site (at least once
per week), we systematically searched the area for banded individuals. Within Program
MARK (White & Burnham 1999), we used the Barker model (Barker 1997) to estimate
apparent monthly survival rather than a traditional Cormack-Jolly-Seber survival model
because the Barker model allows for live encounters (e.g., recapture or resightings)
between capture periods to better estimate survival (Collins & Doherty 2006).
Parameters in the Barker model included: apparent survival (φ), recapture probability (p),
the probability of finding a bird dead (r), the probability a bird lives (R) or dies (R') and

is resighted before the next capture period, the probability a bird staying in the area (e.g., fidelity) and remains at risk of capture in the next capture period (F), and the probability of fidelity to another area (F'). Because no birds were recovered dead, r was set equal to 0. In addition, no birds were captured/resighted during migration or the breeding season, hence, both R and R' were set equal to 0 during this time interval. Fidelity parameters were set equal to one another and constant across time. Our small sample size ($n = 29$) restricted us to running relatively simple models. Apparent monthly survival and recapture probability were modeled as constant and as a function of season. Seasons included 1) winter (constant or different) or 2) between years, which included 2 migration events and the breeding period. Given that Cerulean Warblers exhibited two possible behaviors on the wintering grounds territory-holder or flock member (M. Bakermans, personal observation), we used the term 'territorial' as a covariate. We defined winter territory-holders as birds captured/resighted 2 or more times within the same season with at least 7 days between the events ($n = 20$; Chase et al. 1997). All other remaining birds were classified as flock members ($n = 8$) unless they were seen on greater than 2 occasions in the second season ($n = 1$). Although many flocking birds were resighted within and between seasons, suggesting that they remained in the general study area, we expected that recapture probability would be lower for flock members. We also used age and sex of the bird as covariates in the analyses. Model selection was based on Akaike's Information Criterion (AIC_c) corrected for small sample size. Current Goodness-of-fit tests are not valid for Barker models and were not attempted (Collins & Doherty 2006). In addition, we tested for associations between annual return rate and age and sex (Fisher's exact test).

Flock information

Whenever a mixed-species flock was encountered at sites, we recorded the species composition of Neotropical migrants and residents as well as notes on behavior of individuals. Flocks were located using visual and auditory signals (e.g., contact calls) from members. While following flocks, data collected included date, time, site, bird species, age and sex of birds (if possible), number of individuals for each species, and interactions between species. A flock was defined as ≥ 2 species moving together within 25 m of each other (Hutto 1987). We measured species richness (S), Shannon's index of diversity (H), and Shannon's evenness index (E; see Roth et al. 1994) for migratory bird flocks at each site within and between shade coffee plantations and primary forest. Because of detectability biases and flocks repeatedly moving through our study sites, we used an average number of individuals detected of each species for abundance.

Results

Density

We surveyed 10 transects in shade coffee and 10 transects in primary forest with 14 visits (7 each year) for a total of 280 visits. We recorded 325 Neotropical migrants of 17 species on transects in shade coffee plantations compared to 114 individuals of 15 species observed on transects in primary forest (Appendix F). Of the 280 visits, 77 visits (55%) in primary forest and 21 visits (15%) in shade coffee recorded no migrants. Detection-adjusted density estimates for the 4 most common species were 3–14 times higher in shade coffee than primary forest (Table 3.1). American Redstart was the most abundant species in both shade coffee (3.4 birds/ha) and primary forest (0.9 birds/ha).

Cerulean Warblers were the second most abundant migrant species in shade coffee (2.5 birds/ha) compared to the fourth most abundant species (> 0.2 birds/ha) in primary forest.

Based on transect data, American Redstarts showed marginally significant sexual habitat segregation in primary forest ($n = 31$, P = 0.071; Binomial test) where 68% of birds were male. This is a conservative estimate because some young males (displaying a female-like plumage) may have been included with females. This pattern of segregation, however, was not found in shade coffee plantations ($n = 105$, P = 0.558). Cerulean Warblers did not show sexual habitat segregation in either primary forest ($n = 6$, P = 0.668) or shade coffee plantations ($n = 66$, P = 0.175).

Banding & Body Condition

We captured 283 individual Neotropical migrants in shade coffee compared to only 4 in primary forest (Appendix J). After adjusting for effort, capture rates for shade coffee and primary forest were 4.48 and 0.74 Neotropical migrants/100 net hours, respectively. In shade coffee, banding data for American Redstarts supported an even sex ($n = 35$, P = 0.176, Binomial test) and age (P = 0.500, Binomial test) ratio. Banding data for Cerulean Warblers, though, was marginally biased toward females ($n = 29$, P = 0.061, Binomial test; Appendices H & I), but not for age (P = 1.000, Binomial test). This bias is likely due to the fact that females foraged significantly lower than males (Bakermans et al. Chapter 4) and thus, were more available for capture in mist nets. In addition, Mourning Warblers exhibited sex-based segregation where males were more common than females in shade coffee plantations ($n = 46$, P < 0.001). Seventy-seven individual migrants were recaptured within each season in shade coffee resulting in a

27% recapture rate. Within season recapture rates for some species, such as Northern Waterthrush, were as high as 50% and numerous individuals were caught repeatedly throughout the same season (e.g., a single Northern Waterthrush was captured 7 times within the same season).

Body condition increased with day of the season for Cerulean Warbler ($F_{1,44} = 7.82$, $P = 0.008$), Tennessee Warbler ($F_{1,56} = 5.06$, $P = 0.029$), and American Redstart ($F_{1,43} = 3.98$, $P = 0.053$; Figure 3.1). There were no significant associations between condition and date for Northern Waterthrush ($F_{1,46} = 0.17$, $P = 0.683$) nor Mourning Warbler ($F_{1,60} = 0.02$, $P = 0.893$). Residual body condition did not differ with the age or sex of captured birds for American Redstarts, Cerulean Warbler, Tennessee Warbler, Northern Waterthrush, and Mourning Warbler (ANOVA; all $P > 0.06$).

Apparent Monthly Survival

Twenty-five of the 29 color-banded Cerulean Warblers were resighted within the banding season after the initial banding event. In fact, more than half (22 of 41) of all banded individuals were consistently resighted during at least 60% of the banded weeks within each season. Using program MARK, the highest ranked models include the covariate 'territory-holder' and accounted for 87% of the AICc weights (Table 3.2). Using the top-ranked model, apparent monthly survival for territory-holders and flock members during the study period (i.e., 3 months) was 0.97 (± 0.02 SE, 0.91 – 0.99; 95% CI) and 0.81 (± 0.09 SE; 0.58 – 0.93 CI), respectively. Detection probability was estimated as 0.20 (± 0.08 SE) for territory-holders and flock members.

Between-season return rates for one year were high for Cerulean Warblers in shade coffee plantations. Of 20 Cerulean Warblers banded in the first season, 13 (65%) were recaptured or resighted in the second season. Sex of the bird did not influence whether that bird returned in the second year ($n = 20$, $P = 1.000$, Fisher's exact test). Age, on the other hand, was related to the return rate ($P = 0.070$, Fisher's exact test) such that 89% of adult birds returned compared to 46% of immature birds.

Flocking

We followed flocks on 149 occasions in primary forest ($n = 39$) and shade coffee plantations ($n = 110$). Migrant species commonly present in flocks included Cerulean, Blackburnian, Tennessee, and Black-and-white Warblers, American Redstart, and common residents included Speckled Tanager (*Tangara guttata*), Golden-fronted Greenlet (*Hylophilus aurauntiifrons*), Cocoa Woodcreeper (*Xiphorhynchus susurrans*), Bay-headed Tanager (*Tangara gyrola*), and White-eared Conebill (*Conirostrum leucogenys*). The most common migrant found in mixed-species flocks in primary forest was Blackburnian Warbler, found in 72% of flocks (Table 3.3). In contrast, Cerulean Warblers were the most common migrant detected in mixed-species flocks in shade coffee plantations. Cerulean Warblers were detected in 86% of observed flocks, with a range of 0-9 Ceruleans detected per flock. Mean species richness and diversity were lower for flocks in primary forest than in shade coffee plantations while evenness was similar between habitats (Table 3.4).

Discussion

Densities

Although researchers have suggested that shade coffee plantations serve as refugia for a variety of Neotropical migrants in deforested regions (Wunderle & Latta 1996; Greenberg et al. 1997*c*; Tejeda-Cruz & Sutherland 2004), our study is the first to compare densities of migrants in shade coffee and primary forests after accounting for potential differences in detection probability due to structural features (Komar 2006). Densities of the 4 most common migrant species (American Redstart, and Cerulean, Tennessee and Blackburnian Warblers) were 3 – 14 times greater in shade coffee plantations than in primary forest. Interestingly, Cerulean Warblers exhibited the largest difference with densities in shade coffee 14 times greater than primary forest. Only one other ongoing study in Colombia has estimated density of Cerulean Warblers on wintering grounds. Compared to this study, our densities of Cerulean Warbler were greater in shade coffee (2.1/ha in Venezuela versus 0.8/ha in Colombia) but similar in forest (0.2/ha versus < 0.4/ha, respectively; G. Colorado, personal communication). Reasons for this difference remain unclear. Capture rates of migrant birds per 100 net hours in shade coffee plantations for this study were comparable to those from studies in Costa Rica, Dominican Republic, and Puerto Rico (see Komar 2006). One notable contrast was that unlike Marra and Holmes (2001), who reported that densities of American Redstarts were similar across multiple habitats, including shade coffee, we found substantially lower densities in primary forest.

We found little evidence of age and sex habitat segregation for migratory species. American Redstart, exhibited sex segregation in primary forest where males seemed to

dominate. The only sex segregation found in shade coffee plantations, was for Mourning

Warblers, where males were dominant. Several studies have shown that age and sex

habitat segregation occurs among some birds (Greenberg et al. 1997*b*; Marra & Holmes

2001; Latta & Faaborg 2002; Fernandez & Lank 2006) on the wintering grounds.

Segregation is frequently accompanied by marked differences in condition of males and

females using different habitats. For example, birds in female-biased habitats, which

tend to be of poor quality habitat, frequently lose body mass over the course of the winter

(Marra & Holmes 2001; Latta & Faaborg 2002). In contrast, Greenberg et al. (1997*b*)

found several species, including American Redstart) with higher male: female sex ratios

in shade coffee compared to other types of habitat (i.e., acacia woodlot and gallery

forest), suggesting that shade coffee is the higher quality habitat.

Apparent monthly survival, return rates, and condition

Our banding data indicated that many migrants wintering in coffee plantations

show relatively high site fidelity within and between years. Cerulean Warblers and

American Redstarts exhibited strong site fidelity and the greatest between-year recapture

rates of the 15 migratory species we captured. An important caveat, however, is that nets

were placed in areas to maximize the potential to catch Cerulean Warblers in mixed-

species flocks, and this may have reduced the chances of recapturing birds that do not

join flocks as readily. Interestingly, though, we had few recaptures between years of

other species commonly found in flocks in shade coffee plantations (e.g., Tennessee and

Blackburnian Warblers).

Apparent monthly survival estimates for Cerulean Warblers on our wintering study sites was estimated as 0.97 (0.90 – 0.99; 95% CI) for birds holding territories. Estimates of apparent monthly survival for flock members were lower, but with less precision possibly due to the fact that these birds were more difficult to resight and recapture. In order to accurately assess survival of flock members, radio telemetry may be needed to locate and follow these birds. Age and sex of the bird did not influence apparent monthly survival. Annual return rate for Cerulean Warblers (65%) at our study sites was high compared to studies of migrants elsewhere. Wunderle and Latta (2000) documented an approximately 35% return rates for 3 species (American Redstart, Black-and-white Warbler, *Mniotilta varia*, and Black-throated Blue Warbler, *Dendroica caerulescens*) in the Dominican Republic. However, return rates were higher for these same species in Jamaica (Holmes & Sherry 1992) with a 51% and 46% annual return for American Redstarts and Black-throated Blue Warblers, respectively. Even higher annual return rates were reported by Latta and Faaborg (2002) with an average of 57% return in pine forest, dry forest, and desert for Cape May Warblers in the Dominican Republic. In addition, Koronkiewicz et al. (2006) reported 68% between-year site fidelity for Willow Flycatchers (*Empidonax traillii*) in Costa Rica. Although site fidelity may be adaptive over evolutionary time, high annual return rates may make species particularly vulnerable in regions with extensive and rapid habitat loss, such as in the northern Andes where forest is rapidly being converted to sun coffee and/or open pasture (Stattersfield et al. 1998; Stotz et al. 1996).

Our study is the first to provide evidence of increased body condition of migratory species in shade coffee plantations. Other studies examining seasonal changes

in body condition in forested habitats have produced mixed results. Typically, birds in undisturbed forests have exhibited no change or an increase in body condition (Sherry & Holmes 1996; Strong & Sherry 2001; Latta & Faaborg 2002), whereas birds in disturbed or dry forests often exhibit decreased body condition (Sherry & Holmes 1996; Latta & Faaborg 2002). For example, Latta and Faaborg (2002) documented an increase in muscle mass of Cape May Warblers in pine forest (i.e., high quality) compared to a decrease in muscle mass through the sampling period in desert scrub (i.e., low quality). Several other studies have found that individuals occupying male-dominated habitats often show no change in body condition, whereas individuals in female-dominated habitats often decline in condition as the season progresses (Marra & Holmes 2001; Studds & Marra 2005). Although some species may show a genetic predisposition to sex-based segregation on the wintering grounds, in other species females and young males may be pushed into suboptimal habitat.

Those that have examined body condition in shade coffee habitats, have found measures similar to natural forests (Johnson et al. 2006), but have either seen no change (R. Chandler, personal communication) or a decrease in body condition throughout the wintering season (Strong & Sherry 2000; Johnson et al. 2006). Strong and Sherry (2000) reported that size-adjusted body mass was higher in shade coffee plantations and limestone forest compared to second growth scrub, though body mass declined throughout the season for all habitats. Similarly, size-adjusted body mass values in shade coffee plantations were comparable to the best natural forest habitat in Jamaica. Yet, on average each habitat showed a 3% decrease in body mass by the end of the season (Johnson et al. 2006). In our study, body condition improved for three species (Cerulean

and Tennessee Warblers and American Redstart) as the banding season progressed. High

body condition on the wintering grounds is important because early arrival and body

condition on the breeding grounds are directly correlated with fitness (Price et al. 1988;

Moller 1994; Lozano et al. 1996; Hasselquist 1998). In addition, poor energetic

condition at end of winter season has been found to be correlated with decreased survival

(Marra & Holmes 2001). We suggest that gain in body condition was not related to

either immediate or short-term recovery from southward migration in fall nor migratory

preparation due to the fact that our banding operations in Venezuela started >8 weeks

after birds arrived and >6 weeks before birds departed for northward migration. In fact,

no Cerulean Warblers and < 5% of all migrants had visible furcular fat deposits.

Sociality and flock participation

Sociality may be another driving factor in community structure and habitat

suitability. Mixed-species flocks have been recognized to benefit participants through

improved defense against intruders, predator protection, and information about conditions

(e.g., enhanced foraging efficiency; Hutto 1988; Terborgh 1990). In this study, we

document a shift in principal flock members from primary forest to shade coffee

plantations. Blackburnian Warblers predominated in primary forest flocks while

Cerulean Warblers were greater in shade coffee plantations flocks. Others have

suggested that Cerulean Warblers do not occupy habitats in elevations greater than 1500

m because of increased competition with Blackburnian Warblers (Robbins et al. 1992).

This shift in most common flock member suggests that this competition also could occur

between different habitats. Social interactions with conspecifics may be an important

social component on the wintering grounds for Cerulean Warblers in shade coffee plantations. In both our study and a Colombian study, the majority of observed Ceruleans were members of a mixed-species flock (86% and 82%, respectively; G. Colorado, personal communication). Furthermore, large numbers (up to 9) of Cerulean Warblers have been documented participating in these mixed-species flocks. This is higher than the range (1 to 4) of Cerulean Warblers documented participating in mixed-species flocks in shade coffee plantations on the eastern slopes of the Venezuelan Andes (Jones et al. 2000).

Conservation Implications

Most previous studies have failed to address demographic processes and issues related to body condition of birds using shade coffee plantations. Based on our examination of several demographic and condition parameters (i.e., density, body condition, apparent monthly survival, annual return and sociality), we suggest that shade coffee plantations in the Venezuelan Andes provide important wintering habitat for Neotropical migrants, including Cerulean Warblers. Nevertheless, the traditional agroforestry practice of growing coffee in plantations with a diverse canopy of trees is being lost in many parts of Latin America as farmers switch to intensive and less environmentally-friendly sun coffee plantations and pasture. Indeed, throughout the course of the project, we witnessed the conversion of several surrounding shade plantations into pasture for cattle (M.B., personal observation). Thus, we need to evaluate (e.g., Petit & Petit 2003) and encourage eco-friendly use of the landscape matrix. Future conservation efforts that focus only on preservation of pristine habitats

72

will ultimately be unsuccessful. In regions where little forest habitat remains, agroforestry systems (e.g., coffee, cacao, and allspice) represent habitats of high conservation value.

	Shade coffee plantation			Primary forest		
Species	n	P_a	D (SE)	n	P_a	D (SE)
American Redstart	99	0.58	3.39 (0.67)	32	0.57	0.91 (0.23)
Blackburnian Warbler	46	0.74	1.12 (0.27)	15	0.57	0.42 (0.15)
Cerulean Warbler	63	0.59	2.51 (0.63)	6	0.57	0.17 (0.09)
Tennessee Warbler	48	0.67	1.26 (0.45)	13	0.57	0.37 (0.14)

Table 3.1. Sample size (n), detection probabilities (P_a), and distance-based density estimates (D) generated in Program Distance for the 4 most common species in the Venezuelan Andes, 2005-2007. See Appendix F for scientific names.

Survival model (φ)	AICc	Δ AICc	Model Weight	Number of Parameters
φ 2seasons + territorial, p 2seasons	109.345	0	0.485	8
φ constant + territorial, p constant	111.753	2.41	0.146	7
φ 2seasons + territorial, p 2seasons + territorial	111.918	2.57	0.134	9
φ 2seasons + territorial, p constant	112.167	2.82	0.118	8
φ 2seasons + territorial, p constant + territorial	114.182	4.84	0.043	9
φ constant + territorial, p constant + territorial	114.193	4.85	0.043	8
φ 3seasons, p constant	116.773	7.43	0.012	7

Table 3.2. Apparent monthly survival models for Cerulean Warblers. Apparent monthly survival (φ) was modeled as a function of season using the Barker (1997) model. For instance, a 2-season model included 1 season for both winters (2005/2006 and 2006/2007) and 1 season for between years. Likewise, a 3 season model included 2 seasons for winter (different for each year) and 1 season for between years. Between years included 2 migration events and the breeding period. Covariates included territoriality, age, and sex of bird. Model selection was based on Akaike's Information Criterion (AIC$_c$). Only models with AIC Weight $\geq$0.01 are listed.

| | Primary forest | | Shade coffee plantation | |
Species	Mean ± SE	Proportion	Mean ± SE	Proportion
Cerulean Warbler	1.5 ± 0.2	0.26	2.4 ± 0.2	0.86
American Redstart	1.1 ± 0.1	0.56	1.2 ± 0.1	0.65
Blackburnian Warbler	1.2 ± 0.2	0.72	1.3 ± 0.1	0.56
Tennessee Warbler	1.4 ± 0.2	0.41	1.4 ± 0.1	0.55
Black-and-white Warbler	1.0 ± 0.0	0.31	1.0 ± 0.1	0.23
Mourning Warbler	1.0 ± 0.0	0.03	1.0 ± 0.0	0.10
Yellow-throated Vireo	1.0 ± 0.0	0.03	1.0 ± 0.0	0.09
Canada Warbler	1.0 ± 0.0	0.10	1.0 ± 0.0	0.07
Chestnut-sided Warbler	0.0 ± 0.0	0.00	1.0 ± 0.0	0.05
Northern Waterthrush	0.0 ± 0.0	0.00	1.0 ± 0.0	0.05
Red-eyed Vireo	0.0 ± 0.0	0.00	1.0 ± 0.0	0.05
Summer Tanager	1.0 ± 0.0	0.10	1.0 ± 0.0	0.05
Rose-breasted Grosbeak	2.5 ± 1.5	0.05	1.0 ± 0.0	0.04
Swainson's Thrush	1.0 ± 0.0	0.05	1.0 ± 0.0	0.03
Acadian Flycatcher	1.0 ± 0.0	0.23	1.0 ± 0.0	0.02
Black-throated Green Warbler	0.0 ± 0.0	0.00	1.0 ± 0.0	0.02
Bay-breasted Warbler	1.0 ± 0.0	0.03	1.0 ± 0.0	0.01
Gray-cheeked Thrush	1.0 ± 0.0	0.03	1.0 ± 0.0	0.01
Magnolia Warbler	0.0 ± 0.0	0.00	1.0 ± 0.0	0.01
Golden-winged Warbler	1.0 ± 0.0	0.03	0.0 ± 0.0	0.00

Table 3.3. Proportion of mixed-species flocks containing specific species in primary forest ($n = 39$) and shade coffee plantations ($n = 110$) and mean number of each species detected when in a mixed-species flock, in the Venezuelan Andes, 2005-2007. See Appendix F for scientific names.

Habitat	Site	Index		
		S	H	E
Primary forest	Bosque1	10	2.29	0.99
	Bosque2	10	2.16	0.94
	Bosque3	12	2.45	0.98
Shade coffee	Cafétal1	16	2.76	0.99
	Cafétal2	10	2.17	0.94
	Cafétal3	15	2.67	0.99
Mean ± SE	Forest	10.67 ± 0.67	2.30 ± 0.08	0.97 ± 0.02
	Coffee	13.67 ± 1.86	2.53 ± 0.18	0.97 ± 0.02

Table 3.4. Species richness (S), Shannon's diversity index (H), and evenness (E) for Neotropical migratory birds for 1) each site in shade coffee and primary forest, and 2) the mean for each habitat in the Venezuelan Andes, 2005-2007.

a)

Cerulean Warbler

b)
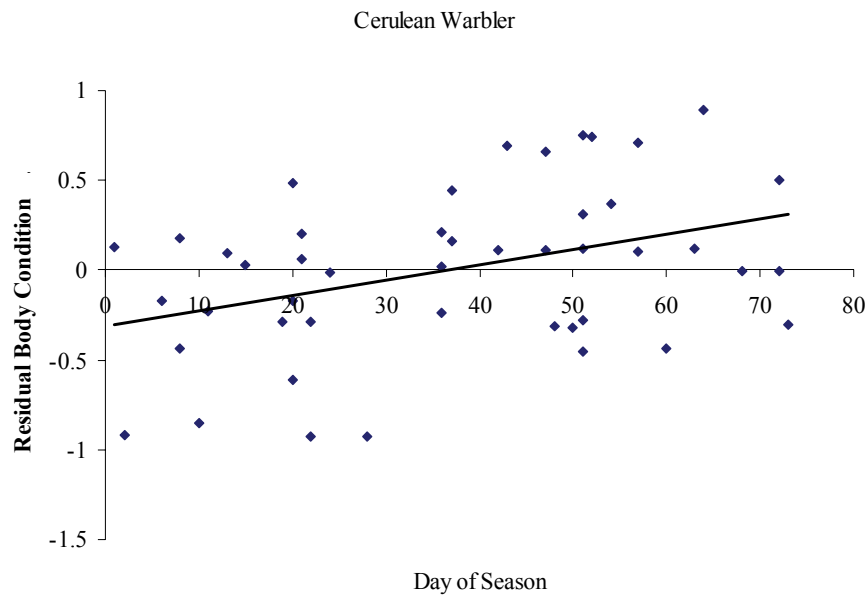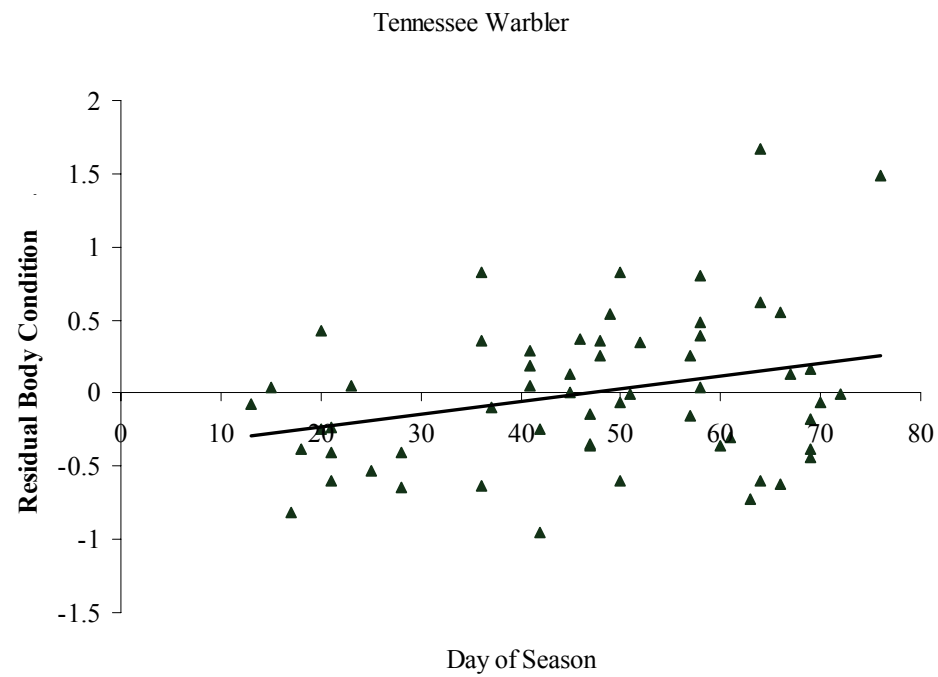
Tennessee Warbler

Figure 3.1. Residual body condition for a) Cerulean Warbler, b) Tennessee Warbler, and c) American Redstarts from 22 November to 8 February, 2005-2007 in Venezuela.

Figure 3.1 (continued)

c)

American Redstart
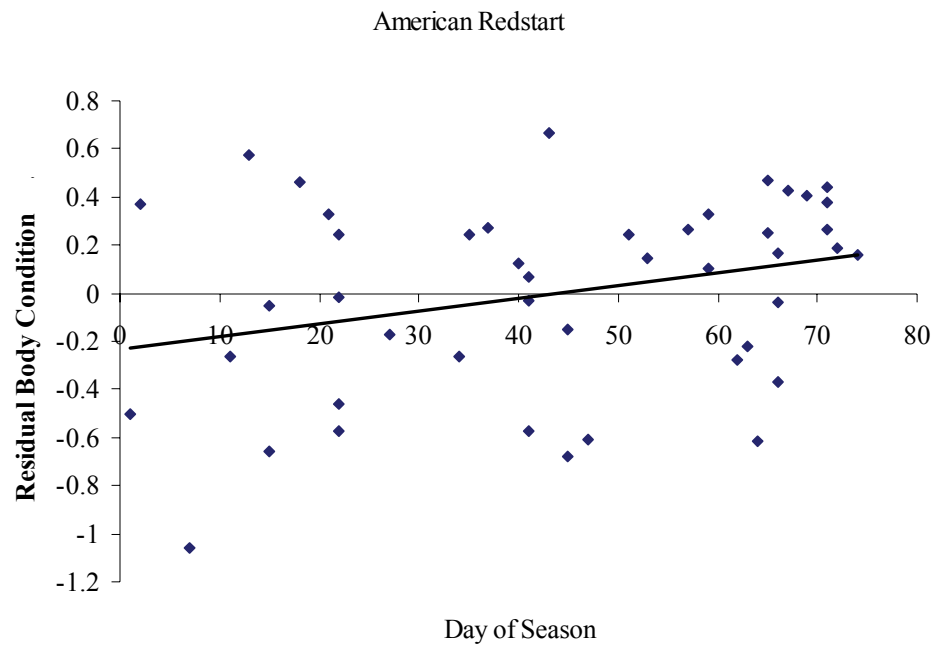
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CHAPTER 4

MIGRATORY BIRD USE OF SHADE COFFEE: THE ROLE OF STRUCTURAL

AND FLORISTIC FEATURES

Running head: Habitat features of shade coffee and migrant bird use

Keywords: Cerulean Warbler, floristic, foraging, habitat, *Inga* spp., Neotropical

migratory birds, shade coffee, structure, redundancy analysis, RDA

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Abstract.– Shade coffee plantations are known to support high levels of Neotropical migratory birds, but relatively little is known about the structural and floristic attributes used by individual species. We identified specific habitat features used by Neotropical migrants in traditional polyculture coffee plantations in the Venezuelan Andes. First, we studied the foraging behavior of Cerulean Warblers (*Dendroica cerulea*), a species of high conservation concern. We found that females forage at significantly lower heights than males. Cerulean Warblers were most often documented foraging in *Inga* spp. trees, and this was in greater proportion than their availability throughout plantations. Next, we used redundancy analysis (RDA), a multivariate approach, to examine if abundance of Neotropical migrants changed with the structure and floristic composition of shade coffee plantations. Analyses showed that abundance of Neotropical migrants was significantly related to both structural and floristic characteristics. Upper canopy foragers (e.g., Cerulean, Blackburnian, and Tennessee Warblers and Summer Tanagers) were closely associated with number of large trees (>38 cm dbh), tree height, and understory vegetation density. Lower canopy and ground foragers were positively associated with numbers of small (8 – 23 cm dbh) and medium (23 – 38 cm dbh) trees and increased canopy cover. Abundances of upper canopy and lower canopy foragers were related to *Erythrina glauca* and *Acnistus arborescens*, respectively, and these two plant species are known to be important for wildlife in the Neotropics. Because habitat structure and floristic composition seemed to strongly affect use of shade coffee plantations by migrant birds, this work suggests that the suitability of plantations may be increased by encouraging farmers to apply specific management practices.

Introduction.–

Among the various agricultural habitats used by wintering Neotropical migratory birds throughout Latin America (see Tejeda-Cruz and Sutherland 2004), agroforestry systems (e.g. coffee, cacao, allspice) are thought to have especially high conservation value because they support more biodiversity than other non-shade agroecosystems (e.g. pasture, sugar cane; Greenberg et al. 1997b, Petit and Petit 2003) and cover large expanses of land in the Tropics (Rice and Ward 1996). In particular, shade-grown coffee is receiving tremendous attention from ecologists and conservationists based on the combined economic, sustainable, and environmental benefits of the practice (Perfecto et al. 1996, Rice 2003). Traditional coffee agroforestry, which involves growing several crops (e.g. coffee, banana, cacao) under mature-tree canopies, generally supports impressive levels of biodiversity. Not only do metrics of species richness and abundance point to the conservation value of shade coffee plantations, but recent data on overwinter survival, site fidelity, and energetic condition also suggest that these areas may provide high quality habitat for Neotropical migrants (Johnson et al. 2006, Bakermans et al. Chapter 3). Thus, encouraging use of shade coffee techniques is thought to be an important conservation strategy.

Broad recommendations to use shade coffee techniques, though, may provide limited guidance for farmers given that coffee can be grown under a wide range of shade intensities – from rustic farms where no canopy trees are removed to low shade conditions that nearly resemble sun coffee plantations (Moguel and Toledo 1999). In general, a decrease in management intensity and an increase in structural and floristic complexity are positively related to species richness and abundance (Calvo and Blake

1998, Cruz-Angón and Greenberg 2005, Van Bael et al. 2007). Specific structural features that have been identified as important factors driving bird-habitat relations include canopy cover (Parrish and Petit 1996, Gordon et al. 2007), canopy height (Greenberg et al. 1997a, Harvey and Villalobos 2007), and tree density (Greenberg et al. 1997, Harvey and Villalobos 2007). Fewer studies have closely examined the value of particular tree species, foraging substrates (e.g., leaves, epiphytes) and food sources (e.g., fruits, nectar, arthropods) for birds.

Clearly, identifying specific vegetation features that are associated with habitat quality in shade coffee plantations is important for implementation of management strategies that can enhance the overwinter survival of migratory birds. Most studies, however, examine avian community response to structure or floristics without considering individual species responses (Komar 2006). For some species of conservation concern, like the Cerulean Warbler (*Dendroica cerulea*), there is still a paucity of information on winter ecology. In this study, we examined habitat use by Neotropical migratory birds in shade coffee plantations that have been identified as high quality habitat for wintering migrants (Bakermans et al. Chapter 3). We evaluated habitat features used by Neotropical migrants by 1) documenting foraging behavior (i.e., height, substrate, maneuver) of Cerulean Warblers, and 2) testing the extent to which abundance of migratory bird species was related to floristic and structural differences in shade coffee plantations.

METHODS

Study system.–We studied Neotropical migrants in shade coffee plantations in the

Cordillera de Mérida of the Andes Mountains in Venezuela from 2005 to 2007. Land

uses within the region are diverse but primary land uses include agriculture (i.e., citrus

and coffee plantations), pasture, urban development, and second-growth and primary

forest. Three study sites, 3-5 hectares each, were selected on the western slope of the

Andes in the state of Mérida facing the Maracaibo basin (8˚ 42'N, 71˚ 25'W). Sites

ranged in elevation from 1050 – 1213 m. These shade coffee plantations correspond to

Moguel and Toledo's (1999) traditional polyculture system. Traditional polyculture

plantations grow coffee in the understory in conjunction with other cultured crops (e.g.,

banana, cacao). Overstory trees are reduced to increase light for understory crops while

encouraging nitrogen-fixing canopy trees (e.g., *Inga* sp.). Shade coffee plantations in the

study contained a mixture of cultivated trees such as coffee, cacao, avocado, and citrus as

well as shade trees such as *Inga* spp., *Erythrina glauca*, *Cedrela mexicana*, and

Heliocarpus americanus. *Inga* spp. and *Erythrina* spp. are the most typical component of

coffee systems in the Venezuelan Andes (Escalante 1995). Shade coffee plantations were

seasonally cleared of all weedy vegetation by manual labor using machetes.

Bird Community.–We sampled the migratory bird community along 10 line transects 80

m in length in shade coffee plantations. Throughout the winter period (December 20 –

February 9, 2005–2007), we surveyed each transect 7 times per season. We recorded all

migrants within sight of the line over a 20-minute time period and recorded distance to

each individual bird. To reduce observer bias, data were collected by the same two fully-

trained individuals each year. Because numbers of birds did not differ by year ($F_{1,26} = 0.14$, $P = 0.709$) we averaged abundance of each species across years.

Foraging observations.–We used a focal individual approach to collect foraging observations. Focal individuals were located by continuously searching sites for Cerulean Warblers throughout the day (~0800 – 1800 hours). Once identified, an individual was followed and observations were taken at ≥1 minute intervals beginning one minute after the initial sighting. Information collected included: age, sex, site, date, foraging height (measured with clinometer and rangefinder), foraging substrate, vertical (lower, middle, or upper) and horizontal (inner, middle, or outer) position in shrub or tree, foraging maneuver (glean, sally, or probe), height of substrate, substrate phenology, and whether the bird was in a flock.

Measurement of Habitat Characteristics.–Habitat characteristics were measured in two 0.04-ha circular plots along each transect (modified from James and Shugart 1970 and Martin et al. 1997). Each plot was randomly located from 0–40 and 41–80 m along each transect with a random distance (0–25 m) and direction from the transect line. At each plot we recorded numbers of trees by species (if identifiable) in three size categories (8–23, 23–38, and > 38 cm dbh, diameter at breast height), standing dead trees (> 15 cm dbh), number of coffee and banana plants > 1 m in height, and canopy height. In addition, percent canopy cover and vertical foliage density (woody shrubs and saplings from 0-3 m) were measured at 2-m intervals along two 20-m perpendicular transects established through the plot center.

Analyses.–We tested for differences in foraging height and strata for Cerulean Warblers (Proc GLM). In addition, we used a chi-square test of the null hypothesis that Cerulean Warblers randomly select tree species in proportion to availability for foraging in shade coffee plantations (Manly et al. 2002). We omitted coffee plants from this analysis because 1) Cerulean Warblers were seldom seen foraging in coffee, and 2) coffee plants are typically <2 m tall which is much lower than average foraging height of both male and female Cerulean Warblers. Because the chi-square test was significant at the $\alpha =$ 0.05 level, we calculated simultaneous Bonferroni confidence intervals (*sensu* Byers et al. 1984) to examine if selection or avoidance of individual tree species occurred. Because Bonferroni adjustments are often too conservative, species with expected frequencies <5 were excluded from analyses (Simes 1986).

We examined if bird community composition was related to vegetation characteristics along transects by applying a direct gradient analysis (ter Braak and Similauer 1998). First, we used a detrended correspondence analysis (DCA) to assess linear or unimodal response of species to environmental variables. DCA is an indirect gradient analysis that seeks major gradients in the species data (ter Braak 1988). The length of the gradient is then used to choose which method of direct gradient analysis is appropriate for analyses. Responses of species are generally expected to be unimodal over a wide range of environmental conditions but linear over a short range of conditions. DCA indicated that a linear approach to ordination was appropriate for the data (all lengths of gradient <3). Therefore, we used a redundancy analysis (RDA) rather than canonical correspondence analysis (CCA) because RDA is based on a linear model of species responses to environmental variables rather than a unimodal response (McCune

and Grace 2002). RDA is a constrained form of multiple regression of the species'

responses on the environmental variables (ter Braak 1988). We used Monte Carlo

permutation tests (with 500 randomizations) to assess the significance of the relationship

between the species and environmental variables.

Multivariate ordination allows for visual interpretation of data associations

through biplots (species and explanatory variables). In these plots, explanatory (i.e.,

environmental) variables are indicated with arrows where the length represents the

importance of the explanatory variable, and the angle between arrows represents

correlations. Locations of species scores indicate environmental preferences (Palmer

1993). Transects were treated as the unit of analysis in this portion of the study. Mean

abundance was estimated by averaging the number of birds (by species) detected on each

line transect for the 10 most abundant species. Although detection of birds is a concern,

there were not enough detections of each species for program DISTANCE to generate

abundance while accounting for detectability. Furthermore, because we were sampling

within shade coffee plantations, we did not expect detectability to vary significantly

between transects. In fact, Bakermans et al. (Chapter 3) found that the 4 most abundant

species had similar detection functions in shade coffee plantations (i.e., 95% confidence

intervals overlapped). Abundance of each species was log-transformed to reduce the

weighting of dominant species. Any non-normal vegetation variables were log-

transformed to improve normality and for each highly correlated pair of variables, one

member was removed from analysis. Because we had a greater number of environmental

variables than samples (i.e., transects), we divided our analyses into two vegetation

models so that we could run a constrained analysis. A constrained analysis can be

performed when the number of environmental variables is less than the number of

samples minus two (Lepš and Šmilauer 2003). We examined if vegetation characteristics

explained abundances of migrants in shade coffee based on two models: 1) structure

(including canopy height, canopy cover, understory vegetation density, and number of

trees in 3 size categories) and 2) floristics (i.e., tree and shrub species). Analyses were

performed using Statistical Analysis System (SAS Institute 1996) and CANOCO Version

4 (ter Braak and Šmilauer 1999).

RESULTS

Bird Community.–We documented 17 species of Neotropical migrants on line transect

surveys in shade coffee plantations (Table 4.1, Appendix J). For the 3 most abundant

species, both American Redstart and Blackburnian Warbler were detected at all transects,

whereas Cerulean Warblers were documented at 9 of the 10 transects (see Table 4.1 for

scientific names). The community of migrants contained several foraging guilds

(DeGraaf et al. 1985) including upper canopy (e.g., Cerulean and Blackburnian Warblers,

Summer Tanager), lower canopy (e.g., American Redstart, Acadian Flycatcher), and

ground/understory (Northern Waterthrush, Mourning and Canada Warbler) foragers.

Foraging observations. –We collected 425 foraging observations on male (n = 189) and

female (n = 237) Cerulean Warblers during 103 occasions. Mean foraging height for

males and females differed significantly ($F_{1,424}$ = 18.09, P < 0.01) with males foraging at

11.4 m ± 0.4 SE (range = 0.5 – 29.0 m) and females foraging lower at 9.4 m ± 0.3 SE

(range = 1.0 – 31.0 m). The most common foraging maneuver was glean (88% of

observations) directed at foliage (92% of observations). Cerulean Warblers foraged throughout the different vertical strata but were found more often in the outer (horizontal) strata of trees and shrubs [χ^2 (2, n = 424) 220.49, P < 0.001]. Males and females did not differ in the vertical ($F_{1,424}$ = 0.650, P = 0.420) or horizontal ($F_{1,424}$ = 0.403, P = 0.525) position within a substrate while foraging. Throughout each season, 76% of observed Cerulean Warblers were moving with mixed-species foraging flocks. Cerulean Warblers foraged in a wide variety of trees and shrubs, including *Inga* spp. and *Acnistus arborescens* (Table 4.2). There was a significant difference in substrates used in foraging versus those available throughout shade coffee plantations [χ^2 (14, n = 418) 207.15, P < 0.001; Table 4.2].

Habitat characteristics.–We identified 13 species of shrubs and trees in transect plots in shade coffee plantations. We were, however, unable to identify 8% of the substrates available in shade coffee plantations. Canopy height ranged from 13 – 24 m (mean = 18.4, SE = 1.1) and canopy cover measured 40 – 65% (mean = 51.8%, SE = 3.05; Table 4.3, Appendices K & L). Although *Inga* spp. were the most common overstory trees in plantations (Table 4.2), half of all large trees (>38 cm dbh) were *Erythrina glauca* (Appendix M).

Species abundance and vegetation structure were significantly related (F = 2.65, P = 0.05), and 75% of the variation in vegetation structure was explained by two RDA axes (Fig. 4.1a). The first RDA axis explained 47.5% of the variation among transects and reflected a decrease in tree size. The second RDA axis explained 27% of the variation and represented an increasing number of mid-sized trees. Most mid- and understory

foragers (e.g., Mourning and Canada Warbler, Acadian Flycatcher) were most closely related to the number of small and medium trees and fell on the positive side of the diagram (right-hand side). Conversely, upper canopy foragers (e.g., Cerulean, Tennessee, and Blackburnian Warblers) were positively associated with an increase in canopy height, number of large trees, and understory vegetation and were on the negative side (left-hand side) of the diagram.

Species abundance was related to vegetation floristics (F = 2.47, P = 0.05), and 72% of the variation among transects was explained by axis 1 (53.2%) and axis 2 (18.7%). The ordination biplot of the floristic model (Fig. 4.1b) illustrated that the foraging guilds were divided with the mid- and understory foragers on the left-hand side of the plot and associated with a common understory shrub, *Acnistus arborescens*. Canopy foragers, on the other hand, were grouped together on the right-hand side of the diagram between two common canopy trees, *Cedrela mexicana* and *Erythrina glauca*, and coffee plants.

DISCUSSION

Although shade coffee plantations are often considered poor habitat for resident understory and ground specialist birds (Roberts et al. 2000), we documented high use of shade coffee plantations in the Venezuelan Andes by 29 species of Neotropical migratory birds representing multiple foraging guilds. Cerulean Warbler, a species of conservation concern, was the second most abundant migrant in shade coffee plantations. Both the proportion and abundance of Neotropical migrant species in our shade coffee plantations

were comparable to those from studies in Columbia, Venezuela, and Panama but slightly lower than studies in Mexico, Central America, and the Caribbean (see Komar 2006).

Relative abundance of Neotropical migrants was significantly related to structural characteristics of shade coffee plantations. This result follows the tenet of shade coffee certification through Smithsonian's Bird-Friendly and Rainforest Alliance programs. The coffee plantations in our study system possessed many of the same qualifications necessary for these shade certifications. In particular, these sites had >40% shade cover, >10 tree species, epiphytes present, and vegetation throughout the shade strata (Philpott et al. 2007).

Wintering migrants were found using the same foraging guild classifications (i.e., upper, lower, and ground) as described by DeGraaf et al. (1985). Upper canopy foraging migrants were most closely associated with taller and larger canopy trees with a thick understory vegetation density. Several upper canopy migrants (e.g., Cerulean and Blackburnian Warbler) show a slight negative relationship with canopy cover. That is, with a decrease in canopy cover, there is an increase in Cerulean Warbler abundance. A decrease in canopy cover or an increase in canopy gaps also allows for light penetration and a thick understory vegetation density. This allows for simultaneous growing of coffee plants while providing habitat for Neotropical migrants. This result, however, differs from other studies (Greenberg et al. 1997a, Parrish and Petit 1996) reporting positive relationships between bird abundance and canopy cover.

Abundance of upper canopy foragers also was associated with an increase in canopy height. An increase in tree canopy may provide additional resources and allow more birds to forage in the canopy. For example, Cerulean Warblers exhibited

significant sex segregation in foraging height where males foraged higher than female Cerulean Warblers. This differs from a study on the eastern slopes of Venezuela which found males and females forage at similar heights (~12m, Jones et al. 2000). Abundance of Acadian Flycatchers, a species with a preference for closed forests (Whitehead and Taylor 2002), showed a strong positive relationship with canopy cover. Lastly, ground and lower story foragers were most closely related to habitat features that provide thick midstory vegetation.

Floristic structure also was significantly related to relative bird abundance. Abundance of upper canopy foraging birds showed a positive relationship with *Erythrina glauca*, a tree species that occupied the largest proportion of the large trees (>38cm dbh). Other studies have shown that plantations with *Inga* spp. and *Erythrina* spp. trees have higher bird species richness and abundance compared to plantations primarily composed of *Pseudalbizzia* spp. or *Gliricidia* spp. (Greenberg et al. 1997a, Johnson 2000, Johnson and Sherry 2001). Our and another study in Colombia (G. Colorado, personal communication) did not observe Cerulean Warblers foraging on *Erythrina* flowers as documented by Jones et al. (2000). Foraging attempts by Cerulean Warblers were most frequently directed at *Inga* trees and were used out of proportion of their availability. Shade coffee plantations dominated by *Inga* spp. have been shown to provide large numbers of arthropod (Johnson 2000, Johnson and Sherry 2001) and nectar resources (Greenberg et al 1997) comparable to natural forest (Pomara et al. 2003). Furthermore, an understory shrub, *Acnistus arborescens*, known to attract over 40 species of birds (Wheelwright et al. 1984) was used by foraging Cerulean Warblers in 12% of observations and was positively associated with ground and lower canopy foragers.

Cerulean and Blackburnian Warblers were tightly associated in ordination graphs and may be selecting similar floristic and structural features. As previously suggested, these two closely related species may compete on the wintering grounds (Robbins et al. 1992). In fact, some have suggested that the restricted elevational range of wintering Cerulean Warblers is a consequence of the greater abundance of Blackburnian Warblers at higher elevations (Hamel 2000). Indeed, on several occasions, we witnessed Blackburnian Warblers initiate aggressive behaviors (e.g., chasing, chipping) directed toward Cerulean Warblers.

Although most attention on habitat conversion in the Tropics has focused on the loss of primary forests, agroforestry systems present a unique opportunity to simultaneously provide economic and environmental benefits. Agroforestry may promote conservation in tropical regions by 1) reducing deforestation pressures, 2) providing suitable habitat for plant and animal species, and 3) creating a hospitable landscape matrix that facilitates movements between existing patches of habitat (Schroth et al. 2004). A traditional polyculture has a complex shade component, a variety of cultivated crops (e.g., banana, fruit, cacao), and a coffee understory, thus, creating a multi-strata system (Greenberg et al. 1997b). Because coffee is grown at altitudes with high deforestation and few designated reserves, traditional shade coffee plantations possess an ever-increasing role in protecting biodiversity (Perfecto et al. 1996). In general, wildlife use of coffee plantations is influenced by structural and floristic complexity, food availability, degree of management, and the surrounding landscape (Somarriba et al. 2004). The value of shade coffee for both sustainable farming and

wildlife benefits can be maximized when incorporating the appropriate structural and floristic characteristics.

ACKNOWLEDGMENTS

Species	Code	Abundance	Foraging Guild
American Redstart, *Setophaga ruticilla*	AMRE	0.70 ± 0.14	Lower canopy
Cerulean Warbler, *Dendroica cerulea*	CERW	0.46 ± 0.11	Upper canopy
Tennessee Warbler, *Vermivora peregrina*	TEWA	0.31 ± 0.11	Upper canopy
Blackburnian Warbler, *D. fusca*	BLBW	0.31 ± 0.07	Upper canopy
Northern Waterthrush, *Seiurus noveboracensis*	NOWA	0.07 ± 0.03	Ground
Black-and-white Warbler, *Mniotilta varia*	BAWW	0.06 ± 0.03	Bark gleaner
Mourning Warbler, *Oporornis philadelphia*	MOWA	0.06 ± 0.03	Ground
Summer Tanager, *Piranga rubra*	SUTA	0.04 ± 0.02	Upper canopy
Acadian Flycatcher, *Empidonax virescens*	ACFL	0.03 ± 0.02	Air /low canopy
Chestnut-sided Warbler, *D. pensylvanica*	CSWA	0.03 ± 0.03	Lower canopy
Bay-breasted Warbler, *D. castanea*	BBWA	0.01 ± 0.01	Upper canopy
Canada Warbler, *Wilsonia canadensis*	CAWA	0.01 ± 0.01	Ground/low canopy
Black-throated Green Warbler, *D. virens*	BTGN	0.01 ± 0.01	Upper canopy
Gray-cheeked Thrush, *Catharus minimus*	GCTH	0.01 ± 0.01	Ground/low canopy
Rose-breasted Grosbeak, *Pheucticus ludovicianus*	RBGR	0.01 ± 0.01	Upper canopy
Swainson's Thrush, *C. ustulatus*	SWTH	0.01 ± 0.01	Ground/low canopy
Yellow-throated Vireo, *Vireo flavifrons*	YTVI	0.01 ± 0.01	Canopy

Table 4.1. Mean abundance ($\pm$ SE) across 10 transects for all Neotropical migratory birds detected on line transects in shade coffee plantations in the Venezuelan Andes, 2005-2007. Foraging guilds follow DeGraaf et al. (1985).

Substrate species / Species code	Proportion Expected	Proportion Observed	Bonferroni confidence interval[a]
Inga spp. / Ing sp	0.43	0.55	$0.474 \leq P_1 \geq 0.626$*
Unknown	0.09	0.18	$0.121 \leq P_2 \geq 0.239$*
Acnistus arborescens / Acn arb	0.17	0.12	$0.070 \leq P_3 \geq 0.170$
Cedrela mexicana / Ced mex	0.11	0.09	$0.046 \leq P_4 \geq 0.133$
Persea americana / Per ame	0.08	0.04	$0.010 \leq P_6 \geq 0.070$**
Erythrina glauca / Ery gla	0.09	0.18	$0.090 \leq P_9 \geq 0.010$**

[a] P_i represents theoretical proportions of occurrence and is compared to proportion of expected use. If the expected proportion is outside the confidence intervals of observed use than the hypothesis of proportional use is rejected.

* = used more and ** = used less than expected by chance (significant at the 0.05 level).

Table 4.2. Tree and shrub species identified in shade coffee plantations and the proportion of each substrate observed in foraging attempts and expected throughout the plantation. Simultaneous Bonferroni intervals were calculated using methods described in Byers et al. (1984). Species with expected frequencies <5 were excluded from analyses, including *Ficus* spp., *Citrus* spp., *Coffea arabica* (Cof ara), *Piper aduncum*, *Cecropia* spp., *Heliocarpus americanus* (Hel ame), *Ceiba pentandra*, *Acacia* spp., *Annona muricata*, *Theobroma cacao*.

Transect	Canopy cover (%)	Canopy height (m)	Number of trees 8-23 cm dbh	Number of trees 23-38 cm dbh	Number of trees >38 cm dbh	Understory vegetation density (0 – 3 m)
1	62.5 (2.5)	17.5 (5.5)	6.0 (1.0)	4.0 (1.0)	0.0 (0.0)	23.5 (2.5)
2	50.0 (10.0)	15.2 (0.6)	6.0 (0.0)	2.0 (0.0)	1.5 (0.5)	18.5 (4.5)
3	62.5 (2.5)	22.2 (2.6)	5.0 (1.0)	2.0 (2.0)	2.0 (1.0)	20.5 (13.5)
4	47.5 (2.5)	16.5 (0.4)	9.0 (0.0)	2.0 (1.0)	2.5 (1.5)	20.0 (5.0)
5	47.5 (2.5)	23.8 (2.0)	6.5 (0.5)	1.0 (0.0)	1.5 (0.5)	19.0 (2.0)
6	47.5 (2.5)	18.1 (2.1)	8.0 (1.0)	2.5 (0.5)	1.0 (0.0)	25.0 (8.0)
7	37.5 (7.5)	17.3 (0.7)	5.5 (1.5)	1.5 (0.5)	1.5 (0.5)	10.5 (10.5)
8	65.0 (0.0)	12.6 (0.1)	12.0 (2.0)	1.5 (0.5)	0.5 (0.5)	8.5 (2.5)
9	57.5 (12.5)	20.1 (4.3)	10.5 (0.5)	2.0 (1.0)	0.0 (0.0)	19.0 (9.0)
10	40.0 (0.0)	20.5 (0.5)	12.0 (0.0)	2.0 (0.0)	0.5 (0.5)	9.0 (2.0)

Table 4.3. Mean (SE) values for habitat features measured at 10 transects in 3 shade coffee plantations in Venezuela, 2006-2007.

a)
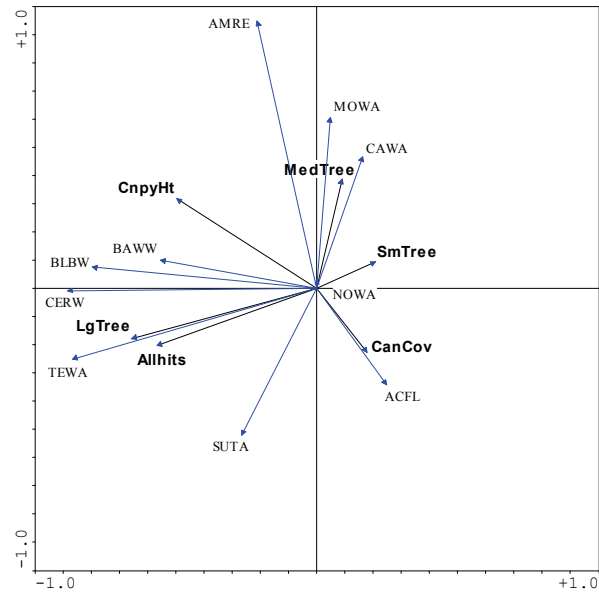
b)
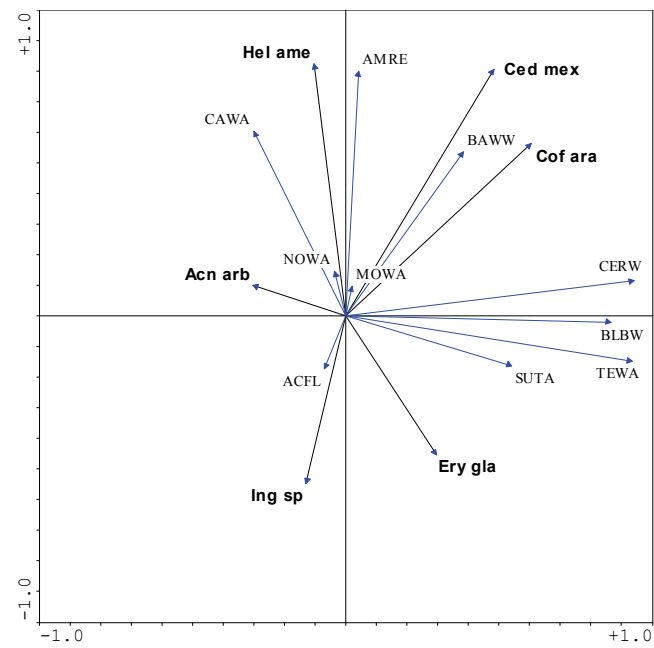
Figure 4.1. RDA biplot of bird and a) forest structure and b) tree species in shade coffee

plantations, Venezuelan Andes. See Tables 4.1 and 4.2 for bird and tree scientific names.

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CHAPTER 5

ESTIMATES OF APPARENT ANNUAL SURVIVAL AND MIGRATION

MORTALITY FOR A NEOTROPICAL MIGRATORY SONGBIRD

Running head: Annual and migration survival of a Neotropical migratory bird

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Summary

1. Despite concern for declining Nearctic-Neotropical avian migrants, few studies have examined populations of species on both the breeding and wintering grounds to assess the relative importance of mortality throughout the annual cycle.

2. We ringed and resighted Cerulean Warblers (*Dendroica cerulea*), a species of high conservation concern, from November – February (2005 – 2008) on the wintering grounds in the Venezuelan Andes to estimate apparent annual survival. Combined with annual survival estimates, we used apparent survival estimates generated on both the breeding (Jones et al. 2004) and wintering grounds (Bakermans et al. Chapter 3) to estimate mortality during migration.

3. Apparent annual survival was best-explained by age-specific models, where adults ($0·73 \pm 0.10$ SE) had higher annual survival than juveniles ($0·45 \pm 0·11$ SE). Apparent monthly migration survival ($0·97 \pm 0·06$ SE) for adults was similar to values throughout the remainder of the annual cycle, though juveniles experienced up to 6x higher mortality during migratory periods.

4. Our study provides an estimate of apparent annual survival for Cerulean Warblers that can be used to re-evaluate other estimates of population growth for this species. In particular, our estimates suggest that several breeding populations that were once considered to be population sinks may now be considered source populations.

Key-words: adult, CJS, Cerulean Warbler, Cormack-Jolly-Seber, demography, *Dendroica cerulea*, juvenile, migration, mortality, survival

Introduction

Concerns of population declines of some Nearctic-Neotropical migrants have prompted studies to focus on limiting factors (e.g. predators, food supply, weather, etc.) of populations. Populations of migratory species, though, are regulated by dynamics that occur throughout the annual cycle (Sherry & Holmes 1995). For migratory birds, most attention has focused squarely on identifying limiting factors on the breeding grounds, with less emphasis focusing on the wintering grounds. Indeed, very few species of Neotropical migrants are studied simultaneously on both breeding and wintering grounds (Holmes & Sherry 1992; Sillett & Holmes 2002).

Demographic parameters, such as survivorship, are among the most influential factors in driving population trends and identifying habitat quality on both the breeding and wintering grounds (Johnson *et al.* 2006; Johnson 2007). Annual survival in migratory bird populations has been linked to reproductive success and wintering-ground body condition (Johnson *et al.* 2006). Annual survival data, however, are difficult to collect and, consequently, are seldom estimated for migratory species. Yet accurate measures of annual survival are critical for proper calculation of population growth rates (Buehler *et al.* 2008). For declining species, this may be of particular interest when identifying source-sink dynamics (Pulliam 1988) and generating conservation strategies.

Although a great deal more is known about habitat requirements and limitations on the breeding and nonbreeding seasons, events during migration also influence population distributions and abundances (Sherry & Holmes 1995). In fact, it is now believed that migration may be the most limiting time period in a migratory bird's annual cycle (Sillett & Holmes 2002; Newton 2008). Yet mortality rates during this period of

time have proven difficult to measure, especially for small passerines, compared to stationary periods (i.e. breeding and wintering periods). Mortality rates are often thought to be much higher during migratory periods due to a combination of loss and degradation of stopover habitats, weather events, and other human-induced factors (Moore *et al*. 1995).

The objective of this study was to evaluate which period of the annual cycle (i.e. breeding, migration, or wintering) had the highest mortality rate for a declining songbird. More specifically, we estimate apparent 1) annual survival and 2) survival during migration for Cerulean Warbler (*Dendroica cerulea*), a Neotropical migrant of high conservation concern. We calculated annual survival from resighting data collected on ringed individuals on the wintering grounds in the Venezuelan Andes. To estimate survival during migration, we used apparent annual survival estimates in combination with within-season survival data generated on the breeding (Jones *et al*. 2004) and wintering (Bakermans *et al*. Chapter 3) grounds.

Methods

STUDY SPECIES

The Cerulean Warbler is a Neotropical migratory songbird that breeds in large tracts of mature deciduous forest concentrated in the mid-Atlantic regions and winters in submontane forests on the slopes of the Andes Mountains in northern South America (Hamel 2000). Since 1966, Cerulean Warblers have declined precipitously throughout their breeding range (-4.0% per year, Sauer 2003), exhibiting one of the steepest declines of any North American bird. Consequently, Cerulean Warblers have a high priority

ranking from conservation groups, which recently petitioned for threatened status for Cerulean Warblers under the Endangered Species Act.

Demography of Cerulean Warblers is notoriously difficult to study on the breeding and wintering grounds because of the canopy foraging and nesting behavior of the species. Most knowledge of Cerulean Warblers comes from habitat associations on the breeding grounds (Oliarnyk & Robertson 1996; Jones *et al.* 2001; Jones & Robertson 2001; Weakland & Wood 2005; Wood *et al.* 2005). Limited data exist for direct measurements of Cerulean Warbler demography (fitness and survivorship), especially on the wintering ground. Cerulean Warblers winter in a narrow elevational range (~500 – 1500m) of the Andes Mountains. This range has been contracting northward from Bolivia, with the majority of individuals of the species wintering in Venezuela and Colombia (Hamel 2000). Cerulean Warblers have a longer migratory route and time-frame (~ 5 months) than most other long-distance passerines (Hamel 2000). This extended migratory phase may exacerbate the risk of mortality during migration for Cerulean Warblers.

STUDY SITES

We studied Cerulean Warblers in shade coffee plantations on the wintering grounds in the Venezuelan Andes. Shade coffee plantations were located in the Cordillera de Mérida, in the state of Mérida, facing the Maracaibo basin (8˚ 42'N, 71˚ 25'W). Sites ranged in elevation from 1050 – 1213m, which corresponds to the altitudes of the most floristically and structurally diverse shade coffee systems in the Venezuelan Andes (Escalante 1995). Plantations were composed of a mixture of canopy shade trees (e.g.,

Inga spp., *Erythrina glauca*, *Heliocarpus americanus*), timber trees (e.g., *Cedrela mexicana*), planted crop trees (e.g., *Citrus* spp, *Theobrama cacao*, *Persea americana*), and coffee (*Coffea arabica*) understorey. These study sites have been documented as high quality habitat for Cerulean Warblers and other wintering Neotropical migrants because birds exhibited increased energetic condition and high persistence and survival during the winter season (Bakermans *et al*. Chapter 3).

FIELD METHODS

We studied Cerulean Warblers in the field in Venezuela during 3 winter seasons including two 3–month seasons in 2005/2006 and 2006/2007 and an ancillary 4 week season in December 2007–January 2008. We mist-netted from late–November to early–February in the seasons 2005–2006 and 2006–2007 and ringed all Cerulean Warblers captured. We placed 10–18 mist nets (12m long, 3m high, 30mm mesh) throughout shade coffee plantations. Because average foraging height for female and male Ceruleans was 9 and 11m, respectively (Bakermans *et al*. Chapter 4), we carefully chose net locations to maximize number of captures. Hence, we strategically placed nets where we observed birds using and/or passing through habitat when in mixed-species foraging flocks. Ideal net placements included hillsides and on limbs of fallen trees. In addition, because a few birds appeared territorial (i.e., displaying aggressive behavior) we opportunistically broadcasted song and chip notes of Cerulean Warbler in an attempt to lure birds into mist nets. Upon capture, all Cerulean Warblers were aged and sexed following Pyle (1997), ringed with a USGS aluminum ring, and individually marked with

a combination of coloured plastic rings. On each visit to a study site, we systematically

searched each study site (at least 1 time per week) for ringed individuals.

STATISTICAL ANALYSIS

We used the Cormack-Jolly-Seber (CJS) model (Pollock *et al*. 1990; Lebreton *et

al*. 1992) in program MARK (White & Burnham 1999) to estimate apparent annual

survival (φ) and detection (ρ) probabilities of 29 Cerulean Warblers. We constructed a

set of candidate models based on factors believed to influence survival and resighting

probabilities based on Cerulean Warbler biology (Hamel 2000). We modeled φ as

constant and as a function of year, age, and sex. Age and sex may influence survival if

older and/or male birds are dominant and exclude young and/or females from high

quality habitat, thus, resulting in lower survival for young and/or females (Marra &

Holmes 2001). Age was classified into two categories: juvenile and adult birds. Juvenile

birds were individuals in their first winter and adults in at least their second winter.

Probability of detection was modeled as constant and as a function of sex. Resighting

may differ between sexes because female Cerulean Warblers forage at significantly lower

heights in the canopy than male Cerulean Warblers (Bakermans *et al*. Chapter 4). Model

selection and parameter estimation were based on Akaike's Information Criterion

corrected (AIC_c) for small sample size. The model with the lowest AIC_c value was

considered the best model given the data. Subsequent models were assessed by their

difference in AIC_c values (ΔAIC_c) and weight of evidence (ω_i). Models with $\Delta AIC_c < 2$

are considered plausible given the data (Burnham & Anderson 2002). We assessed the

support of age, sex, and year in φ by summing ω_i values of all candidate models that

contained that factor. Because our data were sparse, we ran a median chat goodness-of-fit test on the time dependent model (φ_t, ρ_t).

Because apparent annual survival is a product of survival probabilities throughout the annual cycle (i.e. $\varphi_{annual} = \varphi_{breeding} \times \varphi_{migration} \times \varphi_{wintering}$), we were able to calculate survival during migration periods. We used monthly apparent survival estimates ($0{\cdot}98 \pm 0{\cdot}01$) of breeding Cerulean Warblers generated in a 6-year study in Ontario, Canada by Jones et al (2004). Within-season apparent monthly survival estimates ($0{\cdot}97 \pm 0{\cdot}02$) on the wintering grounds were generated from resighting data on the same Cerulean Warbler population (Bakermans *et al*. Chapter 3) used to estimate annual survival in this study. Using Bootstrap resampling methods, we generated a standard error of apparent migration survival based on random combinations from 20 simulated samples of each value for the annual cycle, which were drawn from their respective standard deviations. Although no colour-ringed birds from Ontario were seen on the wintering grounds, we considered individuals sampled on the wintering grounds to be a part of a larger panmictic population because a stable isotopic study by Girvan (2003) documented mixed migratory connectivity where birds breeding in northern latitudes then winter in northern regions of South America. According to Cerulean Warbler biology (Hamel 2000), we defined the breeding period as 3 months (May–July), fall migration as 3 months (August–October), winter period as 4 months (November–February), and spring migration as 2 months (March–April).

Results

ANNUAL SURVIVAL

Variation in apparent annual survival was not well explained by year or sex of the bird. Instead, the best-supported model (φ_{age}, p; Δ AICc = 0, ω_i = 0·32; Table 5.1) included an age-dependent survival estimate with constant detection probability. The second-best model (φ, p; Δ AICc = 1·06, ω_i = 0·19) did not include any age, sex, or time factors. Based on the best-ranked model, adult apparent annual survival was estimated as 0·73 ± 0·10 SE (95% CI: 0·51 – 0·87), whereas juvenile survival was estimated as 0·45 ± 0.11 SE (95% CI: 0·25 – 0·66). Both adult and juvenile birds had a resighting probability of 1·00 ± 0.01. Based on the sum of ω_i, age-specific survival models were 2·2 and 4·1 times better than constant or sex-specific models, respectively. Median chat goodness-of-fit tests indicated a good fit ($\hat{c}$ = 0·98).

MIGRATION SURVIVAL

Because other studies did not specifically look at age in relation to survival, we first calculated apparent migration survival based on the constant survival generated by the second-best survival model (0·59 ± 0·08 SE, 95% CI: 0·44 – 0·73) which did not include an age-dependent estimate. Apparent monthly survival during migration was 0·93 (0·07 SE). When using age-specific annual survival values, apparent migration survival was 0·97 (0·06 SE) and 0·88 (0·07 SE) for adults and juvenile birds, respectively.

Discussion

Accurate estimates of survival throughout the annual cycle are necessary to 1) understand which phase contributes most to mortality and 2) generate veritable values for population growth rates. Our estimate of apparent annual survival ($\varphi_{constant} = 0\cdot59$) in this study is comparable to apparent annual survival rates for other Neotropical migrants. Minimum estimates from other studies range from $0\cdot43$ for American Redstart (*Setophaga ruticilla*) and Blue-winged Warbler (*Vermivora pinus,* Sillett & Holmes 2002; DeSante 2000) to $0\cdot72$ for Willow Flycatcher (*Empidonax trailii,* Koronkiewicz *et al*. 2006). Minimum estimates of annual survival based on annual return rates to the wintering grounds range from 31% from Black-throated Blue Warblers (*Dendroica caerulescens*, Wunderle & Latta 2000) to 57% for Cape May Warblers (*Dendroica tigrina*, Latta & Faaborg 2002), but these do not account for detection probability.

Our study documented large differences in apparent annual survival based on the age of the individual, with adults having 62% greater survival than juvenile birds. Our adult survival estimate was high compared to a study by DeSante (2000), where only two of 27 Neotropical migrant species had higher annual survival rates than we documented in this study. Both Black-and-white Warbler (*Mniotilta varia*) and White-eyed Vireo (*Vireo griseus*) had apparent annual survival of $0\cdot84$ and $0\cdot73$, respectively. Adult apparent annual survival reported in this study ($0\cdot73 \pm 0\cdot10$ SE) was $1\cdot5$ times higher than reported for adult Cerulean Warblers in an Ontario breeding population (Jones *et al*. 2004; $0\cdot49 \pm 0\cdot05$ SE). Johnson *et al*. (2006) also found age-related annual survival differences for American Redstarts wintering in Jamaica where adults had higher survival than juveniles ($0\cdot50$ versus $0\cdot28$). Survival for juveniles, though, may be underestimated

121

in this study if they do not exhibit high site fidelity to the wintering grounds on their second year of return. That is, if there is high dispersal and permanent emigration beyond the study area for the second year of winter, apparent survival will be much lower than true survival (Marshall *et al*. 2000). Our study, did not find sex-related differences in annual survival as found for other passerines (Sillett & Holmes 2002; Morrison *et al*. 2004). We documented an even sex-ratio and no difference in body condition between male and female Cerulean Warblers in shade coffee plantations on the wintering grounds (Bakermans *et al*. Chapter 3), which may explain this pattern.

Detection probability in our study (1·00) is likely overestimated, where estimates in other studies typically range from 0·83 – 0·95 (Sillett & Holmes 2002; Jones *et al*. 2004). To accurately approximate detection probability, birds must not be detected in one period and then detected again in a following period. Our detection probability was high because we never resighted a bird in a subsequent year after it was not detected. Several more years (i.e., > 3 years) in the study system would likely generate a more accurate detection probability. That said, we still believe that not all birds were detected in the study. For example, one male Cerulean Warbler was never resighted at the study site but was captured in a mist net. If indeed detection probability was less than 1, our annual survival rate is biased low.

Our estimate of apparent adult survival is higher than estimates used to calculate population growth rates (λ) for Cerulean Warblers across multiple sites throughout the breeding range (Jones *et al*. 2004; Buehler *et al*. 2008). At all 5 study sites, ranging from Arkansas to Ontario, Buehler *et al*. (2008) found that each population was experiencing negative growth. Based on sensitivity and elasticity analyses, adult survival was found to

have the greatest influence on population change (Buehler *et al*. 2008). Based on their calculations, the 'best' and 'worst' sites need an adult survival rate > 0.65 and > 0.81, respectively, to achieve stable populations (i.e., $\lambda = 1$). Given our estimate of adult survival, several of their study sites (i.e. Ontario and Tennessee) would be considered source populations with positive growth (i.e. $\lambda > 1$), whereas other sites (e.g., Indiana and Mississippi Alluvial Valley) still would be considered sink populations (i.e. $\lambda < 1$).

Apparent monthly mortality rates during migration were $4 - 6$ times higher during migration than summer and winter periods for juvenile Cerulean Warblers. Mortality, especially for inexperienced and/or subordinate juvenile birds, during migration may be higher than stationary periods due to lack of appropriate stopover habitat, adverse weather en route, and barriers (e.g. communication masts, buildings; Newton 2008).

Surprisingly, adult birds had similar monthly survival rates throughout the annual cycle ($0.97 - 0.98$), and survival rates during migration were higher than previously reported for Black-throated Blue and Cerulean Warblers (Sillett & Holmes 2002; Jones *et al*. 2004). This finding is counter to the current assumption that mortality rates are highest during the migratory phase (Sillett & Holmes 2002; Newton 2008). Apparent survival for adult Cerulean Warblers may be higher during migration if survival on breeding and wintering grounds were underestimated. In particular, survival on the wintering grounds may have been underestimated because Cerulean Warblers forage in the canopy and may not be easily detected. Indeed, a pilot study in Colombia on overwintering Cerulean Warblers reported difficulties visually detecting radioed Cerulean Warblers when they were foraging in upper canopies (G. Colorado, personal communication).

Annual survival may be best estimated on the wintering grounds where migratory songbirds show high site fidelity (Holmes & Sherry 1992; Sandercock & Jaramillo 2002). Numerous studies have now documented high site fidelity (50 – 72%) between years on the wintering grounds (Holmes & Sherry 1992; Latta & Faaborg 2002; Koronkiewicz *et al*. 2006, Bakermans *et al*. Chapter 3). In fact, Holmes and Sherry (1992) documented higher site fidelity on the wintering compared to the breeding grounds for Black-throated Blue Warblers. They propose that conditions on the breeding grounds (i.e. habitat quality) have strong yearly variation, thus, causing birds to move greater distances between years on the breeding grounds. Indeed, a stable-hydrogen isotope study of Cerulean Warblers found long-distance dispersal between breeding seasons was common for adult birds (Girvan *et a*l. 2003). Fidelity to the breeding grounds may be based on behavioral decisions of individuals based on predator communities and nest depredation. In fact, several studies have documented that birds with depredated nests show significantly lower return rates than birds with successful nests (Holmes & Sherry 1992; Sandercock & Jaramillo 2002).

Acknowledgements

Survival model (φ)	Number of parameters	AICc	Δ AICc	Model weight (ω_i)
φ_{age}, p	3	59·94	0·00	0·32
φ, p	2	61·00	1·06	0·19
φ_{age}, p_{sex}	4	62·34	2·40	0·10
$\varphi_{age + year}, p$	5	62·79	2·85	0·08
φ_{year}, p	3	62·85	2·91	0·07
φ_{sex}, p	3	63·07	3·13	0·07
φ, p_{sex}	3	63·32	3·38	0·06
$\varphi_{age + sex}, p$	5	64·81	4·87	0·03
φ_{year}, p_{sex}	4	65·30	5·36	0·02
φ_{year}, p_{year}	4	65·30	5·36	0·02
φ_{sex}, p_{sex}	4	65·52	5·58	0·02
$\varphi_{age + year}, p_{sex}$	6	65·53	5·59	0·02
$\varphi_{year + sex}, p$	5	67·31	7·37	0·01
$\varphi_{age + sex}, p_{sex}$	6	67·54	8·00	0·01

Table 5.1. Candidate models describing apparent annual survival for Cerulean Warblers as measured through resighting colour-ringed birds on the wintering grounds in the Venezuelan Andes, 2005 – 2008. Models are ranked according to AICc and Δ AICc values where the best-supported models have smaller (i.e., < 2) ΔAICc values and larger Akaike weights (ω_i). Only models with ω_i > 0.01 are listed.

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Appendix A. Year-round range map of Cerulean Warbler, a Neotropical migratory bird, produced by Cornell by Lab of Ornithology (2003).

Cerulean Warbler
Dendroica cerulea

LEGEND
- Year Round
- Summer (breeding)
- Winter (non-breeding)
- Migration

Map by Cornell Lab of Ornithology
Range data by NatureServe
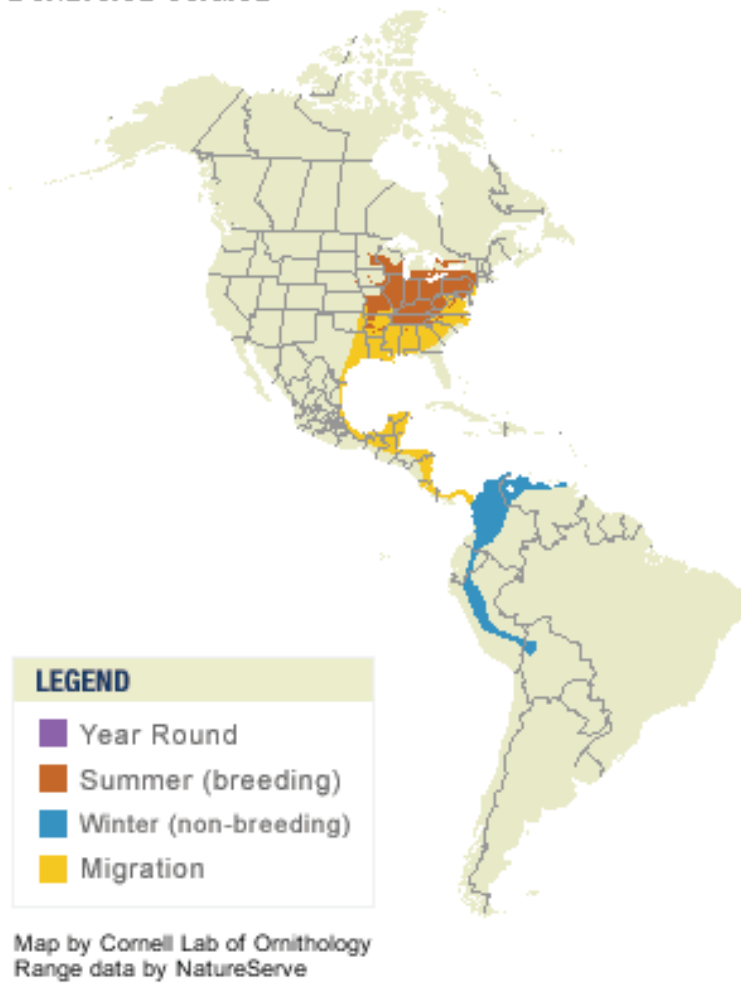
Appendix B. Map of forest cover (shown in green) in the state of Ohio, USA. The red box indicates the southeastern Ohio study region used for breeding ground study sites, 2004-2006.

Appendix C. Map of wintering ground study sites in shade coffee plantations (black dots) and primary forest (red dots) near the town of La Azulita in the Venezuelan Andes, 2005-2007. The two darkest shades of green represent forest with little to no human intervention, light green represents forest of moderate human intervention, and yellow represents forest of heavy human intervention. Agricultural areas are represented by brown (coffee), and pink (pasture or mixed farming). Paramo is represented in white. Vegetation maps were generated and facilitated by the Venezuelan NGO Programa Andes Tropicales-InfoGeo.

Appendix D. Number and proportion of trees with Cerulean Warbler nests measured in nest plots (n = 113) compared to the number and proportion of 'nest' trees in available plots (n = 112) in southeastern Ohio, 2004-2006.

Plant Species	Nest trees	Percent nests	Available trees	Percent available
White oak (*Quercus alba*)	59	52.2	28	25.0
Chestnut oak (*Quercus prinus*)	10	8.8	5	4.5
Yellow poplar (*Liriodendron tulipifera*)	8	7.1	10	8.9
American elm (*Ulmus americana*)	7	6.2	4	3.6
Red maple (*Acer rubrum)*	5	4.4	13	11.6
American sycamore (*Platanus occidentalis*)	5	4.4	3	2.7
Hickory spp. (*Carya* sp.)	4	3.5	11	9.8
White ash (*Fraxinus americana*)	3	2.7	3	2.7
Red oak (*Quercus rubra*)	2	1.8	8	7.1
Shagbark hickory (*Carya ovata*)	2	1.8	4	3.6
River birch (*Betula nigra*)	2	1.8	0	0.0
Ohio buckeye (*Aesculus glabra*)	1	0.9	4	3.6
Black cherry (*Prunus serotina*)	1	0.9	4	3.6
Black walnut (*Juglans nigra*)	1	0.9	2	1.8
Black maple (*Acer nigrum*)	1	0.9	0	0.0
Black locust (*Robinia pseudoacacia*)	1	0.9	0	0.0
Snag (species unknown)	1	0.9	0	0.0
Sugar maple (*Acer saccgarum*)	0	0.0	9	8.0
Hackberry (*Celtis occidentalis*)	0	0.0	1	0.9
Black gum (*Nyssa sylvatica*)	0	0.0	1	0.9
Sourwood (*Oxydendrum arboreum*)	0	0.0	1	0.9
Eastern hemlock (*Tsuga canadensis*)	0	0.0	1	0.9

Appendix E. Nest placement characteristics of Cerulean Warbler nests (n = 113) located in southeast Ohio, 2004-2006.

Variable	Mean	SE	Range
Nest height (m)	19.35	0.52	8 – 36
Nest plant dbh	44.19	1.45	14 – 119
Distance to central axis (m)	4.38	0.22	1 – 15
Distance to nearest foliage edge (m)	0.27	0.05	0 – 5
Canopy height (m)	29.60	0.46	20 – 45
Number of grapevines	3.59	0.51	0 – 23
Slope	7.83	0.64	0 – 20
Aspect	156.42	8.3	-

Appendix F. Number of birds detected by species on line transects in shade coffee plantations and primary forest, 2005-2007 near La Azulita, Venezuela.

Species	No. of individuals detected	
	Shade coffee	Primary forest
Acadian Flycatcher, *Empidonax virescens*	4	9
American Redstart, *Setophaga ruticilla*	105	32
Black-and-white Warbler, *Mniotilta varia*	10	7
Bay-breasted Warbler, *Dendroica castanea*	2	0
Blackburnian Warbler, *Dendroica fusca*	46	15
Black-throated Green Warbler, *Dendroica virens*	1	0
Canada Warbler, *Wilsonia canadensis*	2	3
Cerulean Warbler, *Dendroica cerulea*	66	6
Chestnut-sided Warbler, *Dendroica pensylvanica*	4	0
Golden-winged Warbler, *Vermivora chrysoptera*	0	0
Gray-cheeked Thrush, *Catharus minimus*	1	1
Kentucky Warbler, *Oporornis formosus*	0	1
Magnolia Warbler, *Dendroica magnolia*	0	0
Mourning Warbler, *Oporornis philadelphia*	11	1
Northern Waterthrush, *Seiurus noveboracensis*	11	0
Rose-breasted Grosbeak, *Pheucticus ludovicianus*	1	2
Summer Tanager, *Piranga rubra*	6	3
Swainson's Thrush, *Catharus ustulatus*	1	2
Tennessee Warbler, *Vermivora peregrina*	49	13
Yellow-throated Vireo, *Vireo flavifrons*	4	0
Totals	325	114

Appendix G. Number of Neotropical migrants captured in shade coffee plantations over 2 winter seasons in the Venezuelan Andes, 2005-2007. See Appendix F for scientific names.

Species	Total no. of captures	No. of individuals captured	No. of individuals recaptured within seasons	No. of individuals recaptured between seasons
Acadian Flycatcher	7	5	2	1
American Redstart	46	35	10	5
Black-and-white Warbler	22	15	7	1
Blackburnian Warbler	7	4	2	0
Black-throated Green Warbler	1	1	0	0
Canada Warbler	14	8	5	1
Cerulean Warbler	47	29	11	7
Chestnut-sided Warbler	1	1	0	0
Gray-cheeked Thrush	8	7	1	0
Mourning Warbler	69	46	14	2
Northern Waterthrush	50	26	13	1
Rose-breasted Grosbeak	18	18	0	0
Summer Tanager	14	12	1	1
Swainson's Thrush	9	9	0	0
Tennessee Warbler	60	48	11	1
Totals	373	283	77	20

Appendix H. Age, sex, morphometric measures, and seasons banded and resighted for Cerulean Warblers in shade coffee plantations in the Venezuelan Andes, 2005-2007.

Site	Band	Color bands[a]	Age[b]	Sex[c]	Wing (mm)	Mass (g)	Tarsus (mm)	Season banded[d]	Seasons resighted
C1	2002	R:S	J	F	61.0	8.5	16.0	1	1,2,3
C1	2003	W:S	A	M	66.0	9.0	17.5	1	1,2
P	2005	Y:S	J	M	63.0	9.4	17.0	1	1,2,3
P	2006	V:S	J	F	61.5	8.9	16.6	1	1,2,3
C2	2009	DB:S	A	M	66.5	8.9	17.4	1	1,2,3
C2	2010	S:P	J	F	63.5	8.0	17.0	1	1
P	2012	S:R	J	M	66.0	9.0	16.8	1	1
P	2018	O:S	J	F	59.5	9.0	17.3	1	1,2
C2	2026	S:Y	J	F	61.0	8.9	16.0	1	1
P	2027	W:SDB	J	M	63.0	9.5	15.7	1	1
C1	2028	S:O	J	F	61.5	9.5	16.7	1	1,2
C1	2029	S:G	J	F	60.0	8.9	16.4	1	-
P	2035	S:W	A	F	62.0	9.1	15.7	1	1,2,3
P	2036	RY:S	A	F	62.0	9.6	16.6	1	1,2,3
P	2037	S:LB	A	F	61.5	8.5	15.6	1	1,2,3
C1	2039	LB:S	A	F	63.5	9.2	15.9	1	1,2,3
C2	2041	WO:S	A	F	62.0	9.5	15.7	1	1,2
C2	2051	RLB:S	A	F	60.5	8.9	16.0	1	1,2
C2	2053	VY:S	A	F	63.0	9.7	15.6	1	-
C2	2057	S:OLB	J	M	63.0	8.8	15.6	1	1,2
P	2064	S:P	A	F	62.5	8.4	16.3	2	2,3
P	2069	DBS:Y	A	F	62.0	8.9	16.9	2	2,3

Appendix H (continued).

C2	2062	YS:R	J	M	64.0	8.7	16.2	2	2
C2	2074	LB:OS	A	F	61.5	8.2	16.2	2	2
C2	2078	GS:W	A	M	66.5	9.5	17.7	2	-
P	2082	LB:SR	J	F	62.0	8.6	16.5	2	2
P	2096	S:RO	J	F	61.0	8.9	15.9	2	2,3
C2	2100	S:V	J	F	62.0	8.4	16.5	2	2
P	2113	OS:Y	A	M	67.5	9.7	17.1	2	2,3
P	2116	LBS:LB	J	M	62.0	8.6	16.5	3	3
P	2118	RS:R	J	F	63.0	8.8	16.2	3	3
P	2119	VS:Y	J	F	62.0	8.5	16.1	3	-
P	2120	DBO:S	J	F	63.0	9.5	16.6	3	-
P	2121	VR:S	A	F	68.0	9.0	16.5	3	-

[a] Color band combinations where P=pink, LB=light blue, DB=dark blue, O=orange, Y=yellow, V=violet, W=white, G=green, and S=silver/USGS aluminum band. A combination of VY:S indicates a violet band above a yellow band on the left leg and a USGS aluminum band on the right leg of the bird.

[b] Age where J= juvenile, a bird in its first winter; A=adult, a bird in at least its second winter season

[c] Sex where M=male and F=female.

[d] Season 1=December 2005–February2006, Season 2=December 2006–February 2007, Season 3=December 2008

Appendix I. Measurements of male and female Cerulean Warblers banded in shade coffee plantations in the Venezuelan Andes, 2005-2007. Using multivariate analysis of variance, Cerulean Warbler females (n= 20) are significantly smaller than male (n = 9) Ceruleans (Wilks' Lambda $F_{4,24}$ = 11.20, P < 0.001).

Measurements	Sex		F	P
	Female	Male		
Mean mass (SD), g	8.8 (0.5)	9.1 (0.4)	2.63	0.116
Mean wing chord (SD), cm	61.9 (1.2)	64.9 (1.7)	41.76	< 0.001
Mean tarsus length (SD), cm	16.3 (0.5)	16.9 (0.8)	4.62	0.041
Mean exposed culmen length (SD), cm	9.7 (0.5)	10.0 (0.3)	1.38	0.250

Appendix J.   Mean abundance (SE) of Neotropical migrants (with >3 detections) for
each transect in primary forest and shade coffee plantations, Venezuela 2005-2007.   See
Table 4.1 for species codes.

Appendix J.

Transect	ACFL	AMRE	BAWW	BLBW	CAWA	CERW	MOWA	NOWA	SUTA	TEWA
Primary forest										
1	0.29±0.14	0.50±0.09	0.00±0.00	0.29±0.10	0.07±0.07	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.21±0.25
2	0.00±0.00	0.00±0.00	0.07±0.07	0.07±0.07	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
3	0.00±0.00	0.36±0.14	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
4	0.00±0.00	0.14±0.09	0.29±0.10	0.14±0.09	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.14±0.09
5	0.00±0.00	0.50±0.31	0.07±0.07	0.29±0.10	0.00±0.00	0.14±0.09	0.00±0.00	0.00±0.00	0.14±0.00	0.21±0.25
6	0.00±0.00	0.00±0.07	0.00±0.00	0.21±0.25	0.00±0.00	0.14±0.13	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
7	0.00±0.00	0.14±0.09	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
8	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07
9	0.36±0.14	0.29±0.14	0.07±0.07	0.00±0.00	0.07±0.07	0.14±0.09	0.00±0.00	0.00±0.00	0.00±0.00	0.21±0.10
10	0.00±0.00	0.07±0.07	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Shade coffee										
1	0.00±0.00	1.00±0.12	0.00±0.00	0.07±0.07	0.00±0.00	0.14±0.09	0.14±0.09	0.00±0.00	0.00±0.00	0.00±0.00
2	0.00±0.00	0.29±0.10	0.00±0.00	0.21±0.25	0.00±0.00	0.14±0.09	0.00±0.00	0.00±0.00	0.00±0.00	0.14±0.09
3	0.00±0.00	1.00±0.12	0.00±0.00	0.57±0.18	0.00±0.00	0.71±0.17	0.29±0.10	0.07±0.07	0.00±0.00	0.57±0.13
4	0.00±0.00	0.93±0.13	0.21±0.10	0.43±0.19	0.00±0.00	0.71±0.17	0.00±0.00	0.07±0.07	0.00±0.00	0.79±0.15

Appendix J (continued)

5	0.00±0.00	0.38±0.15	0.21±0.10	0.36±0.10	0.00±0.00	0.71±0.26	0.00±0.00	0.07±0.07	0.14±0.00	0.43±0.15
6	0.07±0.07	0.38±0.10	0.00±0.00	0.71±0.19	0.00±0.00	1.07±0.23	0.00±0.00	0.00±0.00	0.14±0.00	0.93±0.15
7	0.00±0.00	0.50±0.09	0.00±0.00	0.36±0.10	0.00±0.00	0.29±0.10	0.14±0.09	0.07±0.07	0.00±0.00	0.14±0.09
8	0.57±0.07	0.29±0.10	0.00±0.00	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.07±0.07	0.07±0.07
9	0.14±0.09	0.38±0.11	0.00±0.00	0.07±0.07	0.07±0.07	0.50±0.09	0.00±0.00	0.36±0.10	0.00±0.00	0.07±0.07
10	0.00±0.00	1.71±0.26	0.14±0.09	0.29±0.10	0.07±0.07	0.36±0.10	0.07±0.07	0.07±0.07	0.00±0.00	0.00±0.00

Appendix K. Comparison of vegetation structure at primary forest and shade coffee plantations in the Venezuelan Andes, 2006-2007. A multivariate analysis of variance indicated that vegetation structure in primary forest was significantly different from shade coffee plantations (Wilks' Lambda $F_{7,12} = 7.68$, $P = 0.001$).

Variable	Primary Forest		Shade Coffee		F	P
	Mean	SE	Mean	SE		
Canopy Height	20.32	0.26	18.37	0.33	2.15	0.160
Percent Canopy Cover	78.75	0.23	51.75	0.19	32.54	< 0.001
Trees 23-38 cm dbh	3.35	0.14	2.05	0.08	6.84	0.018
Trees >38 cm dbh	1.45	0.10	1.10	0.08	0.73	0.405
Snags > 15 cm dbh	1.55	0.13	0.66	0.05	4.35	0.052
Banana plants	0.60	0.19	13.90	0.64	39.47	< 0.001
Vegetation density	13.15	0.84	15.35	0.64	1.66	0.214

Appendix L. Mean (SE) values of structural characteristics measured in 10 transects in primary forest and shade coffee sites in the Venezuelan Andes.

Transect	Canopy height (m)	Trees 8-23 cm dbh	Trees 23-38 cm dbh	Trees >38 cm dbh	Snags	Canopy cover (%)	Vegetation hits (0-3 m)
Primary Forest							
1	24.2±4.8	14.5±2.5	4.5±3.5	1.5±0.5	1.5±0.5	87.5±0.5	14.5±3.5
2	22.6±2.9	11.5±0.5	3.0±0.0	3.0±1.0	1.0±1.0	85.0±1.0	9.0±1.0
3	21.7±2.8	20.5±6.5	3.5±1.5	2.5±0.5	2.0±2.0	77.5±2.5	7.5±0.5
4	22.3±0.2	20.5±1.5	4.5±1.5	1.5±0.5	3.5±0.5	85.0±0.0	5.5±1.5
5	20.9±0.2	11.0±2.0	5.0±0.0	2.0±0.0	0.5±0.5	72.5±0.5	18.0±1.0
6	16.0±1.0	5.0±5.0	1.5±1.5	0.0±0.0	0.5±0.5	50.0±0.0	32.5±1.5
7	20.8±1.0	38.0±2.0	1.5±0.5	1.0±1.0	4.0±0.0	87.5±0.5	5.0±1.0
8	18.2±1.7	9.5±3.5	5.0±2.0	0.0±0.0	1.5±0.5	77.5±0.5	16.5±1.5
9	19.0±0.5	10.5±3.5	2.5±0.5	2.0±1.0	0.5±0.5	77.5±1.5	16.5±2.5
10	17.6±0.4	36.5±5.5	2.5±0.5	1.0±1.0	0.5±0.5	87.5±0.5	6.5±2.5

Appendix L (continued).

Shade Coffee

1	17.5±5.5	6.0±1.0	4.0±1.0	0.0±0.0	1.0±0.0	62.5±0.5	23.5±2.5
2	15.2±0.6	6.0±0.0	2.0±0.0	1.5±0.5	1.0±0.0	50.0±2.0	18.5±4.5
3	22.2±2.6	5.0±1.0	2.0±2.0	2.0±1.0	1.0±0.0	62.5±0.5	20.5±13
4	16.5±0.4	9.0±0.0	2.0±1.0	2.5±1.5	0.5±0.5	47.5±0.5	20.0±5.0
5	23.8±2.0	6.5±0.5	1.0±0.0	1.5±0.5	1.0±0.0	47.5±0.5	19.0±2.0
6	18.1±2.1	8.0±1.0	2.5±0.5	1.0±0.0	0.0±0.0	47.5±0.5	25.0±8.0
7	17.3±0.7	5.5±1.5	1.5±0.5	1.5±0.5	1.0±1.0	37.5±1.5	10.5±11
8	12.6±0.1	12.0±2.0	1.5±0.5	0.5±0.5	0.0±0.0	65.0±0.0	8.5±2.5
9	20.1±4.3	10.5±0.5	2.0±1.0	0.0±0.0	1.0±0.0	57.5±2.5	19.0±9.0
10	20.5±0.5	12.0±0.0	2.0±0.0	0.5±0.5	0.0±0.0	40.0±0.0	9.0±2.0

Appendix M. Mean (SE) number of plants by genus measured in two 0.04 ha plots at 10 transects in shade coffee, Venezuela.

Transect	Inga	Cedrela	Acnistus	Heliocarpus	Persea	Erythrina	Ceiba	Ficus	Coffea
1	6.5±0.5	0.5±0.5	2.0±2.0	0.0±0.0	0.5±0.5	0.0±0.0	0.0±0.0	0.0±0.0	101.0±15.0
2	3.0±1.0	0.0±0.0	1.5±0.5	0.0±0.0	1.0±0.0	2.0±0.0	0.0±0.0	0.0±0.0	58.5±31.5
3	5.0±3.0	1.0±1.0	0.0±0.0	0.0±0.0	0.5±0.5	0.5±0.5	0.0±0.0	0.0±0.0	91.5±34.5
4	2.5±1.5	1.5±0.5	1.0±1.0	0.0±0.0	0.5±1.0	1.0±1.0	0.0±0.0	0.0±0.0	116.0±20.0
5	0.5±0.5	2.0±0.0	1.5±0.5	0.5±0.5	0.0±0.0	3.0±1.0	0.0±0.0	0.5±0.5	102.5±13.5
6	7.0±2.0	1.5±0.5	1.5±1.5	0.0±0.0	0.0±0.0	0.5±0.5	0.0±0.0	1.0±1.0	123.0±12.0
7	3.5±1.5	0.0±0.0	1.5±0.5	0.0±0.0	0.5±0.5	2.5±0.5	0.0±0.0	0.0±0.0	41.0±33.0
8	11.5±3.5	0.0±0.0	0.5±0.5	0.0±0.0	0.5±0.5	0.0±0.0	0.5±0.5	0.0±0.0	61.5±11.5
9	3.0±2.0	1.0±0.0	5.0±3.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	94.0±27.0
10	0.5±0.5	4.0±1.0	2.5±0.5	2.5±2.5	2.5±2.5	0.0±0.0	0.0±0.0	0.0±0.0	109.5±5.5

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