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# Golden-winged warbler (*Vermivora chrysoptera*) demographics and habitat use and the potential effects of land use change on golden-winged and cerulean warblers (*Dendroica cerulea*) in the Cumberland Mountains of Tennessee

Lesley Penfield Bulluck
*University of Tennessee - Knoxville*

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To the Graduate Council:

I am submitting herewith a dissertation written by Lesley Penfield Bulluck entitled "Golden-winged warbler (*Vermivora chrysoptera*) demographics and habitat use and the potential effects of land use change on golden-winged and cerulean warblers (*Dendroica cerulea*) in the Cumberland Mountains of Tennessee." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

David A. Buehler, Major Professor

We have read this dissertation and recommend its acceptance:

Joseph Clark, Lou Gross, Roger Tankersley

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

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

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Carolyn R. Hodges

Vice Provost and Dean of the
Graduate School

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# GOLDEN-WINGED WARBLER (*Vermivora chrysoptera*) DEMOGRAPHICS AND HABITAT USE AND THE POTENTIAL EFFECTS OF LAND USE CHANGE ON GOLDEN-WINGED AND CERULEAN WARBLERS (*Dendroica cerulea*) IN THE CUMBERLAND MOUNTAINS OF TENNESSEE

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

Lesley Penfield Bulluck
May 2007

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## Abstract

The golden-winged warbler (*Vermivora chrysoptera*) is an early successional Nearctic-Neotropical migrant songbird undergoing population declines range-wide. The Cumberland Mountains contain one of the southernmost populations where golden-wingeds occur in relatively high densities on old reclaimed surface mines. The three objectives of this research were to (1) describe the basic demography and habitat use of this population, (2) compare the demography of the Cumberland population to a population in Ontario, and (3) to model alternative land use scenarios and the impacts on both the golden-winged warbler and the cerulean warbler (*Dendroica cerulean*), another declining Nearctic-Neotropical migrant that occupies mature forests. Specifically, I modeled daily nest survival rate as a function of biologically meaningful covariates (Part 2) and the relative effects of habitat and demographic factors on territory size variation (Part 3) for the Tennessee population. There was some evidence of annual variation in nest survival rates and a decline throughout the nesting season, but I found little evidence that local habitat characteristics measurably affected nest survival. Territory size varied with the percent cover of vines and the number of snags. The single demographic factor related to territory size was nest success; birds with larger territories had a greater rate of nest success. I compared annual adult survival, fecundity, rate of population growth ($\lambda$), and mean time to extinction for Tennessee and Ontario populations (Part 4). Adult survival and fecundity were similar for the two populations such that predictions based on the theory of life history variation with latitude were not supported. Lambda estimates suggested that both populations were declining and I projected extirpation within 20-30 years without immigration. To further explore avian populations in the Cumberlands, I modeled coal mining, reclamation, and timber harvesting under a base-case scenario (as described by landowners and industries) as well as for alternatives that limited the amount of disturbance (Part 5). None of the scenarios were sustainable alternatives for cerulean and golden-winged warbler populations. My results suggest that future disturbances should be significantly limited to meet cerulean population goals and existing early successional habitat should be maintained and enhanced to sustain golden-winged warbler populations.

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# Part 1

# PART 1: INTRODUCTION

The amount of early successional habitat in the eastern United States has significantly declined during the last half-century. Extensive land clearing for agriculture and grazing occurred with the arrival of Europeans in the 18th and 19th centuries, followed by an increase of early successional habitat after farmland abandonment and general succession (Litvaitis 2003). Since then, the suppression of natural disturbance (fire), the succession of forests following reduced logging, and land use change associated with a rapidly growing human population (Askins 2001, Lorimer 2001, Trani et al. 2001, Lorimer and White 2003) have resulted in a dominance of even-aged forests in the eastern US (Litvaitis 2003). Because these forests lack the diversity of vegetation structure and seral stages present in mature forests where natural disturbance is a dynamic force, the diversity of habitats for many wildlife species have also declined in abundance (Litvaitis 2003). Indeed, 56% of grassland bird species and 39% of shrubland bird species have experienced significant population declines between 1966 and 1998 (Brawn et al. 2001, *sensu* Sauer et al. 2000). The severity of these declines has heightened interest in management of early successional habitats.

The golden-winged warbler (*Vermivora chrysoptera*) is a disturbance-dependent Nearctic-Neotropical migratory songbird that has experienced significant range-wide population declines (Sauer et al. 2005) that correspond with the decline in early successional habitat. The golden-winged breeding range (Figure 1.1, all tables and figures appear in appendices to each part) covers the northeastern and upper midwestern United States and Ontario, Canada and extends down the southern Appalachian Mountains into portions of West Virginia, southwestern Virginia, eastern Kentucky, western North Carolina, eastern Tennessee and northern Georgia (Confer 1992). In addition to the loss of early successional habitat, hybridization with blue-winged warblers (*Vermivora pinus*) and nest parasitism by brown-headed cowbirds (*Moluthrus ater*) also pose threats to the golden-winged on the breeding grounds (Confer 1992). Habitat loss occurring on the tropical wintering grounds of Central and South America more than likely contribute to this species' decline, but the magnitude of this threat relative to that on the breeding grounds is unknown (Confer 1992, Buehler et al., in press).

The extent and cause of population declines differ across this species' breeding range (Buehler et al., in Press). Hybridization with the blue-winged warbler is occurring throughout their overlapping breeding range, but most rapidly and persistently in the northeastern and upper midwestern United States. Similarly, parasitism by brown-headed cowbirds is greatest in these regions where grazing and human land uses benefit this nest parasite. In the southern portion of the range, overlap with blue-wingeds is restricted to lower elevations (< ~450 m) and brown-headed cowbird parasitism is occurring at low levels (Klaus and Buehler 2001, Welton 2003, and this study). Therefore, high-elevation sites in the southern Appalachians appear to provide refugia for more genetically pure (i.e., less introgressed) populations of golden-wingeds. These high elevation populations are geographically disjunct from the northern golden-winged populations in New York, Ontario and the upper Midwest, and the amount of dispersal (and therefore gene flow) between these two major portions of their range is unknown. A complete extirpation of these southern populations could occur if the blue-winged warbler expands its range into these high-elevation sites and/or habitat loss takes place via forest succession or land use change. The consequences of loss of these southern populations in terms of rangewide population viability and evolutionary adaptability are unknown.

A relatively large number of golden-winged warblers are present in the Cumberland Mountains of northeastern Tennessee (Figure 1.2) compared to the rest of the southern Appalachian region. Similar to other areas in the southern Appalachians, golden-wingeds exhibit a near complete separation from blue-wingeds by elevation in the Cumberland Mountains, with blue-wingeds most often occupying sites < 450 m in elevation (Welton 2003 and personal observation). Golden-wingeds in Kentucky are contiguous with the Tennessee Cumberlands population and also inhabit reclaimed surface mines, but at lower elevations where pines dominate and there are greater densities of blue-wingeds (Patton 2007). Because these species are currently separated by elevation and because hybridization may threaten the long-term persistence of golden-wingeds at a given site (Gill 1980), it is appropriate to focus research and management efforts on golden-wingeds at high elevations in the Tennessee Cumberlands. An additional reason this population warrants active management is the isolation of these birds from other southern Appalachian populations. The next closest populations are in northern Georgia and along the Tennessee/North Carolina state line where they inhabit abandoned farmland, grazed pastures, beaver wetlands, and recent clearcuts in the Cherokee and Nantahala National Forests (Klaus and Buehler 2001). The birds in northern Georgia are few (<20 pairs) and their numbers fluctuate as forests are harvested for timber, burned, and allowed to succeed (Klaus 2004).

The Cumberland Mountains provide a unique management opportunity for golden-winged warblers for two reasons: (1) much of the landscape is publicly owned by the Tennessee Wildlife Resources Agency (TWRA) who is willing to manage for successional species; and (2) the intact nature of forest cover on the landscape. More than 50,000 ha of state-owned Wildlife Management Area (WMA) lands exist in this region, with approximately 15% in early stages of succession from the extensive surface mining of coal. TWRA is willing to actively manage these lands for golden-winged warblers and other species with early successional habitat requirements such as white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), wild turkey (*Meleagris gallopavo*) and ruffed grouse (*Bonasa umbellus*).

The early successional habitats in the Cumberlands are patchily distributed throughout >80,940 ha of contiguous forests. The proportion of early successional and mature forest in this region may be similar to the effects of historical natural disturbance at the landscape level. Litvaitis (2003) suggested that land use change and forest fragmentation preclude the use of pre-Columbian conditions as a relevant baseline for the amount and distribution of early successional habitat. However, relatively intact landscapes, such as the Cumberland Mountains, may be managed successfully by attempting to mimic natural disturbance regimes (Litvaitis 2003). Moreover, the distribution of disturbed area within a predominantly forested matrix allows for management of disturbance-dependent species without negatively impacting mature forest-interior species. This is fortunate considering that the cerulean warbler (*Dendroica cerulea*), a mature forest-interior species exhibiting a rapidly-declining population range-wide, occurs in relatively high densities in this same area. Given the juxtaposition of the golden-winged and cerulean warblers, in addition to the occurrence of numerous other declining forest songbirds (Ford 2000), the Cumberland Mountains region has been identified as an important area in several conservation and planning initiatives. Specifically, this ecoregion has been designated as an important bird area (IBA) by the American Bird Conservancy (www.abcbirds.org), as a portfolio site by The Nature Conservancy (www.nature.org/), and as having a high biodiversity index by the Tennessee GAP project (http://www.state.tn.us/twra/thcp/Appendix_1.pdf).

The historical distributions of the golden-winged and cerulean warblers are unknown in the Cumberland Mountains region. Although early successional habitats were likely distributed throughout the landscape as patchy wetlands and following natural and anthropogenic fires, the landscape was probably extensively forested (Küchler 1964). The contemporary core of the golden-winged warbler breeding range is in the upper midwestern U.S. (Figure 1.1). The southern populations occupying high-elevation sites following anthropogenic disturbance are considered by some as relict populations less worthy of conservation (L. Bulluck, personal observation). Alternatively, the core of the cerulean warbler range is in the southern Appalachian region, specifically in West Virginia, Ohio, Kentucky, and Tennessee (Figure 1.3), making it a priority for conservation. Because the core of the cerulean range lies in this region, there are an estimated 40,000+ breeding pairs here (Buehler et al. 2006). This relatively large population of ceruleans has led to the urgency of cerulean conservation in the region th be the center of some debate. Simultaneous management of species with conflicting habitat requirements within the same landscape is complicated and has involved disagreement over species prioritizations.

Management by TWRA, coal mining, and timber harvesting contribute to the creation and maintenance of early successional habitat in this region. However, in the last decade there has been an increase in timber harvesting and coal mining in the region. Timber and mineral rights are not always owned by the state agencies who own the surface lands, and even state-owned WMAs are undergoing drastic land use change. Furthermore, recent mine-reclamation procedures involve the planting of non-native, invasive species such as cool season grasses (*Festuca* spp.) and *Lespedeza* spp. that help to prevent soil erosion and restore nitrogen to the mining-depleted soils. Immediate soil stabilization is mandatory under the Surface Mining Control and Reclamation Act (SMCRA) of 1977. This legislation has resulted in some positive steps toward restoring habitats affected by surface mining, particularly for aquatic systems because soil is better stabilized following reclamation (Olyphant and Harper 1995). SMCRA mandates for restoring terrestrial systems, however, have been less successful in terms of habitat quality for wildlife. The planting of non-native, invasive groundcovers is not beneficial to shrubland birds because the groundcovers greatly delay establishment of native shrubs and forbs; mines reclaimed in this manner 10 years ago still do not have the shrub/sapling components that make them suitable breeding habitat for golden-wingeds. Conversely, sites that were mined 30 or more years ago (pre- SMCRA) were often not reclaimed at all and have slowly become colonized by black locust (*Robinia pseudoacacia*), yellow poplar (*Liriodendron tulipifera*) and maple (*Acer* spp.) that shade out much of the herbaceous cover. Therefore, despite an abundance of early successional habitat in the Cumberland region, much of it is not suitable for golden-winged warblers.

The Cumberland Mountain golden-winged warbler population has only just recently been extensively surveyed (Welton 2003) despite its conservation importance. There has been little research to date on golden-winged warbler demographics in any population throughout the breeding range. As a result, we cannot be sure if golden-winged warbler populations are limited by different factors in different portions of their range. For example, the more northerly breeding populations may be limited by adult survival whereas the southern populations may be limited by nest survival. Regional conservation measures should reflect these differences. Until we know whether regional differences in demography exist, our current conservation efforts may be of limited effectiveness.

This dissertation research was initiated to address the overall lack of demographic data for golden-winged warblers, and to address the potential impacts of land-use change associated with increasing mining and timber harvesting in the Cumberlands. The four objectives of my study were to (1) describe the demographics and habitat relationships of the Cumberland Mountain golden-winged warbler population (Part 2), (2) assess the effects of habitat and demographic factors on golden-winged warbler territory size (Part

3), (3) compare the demographics of the Cumberland population to a population in Ontario (Part 4), and (4) evaluate alternative land use scenarios and the impacts on both golden-winged and cerulean warblers (Part 5). I present the conservation implications of this research in Part 6. With the exception of Parts 1 and 6, individual parts are written as stand-alone manuscripts for future publication.

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# Appendix

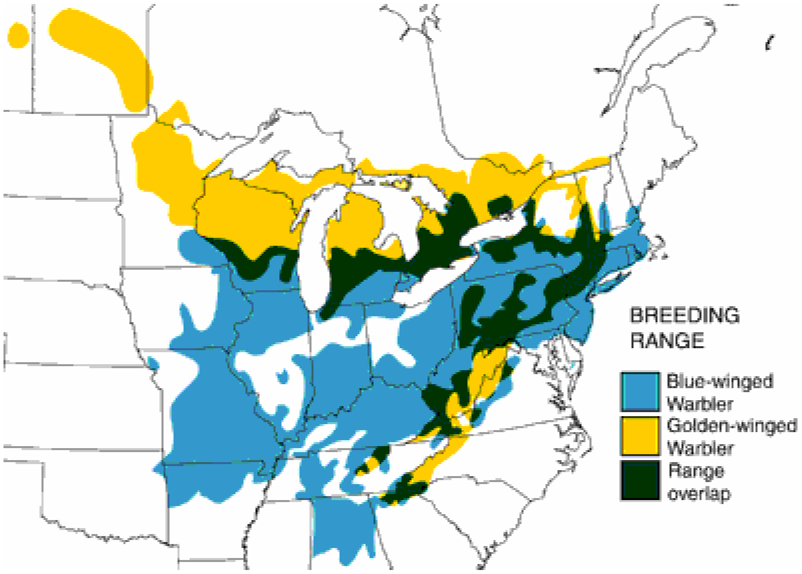

**Figure 1.1:** Map of golden-winged (*Vermivora chrysoptera*) and blue-winged warbler (*V. pinus*) occurrences and areas where their ranges overlap produced by the Cornell Lab of Ornithology for the Golden-winged Warbler Atlas Project (GOWAP, unpublished data).

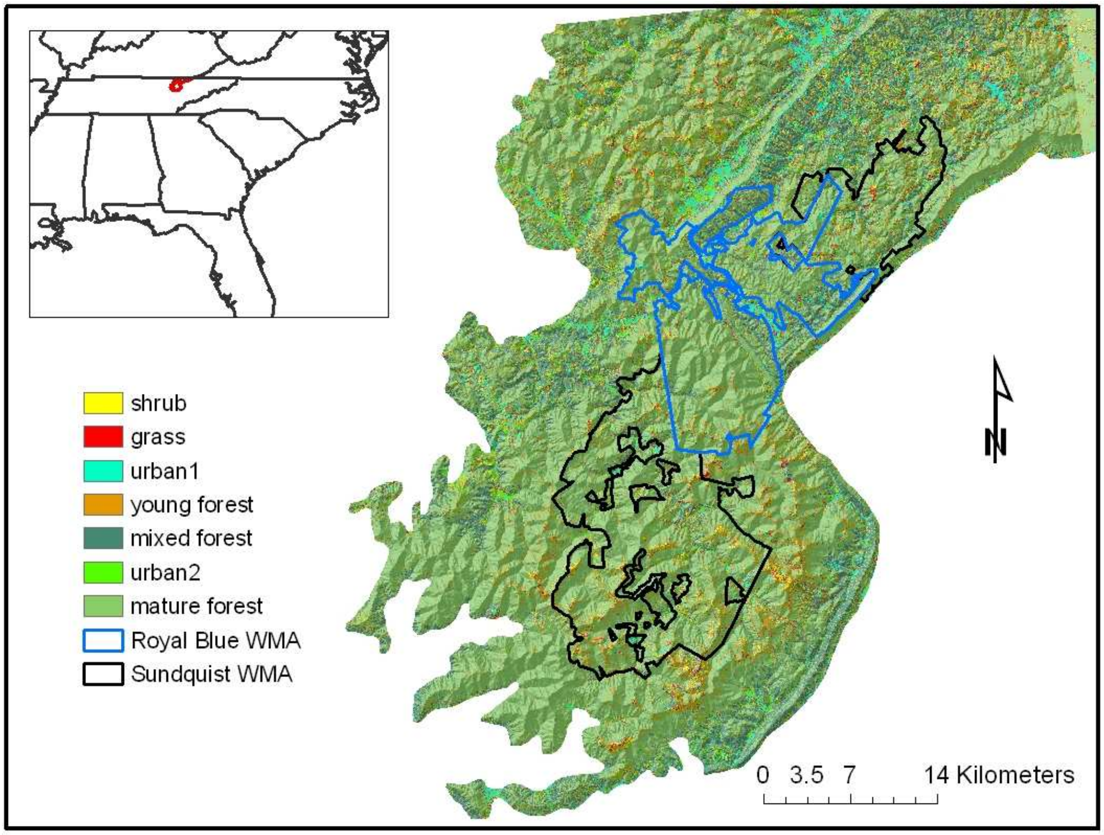

**Figure 1.2:** The Cumberland Mountains ecoregion in northeastern Tennessee and the location of two Wildlife Management Areas (WMA). The landcover map is from a classified Landsat TM satellite image, September 2000.

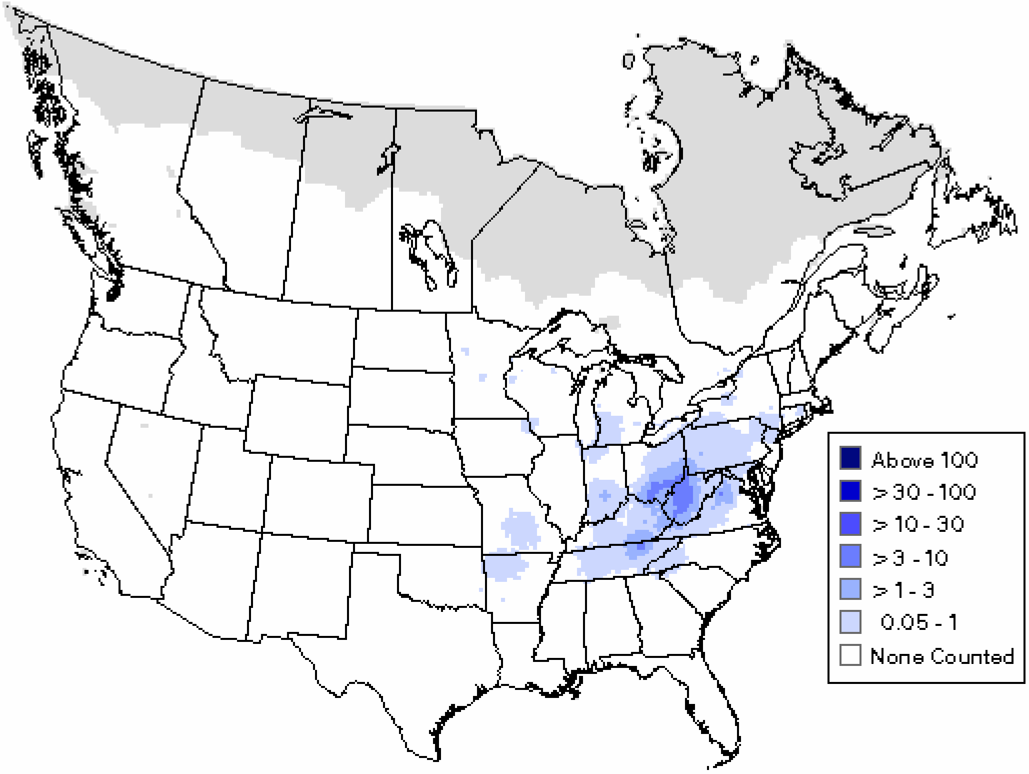

**Figure 1.3:** Breeding distribution of the cerulean warbler (*Dendroica cerulea*) based on Breeding Bird Survey (BBS) data (Sauer et al. 2005).

# Part 2

# PART 2: FACTORS INFLUENCING GOLDEN-WINGED WARBLER (*Vermivora chrysoptera*) NEST-SITE SELECTION AND NEST SURIVIVAL

The following manuscript was written for submission to the
journal *Auk.* “We” throughout the manuscript refers to:
Bulluck, L. P. and D. A. Buehler

## Abstract

Studies of reproduction and habitat use are essential parts of any species assessment, especially for declining populations. We compared habitat attributes associated with nest sites to sites randomly sampled within golden-winged warbler (*Vermivora chrysoptera*) territories. We also modeled the effects of temporal and biotic factors on daily nest survival using Program MARK. In addition, we used Monte Carlo simulation to evaluate the performance of any model(s) that performed better than the null model (constant survival). Of the nine vegetation variables assessed, four differed significantly between nest-sites and randomly selected non-nest sites within golden-winged territories -- the percent cover of saplings at the nest plot level was greater in non-nest sites, the percent cover of forbs and grass within a 1-m sub-plot were greater at nest sites, and the percent cover of woody vegetation within a 1-m sub-plot was greater at non-nest sites. There was some support ($\Delta$AIC < 2) for models with annual variation in nest survival rates and a decline in nest survival throughout the nesting season, but the constant survival model performed equally well. One vegetation parameter (the presence of a woody stem in the nest substrate) performed better than the constant survival model; nests with a woody stem in the substrate had a lower nest survival rate than nests without a woody stem. The mean AIC weights based on 100 simulated datasets did not differ for the constant survival model and the model with the woody stem variable. The constant survival model was selected as the better model in 57% of the simulated datasets, indicating that the woody stem habitat effect did not appear to have a strong effect on nest survival. We conclude that nest-site selection was non-random such that golden-winged warbler females use specific criteria to select a nest site within a territory.

However, micro-scale habitat characteristics did not appear to affect daily nest survival, and therefore predation rates. Conservation strategies that attempt to increase the amount of breeding habitat with specific nest site features may be more successful than attempts to directly control nest survival until factors that affect predation rates are better known for this population.

## Introduction

Studies of reproduction and habitat use are particularly important for species experiencing significant population declines. However, because it is difficult to collect these data, management recommendations for declining species are often solely based on species occurrences or population densities (Van Horne 1983, Scott et al. 2002.). Assessing habitat use versus availability is more informative than comparing used with unused habitat (Johnson 1980, Jones 2001) because in addition to the expected avoidance of some environmental factors, biological factors such as competition, predation, and density can lead to non-use (Rotenberry and Wiens 1980, Haila et al. 1996). When productivity data are available for avian species, only apparent nest success estimates or Mayfield nest survival estimates (Mayfield 1961) are typically provided, which assume constant survival over time. Only recently have analysis methods become available that allow daily nest survival to vary with time and as a function of biologically meaningful covariates (Dinsmore et al. 2002, Shaffer 2004). As a result, researchers can gain a deeper understanding of the factors that influence daily nest survival rates to answer questions about variation within a region or across habitats and to make more informed management decisions.

The golden-winged warbler (*Vermivora chrysoptera*, hereafter, ‘golden-winged’) is a Nearctic-Neotropical migratory songbird that requires early successional breeding habitat. Golden-wingeds nest on the ground in areas with sparse trees and shrubs and an herbaceous understory of grasses and forbs found in either upland or wetland settings (Confer 1992). Golden-winged populations are declining throughout their range as early-successional habitats revert to mature forest and as upland and wetland habitats are lost to human development (Confer 1992, Buehler et al. In Press). These population declines are leading to extirpation of the species from areas that have supported golden-winged warblers for the last several centuries (i.e., Georgia, South Carolina, Virginia, Massachusetts, Connecticut, Rhode Island, Vermont, New Hampshire, Indiana, Illinois, and Ohio) (Buehler et al., In Press). The range expansion of the blue-winged warbler (*Vermivora pinus*) and resulting hybridization may also be contributing to golden-winged population declines. This phenomenon is occurring range-wide, but currently is a major problem in the northeastern U.S. Based on Breeding Bird Survey (BBS) data, populations have declined an average of 2.5% per year survey-wide ($P < 0.001$; $n = 274$ routes) and 3.4% per year in the U.S. ($P < 0.001$; $n = 242$ routes) over the last 40 years of monitoring (1966-2005; Sauer et al. 2005). Populations in the southeastern U.S. are so low that estimating recent population trends is problematic (-6.7%/year, $P = 0.74$, with only 11 routes remaining with golden-winged warblers). Consequently, the golden-winged is considered a high priority species for conservation by Partners in Flight (PIF) and the U.S. Fish and Wildlife Service.

Published data on golden-winged warbler breeding biology are rare. Confer et al. (2003) demonstrated that herb and shrub cover were positively correlated with golden-winged warbler clutch size, increased tree cover was positively correlated with number of fledglings, and herbaceous cover was correlated with more brown-headed cowbird (*Moluthrus ater*) eggs. Klaus and Buehler (2001) illustrated that nest sites had fewer saplings and less canopy cover than randomly-selected sites within a territory. Although this information is useful, no studies have used rigorous statistical methods to assess whether daily nest survival rates of golden-winged warbler vary with time or other biologically meaningful covariates.

The Cumberland Mountains population of golden-winged warblers deserves conservation attention for several reasons. Most published studies of nesting success and habitat use were conducted in New York where habitats greatly differ from the Cumberland Mountains. Most golden-wingeds in the Cumberlands occupy coal surface mines that were reclaimed 15-30 years ago. With the resurgence of mining in the region (see Part 5), there is interest in reclamation strategies that provide quality early successional habitats for priority species such as the golden-winged warbler. Furthermore, little hybridization is occurring because of elevational separation of golden-winged and blue-winged warblers, such that loss of habitat and/or nest predation may be limiting factors in this region. Finally, the potential for management is great for this population considering the large amount of state-owned land and the intact nature of the forests. The current proportion of early and late successional habitats in the Cumberlands may mimic natural disturbance at the landscape scale while still maintaining large core areas of mature forests. Indeed, the Cumberland Mountains region is >70% forested. Such a distribution of successional habitat may provide highly productive nesting sites compared with disturbed areas in a more developed landscape that may experience more nest predation and parasitism.

The objectives of our research were to (1) compare habitat attributes associated with nest sites to attributes in sites sampled randomly within golden-winged territories, and (2) determine if there is a relationship between daily nest survival and year-, time-, nest age-, climate-, and habitat-specific covariates. An additional objective was to (3) use Monte Carlo simulation to evaluate the performance of the model(s) that rank higher than the null/constant survival model. Increased understanding of factors influencing golden-winged warbler nest-site selection and nest survival are imperative if breeding season management efforts are to be successful.

## Methods

### *Study area*

The Cumberland Mountains in northeastern Tennessee compose the southwestern portion of the Appalachian Mountains. The mean elevation is 580 m with the highest ridges reaching 1,075 m. More than 50,500 ha of this landscape is publicly owned by the Tennessee Wildlife Resources Agency (TWRA); our study sites are located within the Sundquist Forest Wildlife Management Area (Figure 1.2). The predominant landcover of the region is mixed-mesophytic forest; approximately 15% is in early succession because of the surface mining of coal and timber harvests (see Part 5). The Cumberland Mountains region is located near the southern extreme of the golden-winged warbler range. In this region, golden-winged warblers primarily occupy reclaimed coal surface mines, and they ephemerally occupy sites associated with timber harvests (5-15 years post-harvest) at lower densities (Welton 2003).

We conducted this study on four reclaimed coal surface mines; two were reclaimed in ~1990 and the other two were reclaimed in ~1980 (Table 2.1). Mine reclamation on these sites typically involved planting black locust (*Robinia pseudoacacia*) saplings and a thick herbaceous layer of grasses and forbs to prevent soil erosion. Since reclamation, maples (*Acer* spp.), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), and thickets of blackberry (*Rubus* spp.) have become established. Periodic arson fires have maintained the thick herbaceous cover and created numerous snags in all sites. All study sites were at approximately the same elevation (mean = 850 m, range = 770-950 m). We selected these sites based on the relatively high concentration of breeding golden-winged pairs per site to efficiently focus our daily nest searching and monitoring efforts. We estimated the Cumberland Mountains golden-winged warbler population to be about 369 (± 122) breeding pairs (Bulluck and Buehler, unpublished data). The four sites in this study support about 85 breeding pairs, or 17-34% of the region's population.

### *Field methods*

From 20 April to 30 June 2004-2006, we visited each site every two-three days from sunrise (~0600 h) to mid-afternoon (~1400 h). We spent the early morning hours (until 1000 h) observing behavior, mapping territories (2005 and 2006 only), and locating nests. To map territories, we followed individual males during one 30-min visitation period per day and marked his location every three minutes for a total of ten potential locations per day (see Part 3 for details). We mapped each male's territory over five visits from 1 May to 15 June and at least once early and late in the morning to ensure we accounted for variation in behavior throughout the morning. Our goal was to collect 40 to 50 locations for each male across the breeding season. We marked points using flagging tape and a Trimble GeoExplorer XM GPS unit. We collected vegetation data in an 11.3-m radius plot (0.04 ha) around each nest as well as at three randomly-selected locations within the territory. Three non-nest vegetation plots per mapped territory were randomly selected using a random point generator extension (Jenness 2005) in ArcView 3.2 (ESRI 1999) with all points located ≥25 m from each other and the nest.

In each vegetation plot we recorded the number of snags (i.e., a dead tree with >5 cm diameter at breast height [DBH]) and estimated average shrub and sapling height (m). We used an ocular tube (James and Shugart 1970) to determine the percent cover of vines, forbs, grass, shrubs, saplings both above and below 1 m in height, and canopy trees

(trees were defined at those >10 cm DBH). Ocular tube readings were taken at 20 points within the 11.3-m plot along four transects in the cardinal directions (5 readings per transect). Observers recorded the presence of each cover type when looking though the ocular tube downward from the line of sight 45 degrees and straight up at each point. Ocular tube readings provided an objective measure of percent cover within plots (# readings with cover type/20*100). Within 1 m of the plot center (which was a nest for nest sites), we also visually estimated the percent cover of grass, forbs and woody vegetation.

To locate golden-winged warbler nests, we observed male and female behavior, especially during nest building and nestling periods when bird visits to the nests were frequent. We opportunistically located nests during the laying and incubation periods while systematically walking through territories and while mapping male territory boundaries. We found the majority (~70%) of nests during the nest-building stage.

We monitored all nests every 2-4 d until the nestlings fledged or the nest failed. The golden-winged nestling cycle typically spans 25 days. The egg laying stage is four days; the average clutch size is five and incubation begins when the final egg is laid. Incubation is typically 10-11 days and the nestling stage is typically 9-10 days (Ehrlich et al. 1988, Confer 1992). If the exact age of a nest was known and the female's presence on the nest could be determined from a distance, we did not flush the female during incubation or brooding nest visits to minimize observer impacts on nest survival. Furthermore, we took care to minimize disturbance to nest-site vegetation to limit observer impacts on nest survival.

### ***Data analyses***

#### Nest-site selection

We compared vegetation characteristics at nests and randomly-selected non-nest sites within golden-winged territories using Student's t-tests in JMP statistical software (version 6.0). Several variables did not meet the assumption of normality, but our sample sizes for each group (nests = 104 and non-nests = 188) were large such that non-normality was considered not to be an issue according to the Central Limit Theorem

(Samuels and Witmer 1999). We compared nine vegetation characteristics and used a Bonferroni adjustment (Samuels and Witmer 1999) to determine significant differences (adjusted $\alpha = 0.006$). Specifically, we compared the number of snags, basal area, and percent cover of saplings, shrubs, forbs and grass within an 11.3-m sampling plot at nest and non-nest sites. Within a 1-m sampling plot, we also compared the percent cover of woody vegetation, forb, and grass cover between nest and non-nest sites.

### Nest survival

We modeled the relationship between daily nest survival rate (DSR) and several variables based on a priori hypotheses and we used a hierarchical modeling procedure with four suites of models (Table 2.2) and $AIC_c$ as the model selection criteria (Burnham and Anderson 2002). We decided a priori to carry over any model that had a $\Delta AIC_c$ value < 2 to be included in the next suite of models (Hood and Dinsmore, In Press). The first set of models considered the influence of two grouping parameters (site and year) on DSR. Annual variation in nest survival was expected because of changes in regional weather patterns and/or annual fluctuations in predator abundance. Likewise, inter-site variation in nest survival was expected if there were differences in vegetation, microclimate and/or predator communities among sites.

The second set of models assessed the influence of two climate covariates (minimum daily temperature and mean daily precipitation), nest stage (laying, incubation, brooding), and whether DSR varied linearly or quadratically with time and nest age (Table 2.2). We hypothesized that low temperatures and/or precipitation could impact daily nest survival rate by forcing the female to incubate or brood less often, as has been demonstrated in previous studies (Siikamaki 1996, Radford et al. 2001, but see Chase 2005). We obtained temperature and precipitation data from the National Oceanic and Atmospheric Association (NOAA) Climatic Data Center (station # 723246 KOQT Oak Ridge). This station was the closest one to our study sites and was located ~25 km south of the study sites and ~550 m lower in elevation. Because of the difference in elevation, there were likely differences in the minimum temperature and precipitation on the study sites compared to the Oak Ridge data, but the data were likely correlated with the actual study site values.

Several studies have demonstrated that nest survival decreases over time and within a season (Ainsley and Schlatter 1972, Grant et al. 2005), and some studies have even documented that DSR varies with time such that a quadratic or cubic function fits the relationship best (Grant et al. 2005). We hypothesized that golden-winged DSR may decrease linearly or show a quadratic relationship with time because of increased activity of ground-nest predators as the breeding season progresses. We also tested for a relationship between DSR and nesting stage and nest age. These parameters are related, but different enough that we decided to test for each effect independently. For example, nest predation is hypothesized to be greatest in the brooding stage when activity is greatest near the nest because of increased parental feeding activity. We might then expect there to be clear differences in DSR among different nest stages. The nest stage model assumes that DSR is constant within a stage. However, we might expect survival to vary within the brooding stage because activity near the nest may be greatest near the end of this stage. For example, the female typically broods the newly-hatched nestlings such that there is very little additional activity compared with the incubation stage until the end of the nestling stage when both male and female adults continuously bring food to the rapidly-growing nestlings. DSR may then be relatively unchanged throughout the nesting cycle and then decrease towards the end of the brooding stage. In this scenario, a model of nest age may be more appropriate than nest stage that assumes constant survival within a stage.

We used the third and fourth sets of models to assess how DSR varied as a function of the vegetation around the nest at the 11.3-m plot level and within 1 m of the actual nest, respectively. Because golden-winged warblers occupy a broad range of successional seres, from very open with scattered woody vegetation to mature woodlands with an herbaceous understory, it is not known if there is a reproductive advantage to any portion of this continuum (i.e., if DSR varies with the cover of herbaceous and woody vegetation). Therefore, these vegetation-specific models of DSR are somewhat exploratory because our a priori models do not test specific hypotheses (i.e., increased shrub cover may increase or decrease DSR). At the plot level, we considered the following three parameters: distance to forest edge, the percent cover of herbaceous vegetation (additive model with forb and grass cover), and the percent cover of woody vegetation (additive model with sapling and shrub cover) (Table 2.2). Nest predators may occur in greater densities near forest edges (Wilcove 1985, Chalfoun et al. 2002, Bloun-Demers and Weatherhead 2001, Carfagno and Heske 2006); yet, forest edges are often a primary component in golden-winged warbler territories. At the nest-site level (1-m sub-plot), we considered the following parameters: nest height, the presence of a woody stem in the nest substrate, and the percent cover of woody vegetation, grass and forbs. Although golden-wingeds nest on the ground, there is some variation in the height of the nest rim related to the size of the nest and the type of substrate in which the nest is built. We hypothesized that nests that extend further off the ground may be more visible to predators than nests with all materials closer to the ground and therefore have lower nest survival rates. Many nests are built solely in herbaceous vegetation (grass and forbs) whereas others are at the base of a woody stem such as a blackberry or small sapling. We hypothesized that nests with a woody stem in the substrate may be more noticeable to predators than those built solely in herbaceous cover.

## Modeling procedure

We used the nest survival module in Program MARK (White and Burnham 1999, Rotella et al. 2004) to compare nest survival models and to obtain estimates of daily nest survival. With the logit link, daily survival rate of a nest on day *i* is modeled as

$$DSR = \frac{\exp(\beta_0 + \sum_j \beta_j x_{ji})}{(1 + \exp \sum_j \beta_j x_{ji})}$$

where the $x_{ji}$ (j=1,2,…..,J) are values for *j* covariates on the day *i* and the $\beta_j$ are coefficients to be estimated from the data (Rotella et al. 2004). We assumed a 25-day nesting cycle for golden-winged warblers with 4 days for laying, 11 days for incubation and 10 days for brooding. Year (n = 3), site (n = 4), and nest stage (n = 3) were modeled as groups in the nest survival module resulting in 36 groups. For each nest we also included 65 individual covariates. The two climatic variables and eight vegetation variables accounted for ten of the covariates and the remaining 55 covariates account for daily age of the nest across the nesting cycle. Throughout the three years of study, golden-winged warbler nests were active from 5 May (first egg date) to 28 June, for a 55-day nesting cycle. Data structure and entry followed those of Dinsmore et al. (2002). As suggested by Dinsmore et al. (2002) and Rotella (2006), we did not standardize individual covariates because the unstandardized covariates did not affect numerical optimization.

Within each model set, we decided a priori to create an additional additive model using all variables from models that have $\Delta AIC_c$ values < 2. Models meeting the $\Delta AIC_c < 2$ criterion should *not* be ruled out as being the best model given the data (Burham and Anderson 2002). We also decided a priori to carry over any models with $\Delta AIC_c$ values < 2 on to the next suite of models. We did this to allow for combinations of important variables from the different suites of models without having to run all possible subsets with all possible variables. We chose variables of interest a priori as well as the criteria for future combinations of variables; we believe this framework leads to more parsimonious model subsets than the alternative of running hundreds of models for a single analysis, and thus running the risk of finding spurious results (S. Dinsmore, personal communication).

### Monte Carlo simulation

When a nest-survival model including habitat covariates performs better than the constant survival, intercept only model, there is some evidence for a real effect of that habitat parameter. However, model-selection uncertainty is common where the "best" model according to $\Delta AIC$ values may be equally as supported as others, including the null model of constant survival. We used Monte Carlo simulation to create 100 replicate data sets and determined how consistently a given model was selected as best (using AIC model selection criteria). We used a SAS code developed by J. Rotella (available at www.montana.edu/rotella/research.htm) as a starting template for our simulations and adjusted the code as necessary for our objective. The characteristics of simulated datasets were based on our real world data (i.e., a sample size, nest check intervals, etc.). We assumed the nest-initiation dates and the age of nests when found in these simulated data were uniformly distributed and the nest check interval lengths were uniformly distributed between 1-4 d. For each simulation, we fit survival models for the intercept-only, constant survival model and for any other model that performed better than the null model. We then calculated the Akaike weights from all models and summarized the Akaike weights from all simulations to determine the degree of model selection uncertainty in our model set and in so doing quantify the evidence for an effect of the covariates. For example, if a covariate model had a greater AIC weight than the null model in >90 of the 100 simulations, we would be confident that the effect was real.

## Results

We monitored 102 golden-winged warbler nests during the 2004-2006 breeding seasons for 1,613 exposure days across a 55-d interval. The raw nest success (number of successful nests/total number of nests*100) across the three years was 58.8%, and 90% of the failed nests were attributed to predation. No evidence of double-brooding was observed. The mean age of nests when they were found was 5.6 d (SE = 0.66) and 70% of all nests were found before incubation began (during nest construction).

### *Nest-site selection*

Of the nine vegetation variables assessed, four differed between nests and randomly-selected non-nest sites within golden-winged territories (Table 2.3). The percent cover of saplings in the 11.3-m radius plot and the percent cover of woody vegetation, forbs and grass within a 1-m radius plot differed ($P < 0.006$) between nest and non-nest plots. Nest sites had more snags, more grass cover at both the plot and 1-m scale, more forb cover at the 1-m scale, fewer saplings at the 11.3-m plot scale and less woody cover at the 1-m plot scale (Table 2.3).

### *Nest survival*

In the first set of models assessing the effects of study site and year, the constant survival model had the most support ($AIC_c$ weight = 0.57), indicating that golden-winged warbler daily nest survival may not vary significantly across sites and years (Table 2.4).

However, the model with a year effect also had good support ($\Delta AIC_c = 0.98$, AIC weight = 0.35), suggesting that there may be some degree of annual variation in DSR. The actual estimates of DSR (Table 2.5) overlapped considerably and the confidence intervals for the year-effect beta coefficients included zero. Based on the low $\Delta AIC_c$ value, the year effect was added to the second suite of models. The site model and the additive site and year model received little support from the data ($\Delta AIC_c$ values > 4), and were not added to subsequent model sets.

In the second set of models, a constant survival model was again most supported by the data ($AIC_c$ weight = 0.19), however several models had $\Delta AIC_c$ values < 2 that were transferred to the third suite of models: the linear and quadratic time models and the effects of minimum temperature, year, and daily precipitation (Table 2.6). In the third set of models, these same parameters had $\Delta AIC_c$ values < 2 in addition to a model with the percent cover of shrubs and saplings and another with distance to forest edge (Table 2.7). For the final set of models, several models had $\Delta AIC_c$ values < 2 (Table 2.8), but parameter estimates for all covariates included zero (Table 2.9) and the constant survival model had equal support. We did not use model averaging to obtain estimates of covariate effects because covariates were not typically present in more than one model.

Our model-selection results provided evidence that daily nest survival rates decreased as daily minimum temperature increased (Figure 2.1a), decreased over time (Figure 2.1b), increased with increasing shrub cover (Figure 2.1c), and decreased with increasing sapling cover (Figure 2.1d). In addition, the presence of a woody stem in the nest substrate performed better than the constant survival model, such that nests with a woody stem had a lower DSR than nests without a woody stem (Figure 2.2). The AIC weights for this model and the constant survival model, however, were very similar (Table 2.8). The estimate for golden-winged warbler DSR from the constant survival model was 0.973 (SE = 0.004).

### *Monte Carlo simulation results*

The mean AIC weights across all simulations did not differ for the constant survival model and the woody stem model ($w_i = 0.497$ and 0.503 for the constant survival and subwood models, respectively, t = 1.66, P = 0.488), indicating that the presence of a woody stem in the nest substrate did not have a strong effect on nest survival. Furthermore, the constant survival model was selected as the best model (i.e., it had a lower $AIC_c$ value) over the subwood model in 57% of the simulated datasets. The distribution of model weights for the constant survival model was skewed low (Figure 2.3), with no model weight over 0.732. Conversely, the distribution of model weights for the subwood model was skewed high (Figure 2.3), with no model weight less than 0.268.

## Discussion

### *Nest-site selection*

Golden-winged warbler nest-site selection appears to be non-random, such that females select nest sites with specific habitat attributes. Nests sites had more grass and forb cover and less woody vegetation cover within 1 m and had fewer saplings within 11.3 m (Table 2.3). In theory, female golden-wingeds should select nest-site characteristics that reduce the probability of nest predation (Martin 1988a). This hypothesis would be supported if similar habitat attributes affected nest-survival rates as demonstrated by Martin (1998). However, recent studies have demonstrated non-random nest-site selection with no apparent relationship between selected habitat attributes and nest survival (Wilson and Cooper 1998, Wilson and Gende 2000, Siepielski et al. 2001). Likewise, we did not find any habitat variables, except potentially one (the presence of a woody stem in the nest substrate), that seemed to influence nest survival rates (see next section). Golden-winged warblers may simply be very effective at identifying nesting sites with low predation rates. Alternatively, the habitat characteristics associated with golden-winged warbler nest sites in the Cumberland Mountains of Tennessee may be more of a reflection of resource partitioning than a mechanism for optimizing nest survival. Martin (1988b) suggested that bird species partition nest sites because of density-dependent predation pressures, allowing for coexistence of similar species. If all species had similar nesting habits, predator search efficiency would be high. Regardless of the mechanism or degree to which it is adaptive, golden-wingeds selected nest sites with specific habitat attributes and assuring the presence of these preferred nest site characteristics in the landscape is important for the conservation of this species.

### ***Nest survival***

Our nest survival results did not identify any strong relationships between the factors we considered and daily nest survival. All parameter estimates included zero and only one model had performed better than the constant survival model. This model that performed better actually had equal support (i.e., $AIC_c$ weight). However, several models had $\Delta AIC_c$ values < 2 suggesting that of the models considered, these variables may have some effect on daily nest survival.

Daily nest survival rate tended to decrease with increasing minimum daily temperature and tended to decrease over time, but the constant survival model performed equally well as models with either of these covariates. These two covariates were also correlated; as the nesting season progressed, the daily minimum temperature increased. We predicted the opposite trend with lower nest survival earlier in the season when the temperatures were cooler. However, an alternative explanation is that nest predator activity increases throughout the nesting season as temperatures rise. Small mammals (Soderstrom et al. 1998) and snakes (Thompson and Burhans 2003, Weatherhead and Bloun-Demers 2004) make up the dominant nest predator community for ground-nesting birds, such as golden-winged warblers. Snakes are very abundant on our study sites because of the dense cover of herbaceous vegetation, and do not typically become active until later in the season (Stake et al. 2005 and L. Bulluck, personal observation) when the temperatures are greater and potentially more food is available. Burhans et al. (2002) and Davis (2005) also found temporal models were related to nest survival rates and they expressed a need to better understand the mechanisms behind these temporal differences. More study is needed regarding the specific causes of nest failure for golden-winged warblers (i.e., frequencies of nest predation events by specific predators), especially considering that >95% of the nest failures were caused by predation (n = 2 failed nests with known fates not caused by predation). Such studies that address predation of songbird nest should explore further the relationship between time of season and nest predator activity.

A model with two covariates representing sapling and shrub cover at the 11.3-m plot scale was also supported ($\Delta AIC_c < 2$). DSR increased as shrub cover increased and decreased as sapling cover increased (Figure 2.1c-d), however, the parameter estimates for these covariates included zero. We did not have specific a priori hypotheses regarding these vegetation components. A posteriori, we can speculate why these vegetation characters may be marginally associated with nest survival. Increased shrub cover may provide additional cover for adults while feeding nestlings that make their frequent visits less conspicuous to predators. The majority of shrub cover in this study area was comprised of blackberry, which grows in very dense thickets that may provide a barrier to movement for predators that travel on the ground. The inverse relationship between sapling cover and nest survival is less intuitive. Saplings have the opposite structure of shrubs with open areas near the ground and dense cover >2 m. This structure does not provide dense cover for adults during the nestling stage nor does it provide a barrier to movement for predators. Despite the weak support for this model, the influence of vegetation structure on golden-winged warbler nest survival, if any, requires more study.

Only one model with one habitat covariate (the presence of a woody stem as the nest substrate) performed better than the constant survival model in all model sets (i.e., it had a greater model weight). A simulation exercise indicated that if we were to collect these data on 100 different occasions, more than half of the time the constant survival model would perform better than the habitat model. This suggests that the presence of a woody stem in the nest substrate may not significantly affect nest survival.

Our model results indicate that either nest survival is a random process in this system, golden-wingeds consistently select sites with low predation rates, or nest survival is a dynamic and complex process driven by a myriad of factors, some of which were not measured in this study. Other studies of avian nest success have speculated that predation may be a random process (Holway 1991, Filliater et al. 1994, Howlett and Stutchbury 1997, Wilson and Cooper 1998). However, there are alternative possible reasons that we found no habitat factors to appreciably influence nest survival rates. While our four study sites are different (Table 2.1), there may be too little variation in habitat types across these sites to display a difference in nest survival rates from our sample of nests. Our study sites comprised a large portion of the broad successional spectrum that golden-wingeds occupy, though the extremes were not present. The drastic increases or decreases in nest survival may occur in habitat components present in these extremes. Further, our sample size (n = 102 nests) may have been too small to detect an existing effect. At the same time, this sample size is comparable to other studies that have found effects. Finally, we may not have measured the appropriate variables that truly affected golden-winged warbler nest survival.

Several other studies of factors influencing avian nest survival have found no or little effect of microhabitat or vegetation (Filliater et al. 1994, Wilson and Cooper 1998, Huhta et al. 1999, Wilson and Gende 2000, Siepielski et al. 2001, Burhans et al. 2002, Chase 2002, Davis 2005). Several hypotheses for this have been presented. Temporal factors may be at play such that current nest-site selection criteria may reflect historical predator communities and/or densities (Martin 1988b, Siepielski et al. 2001). Indeed, Misenhelter and Rotenberry (2000) found that birds preferred to nest in areas in which they did not reproduce successfully (i.e., “an ecological trap”), perhaps caused by the redistribution of nest predators following anthropogenic disturbance. Alternatively, spatial and temporal variation in predation may lessen the response of a species to natural selection pressures, leading to the lack of a strong relationship between nest-site characteristics and nest survival (Chase 2002). Nest-site selection may also be controlled by other factors than nest predation, such as food availability (Lennington 1980), foraging efficiency (Huhta et al. 1999), or landscape-level factors (Rodewald and Yahner 2001).

### *Study Implications*

Golden-winged warbler nest-site selection is non-random and consequently may provide guidance for future conservation efforts. The importance of maintaining early successional habitats with an abundance of diverse herbaceous ground cover appears to be critical for golden-winged warbler nesting; the percent cover of both forbs and grass were greater on nest sties compared with non-nest sites. Nest sites also had more snags, fewer saplings, and less woody cover than non-nest sites. The vegetation criteria that golden-wingeds appear to select for nest sites are all characteristic of areas that have been burned in the recent past. Bulluck and Buehler (2006) demonstrated that early successional habitats vary in their vegetative characteristics and in the avian communities they support and thus should not be considered equivalent when trying to manage for the entire suite of early successional bird species in a region. The results presented here provide additional evidence for this; only early successional areas with diverse herbaceous and woody cover are suitable for golden-winged warbler nesting. Timber harvests are an important source of early successional habitat in deciduous forests of the eastern U.S. However, regenerating forests in the Cumberland Mountains of Tennessee do not typically have the abundant herbaceous cover required by nesting golden-wingeds. Older reclaimed surface mines, on the other hand, if re-vegetated with a mixture of herbaceous and woody vegetation, provide suitable habitat for golden-winged warblers in addition to a variety of early and late successional bird species (Bulluck and Buehler 2006).

Golden-winged warbler nest survival appears to be complex and dynamic, with no covariates measured showing strong relationships to daily nest survival rate. Further study of the weakly-associated covariates is warranted in addition to others not considered here. The negative relationship between nest survival and both time throughout the season and minimum daily temperature may be associated with predator activity. A study that explicitly tests this hypothesis by monitoring predator activity through time with cameras at golden-winged nests is needed. The positive relationship between nest survival and the percent cover of shrubs may have to do with predator mobility and/or visibility being hindered by the dense shrub cover near the nest. The negative relationship between nest survival and sapling cover and the presence of a woody stem in the nest substrate are more difficult to explain. The relationships suggested from this study provide an excellent pool of potential hypotheses to test both within the Cumberland Mountains population and throughout the species' range.

However, until the mechanisms behind the factors related to nest survival are better understood, habitat-based management attempting to increase nest survival may be ineffective.

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# Appendix

**Table 2.1:** General summary information about each field site in the Cumberland Mountains of Tennessee, 2004-2006. The number of years since reclamation was estimated based on vegetation succession and federal documents from the Office of Surface Mining. The number of territorial males is a range based on variation among years.

| Site | Year of reclamation | Size (ha) | Number of birds | Number of nests |
|---|---|---|---|---|
| Ash Log Mountain | ~1990 | 125 | 35-40 | 44 |
| Bootjack Mountain | ~1980 | 50 | 12-15 | 20 |
| Burge Mountain | ~1990 | 50 | 12-17 | 22 |
| Fork Mountain | ~1980 | 40 | 12-15 | 16 |

**Table 2.2:** Description of the four suites of models for daily nest survival rate and the corresponding notation used in later results tables. Constant survival models ($S_{(.)}$) containing the intercept only and global models ($S_{(global)}$) containing all parameters in a given suite were also assessed but not included in this table.

| Model Suite | Model | Notation |
|---|---|---|
| I. Nuisance Models | Year | $S_{(year)}$ |
| | Site | $S_{(site)}$ |
| | Year and site | $S_{(year + site)}$ |
| II. Climate, time, age, and stage models | Linear time | $S_{(T)}$ |
| | Quadratic time | $S_{(TT)}$ |
| | Minimum temperature | $S_{(mintemp)}$ |
| | Daily precipitation | $S_{(precip)}$ |
| | Temperature and precipitation | $S_{(mintemp + precip)}$ |
| | Nest stage (Lay/Incubation/Brood) | $S_{(stage)}$ |
| | Linear Age | $S_{(age)}$ |
| | Quadratic age | $S_{(age2)}$ |
| III. Plot-level vegetation models | Sapling and shrub cover | $S_{(saps + shrubs)}$ |
| | Distance to forest edge | $S_{(dedge)}$ |
| | Grass and forb cover | $S_{(grass+ forbs)}$ |
| IV. Nest-level vegetation models | Woody stem in nest substrate (0/1) | $S_{(subwood)}$ |
| | Grass cover within 1 m of nest | $S_{(mgrass)}$ |
| | Forb cover within 1 m of nest | $S_{(mforb)}$ |
| | Woody vegetation within 1 m of nest | $S_{(mwood)}$ |
| | Nest height | $S_{(nesthgt)}$ |

**Table 2.3:** Mean and standard error (in parenthesis) of nine vegetation characteristics at nest sites and randomly-selected non-nest sites within golden-winged warbler territories in the Cumberland Mountains of Tennessee, 2004-2006. Parameters with asterisks were significantly different (P < 0.05) and those with double asterisks were significant after the Bonferoni adjustment (P < 0.006).

| Scale | Vegetation parameter | Nests | Non-nests | P |
|---|---|---|---|---|
| Plot level (11.3-m radius) | Basal Area | 21.1 (2.0) | 18.2 (1.5) | 0.348 |
| | Number of snags* | 6.7 (0.4) | 5.3 (0.3) | 0.014 |
| | Percent cover grass* | 70.2 (2.5) | 62.4 (1.9) | 0.012 |
| | Percent cover forbs | 79.1 (1.8) | 78.7 (1.3) | 0.843 |
| | Percent cover shrubs | 36.5 (2.6) | 42.7 (1.9) | 0.077 |
| | Percent cover saplings** | 31.4 (2.8) | 44.5 (2.1) | <0.001 |
| Subplot-level (1-m radius) | Percent cover woody** | 34.5 (3.0) | 47.2 (2.2) | <0.001 |
| | Percent cover forbs** | 49.3 (2.6) | 39.9 (1.9) | 0.003 |
| | Percent cover grass** | 52.3 (3.0) | 39.3 (2.2) | <0.001 |

**Table 2.4:** Summary of model selection results from the first suite of models for the nest survival of golden-winged warblers in the Cumberland Mountains of Tennessee, 2004-2006. Model notation is described in Table 2.2. The AIC values are different in this suite than in future suites for the exact same models because the nest stage grouping effect was removed.

| **Model** | **K** | **AIC$_c$** | **ΔAIC$_c$** | ***$w_i$*** |
|---|---|---|---|---|
| $S_{(.)}$ | 1 | 312.32 | 0 | 0.565 |
| $S_{(year)}$ | 3 | 313.30 | 0.98 | 0.347 |
| $S_{(site)}$ | 4 | 317.10 | 4.78 | 0.052 |
| $S_{(year+site)}$ | 6 | 317.84 | 5.51 | 0.036 |

**Table 2.5:** Golden-winged warbler nest survival estimates (daily survival rates (DSR)) for year and site, Cumberland Mountains, 2004-2006. The differences among sites are marginal whereas the annual variation in DSR is more apparent.

| **Nuisance Parameter** | | **Mean DSR** | **SE** | **95% CI** | |
|---|---|---|---|---|---|
| | | | | **Lower** | **Upper** |
| Site | Ash Log | 0.9753 | 0.005 | 0.9616 | 0.9842 |
| | Bootjack | 0.9783 | 0.009 | 0.9526 | 0.9902 |
| | Burge | 0.9752 | 0.009 | 0.9489 | 0.9881 |
| | Fork | 0.9635 | 0.012 | 0.9313 | 0.9809 |
| Year | 2004 | 0.9834 | 0.006 | 0.9656 | 0.9921 |
| | 2005 | 0.9738 | 0.006 | 0.9597 | 0.9830 |
| | 2006 | 0.9641 | 0.009 | 0.9403 | 0.9786 |

**Table 2.6:** Summary of model selection results for the second suite of models for the nest survival of golden-winged warblers in the Cumberland Mountains of Tennessee, 2004-2006. Model notation is described in Table 2.2.

| Model | K | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| $S_{(.)}$ | 1 | 318.35 | 0 | 0.192 |
| $S_{(minTemp)}$ | 2 | 318.43 | 0.09 | 0.184 |
| $S_{(T)}$ | 2 | 318.99 | 0.65 | 0.139 |
| $S_{(TT)}$ | 3 | 319.52 | 1.17 | 0.107 |
| $S_{(year)}$ | 3 | 320.08 | 1.73 | 0.081 |
| $S_{(precip)}$ | 2 | 320.10 | 1.76 | 0.080 |
| $S_{(precip\ +\ minTemp)}$ | 3 | 320.21 | 1.86 | 0.076 |
| $S_{(age)}$ | 2 | 320.35 | 2.01 | 0.070 |
| $S_{(age2)}$ | 3 | 321.93 | 3.59 | 0.032 |
| $S_{(stage)}$ | 3 | 321.99 | 3.65 | 0.031 |
| $S_{(T\ +\ TT\ +\ minTemp\ +\ precip\ +\ year)}$ | 7 | 324.67 | 6.32 | 0.008 |
| $S_{(year\ +\ T\ +\ TT\ +\ minTemp\ +\ precip\ +\ age\ +\ age2\ +\ stage)}$ | 11 | 330.22 | 11.87 | 0.000 |

**Table 2.7:** Summary of model selection results from the third set of models for the nest survival of golden-winged warblers in the Cumberland Mountains of Tennessee, 2004-2006. Model notation is described in Table 2.2.

| Model | K | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| $S_{(.)}$ | 1 | 318.35 | 0 | 0.168 |
| $S_{(minTemp)}$ | 2 | 318.43 | 0.09 | 0.161 |
| $S_{(T)}$ | 2 | 318.99 | 0.65 | 0.121 |
| $S_{(saps + shrubs)}$ | 3 | 319.11 | 0.77 | 0.114 |
| $S_{(TT)}$ | 3 | 319.52 | 1.17 | 0.093 |
| $S_{(year)}$ | 3 | 320.08 | 1.73 | 0.071 |
| $S_{(precip)}$ | 2 | 320.10 | 1.76 | 0.070 |
| $S_{(dedge)}$ | 2 | 320.18 | 1.83 | 0.067 |
| $S_{(precip + minTemp)}$ | 3 | 320.21 | 1.86 | 0.066 |
| $S_{(saps + shrubs + dedge)}$ | 4 | 321.10 | 2.75 | 0.042 |
| $S_{(grass + forbs)}$ | 3 | 322.23 | 3.89 | 0.024 |
| $S_{(year + T + TT + minTemp + precip + saps + shrubs + grass + forbs + dedge)}$ | 10 | 327.70 | 9.35 | 0.002 |

**Table 2.8:** Summary of model selection results from the final set of models for the nest survival of golden-winged warblers in the Cumberland Mountains of Tennessee, 2004-2006. Model notation is described in Table 2.2.

| **Model** | **K** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** |
|---|---|---|---|---|
| $S_{\text{(subwood)}}$ | 2 | 318.22 | 0 | 0.136 |
| $S_{\text{(.)}}$ | 1 | 318.35 | 0.13 | 0.128 |
| $S_{\text{(minTemp)}}$ | 2 | 318.43 | 0.21 | 0.123 |
| $S_{\text{(T)}}$ | 2 | 318.99 | 0.78 | 0.092 |
| $S_{\text{(saps + shrubs)}}$ | 3 | 319.11 | 0.90 | 0.087 |
| $S_{\text{(TT)}}$ | 3 | 319.52 | 1.30 | 0.071 |
| $S_{\text{(mgrass)}}$ | 2 | 319.78 | 1.56 | 0.062 |
| $S_{\text{(year)}}$ | 3 | 320.08 | 1.86 | 0.054 |
| $S_{\text{(precip)}}$ | 2 | 320.15 | 1.94 | 0.052 |
| $S_{\text{(dedge)}}$ | 2 | 320.18 | 1.96 | 0.051 |
| $S_{\text{(mwood)}}$ | 2 | 320.29 | 2.07 | 0.048 |
| $S_{\text{(Nesthgt)}}$ | 2 | 320.34 | 2.12 | 0.047 |
| $S_{\text{(mforb)}}$ | 2 | 320.35 | 2.13 | 0.047 |
| $S_{\text{(subwood + minTemp + T + TT + saps + shrubs + mgrass + year +precip + dedge)}}$ | 12 | 327.77 | 9.55 | 0.001 |
| $S_{\text{(subwood + minTemp + T + TT + saps + shrubs + mgrass + year +precip + dedge + Nesthgt \_mwood + m forb)}}$ | 15 | 332.13 | 13.91 | 0.000 |

**Table 2.9:** Beta estimates and 95% CI for parameters in the top models (i.e., those with ΔAIC values < 2) in the final and fourth set of models for the nest survival of golden-winged warblers in the Cumberland Mountains of Tennessee, 2004-2006.

| **Parameter** | **Estimate** | **95% CI** | |
|---|---|---|---|
| | | **Lower** | **Upper** |
| Woody stem as nest substrate | -0.458 | -1.072 | 0.1562 |
| Linear time | -0.018 | -0.0477 | 0.0120 |
| Quadratic time | -0.001 | -0.0035 | 0.0008 |
| Sapling cover | -0.008 | -0.0197 | 0.0029 |
| Shrub cover | 0.010 | -0.0042 | 0.0241 |
| Grass cover in 1m | 0.004 | -0.0071 | 0.0161 |
| Minimum temperature | -0.033 | -0.0797 | 0.0145 |
| Daily precipitation | -0.301 | -1.2938 | 0.6914 |
| Distance to forest edge | -0.003 | -0.0141 | 0.0091 |

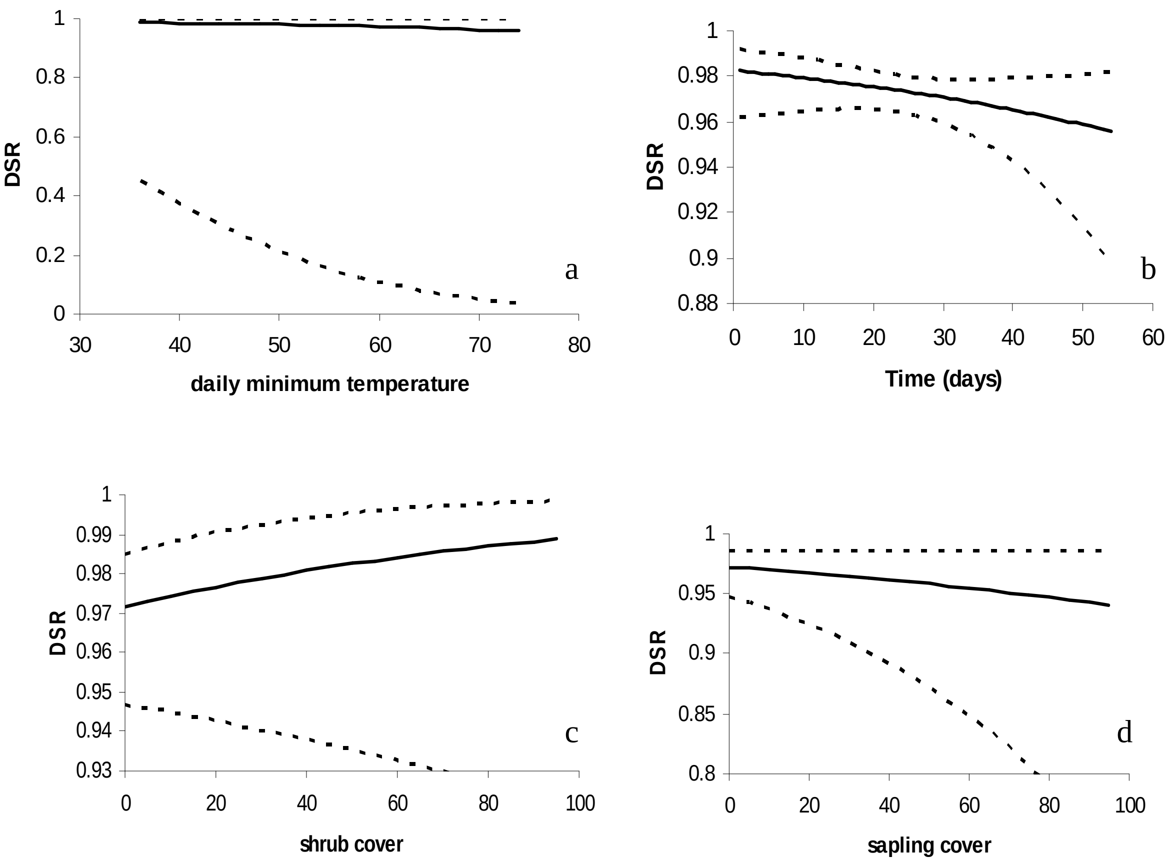

**Figure 2.1:** Golden-winged warbler daily nest survival rate (DSR) as a function of daily minimum temperature (a), time throughout the nesting season (b), percent shrub cover (c) and percent sapling cover (d), Cumberland Mountains, 2004-2006. Dashed lines represent standard errors.

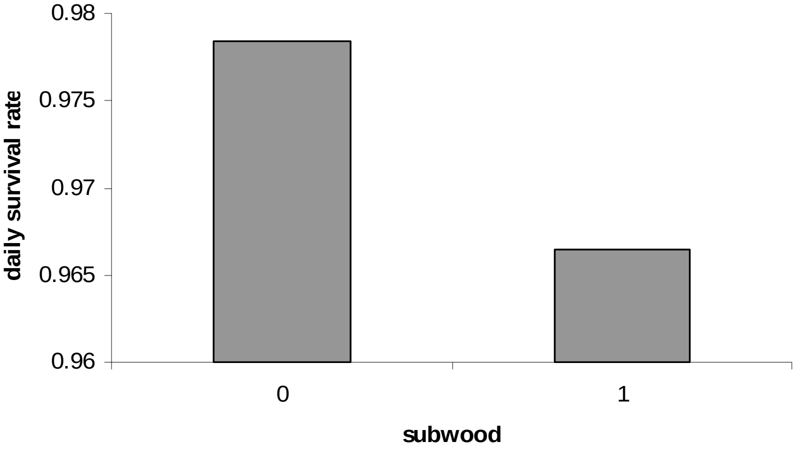

**Figure 2.2:** Mean daily nest survival rate for golden-winged warbler nests with (1) and without (0) a woody substrate, Cumberland Mountains, Tennessee, 2004-2006.

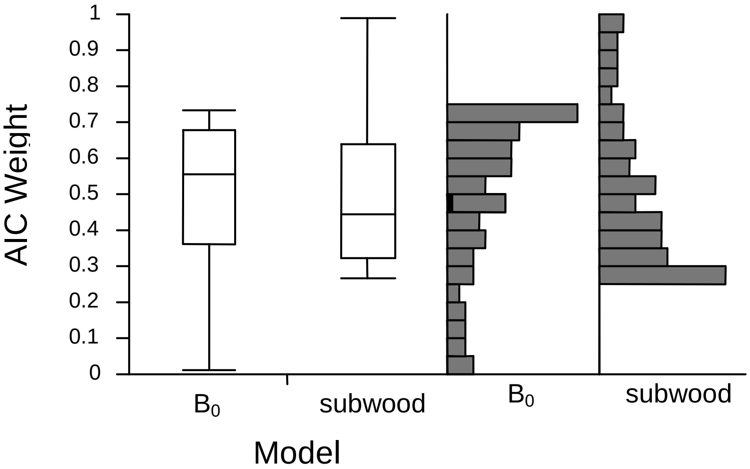

**Figure 2.3:** Summary of Monte Carlo simulation results. The distribution of AIC weights from the 100 simulation model runs for the constant survival ($B_0$) model and the model with a variable for the presence of a woody stem as the nest substrate (subwood).

# Part 3

# PART 3: THE ROLE OF HABITAT AND DEMOGRAPHY IN GOLDEN-WINGED WARBLER (*Vermivora chrysoptera*) TERRITORY SIZE VARIATION

The following manuscript was written for submission to
*Oecologia* or *Biological Conservation*. "We" throughout
this manuscript refers to: Bulluck, L.P., D.A. Buehler, and
K. Caruso

## Abstract

Intraspecific variation in territory size can be significant and is often thought to be a function of territory quality. Because of the complex interactions between con-specifics and the often heterogeneous distribution of resources, territory size variation is likely related to both habitat quality and demographic factors (e.g., male age and density). The golden-winged warbler (*Vermivora chrysoptera*) is a territorial migratory songbird that breeds in early successional habitats and has been documented to have high rates of extra-pair paternity (EPP). We modeled the relative effects of habitat and demographic factors on golden-winged territory size variation. We used the fixed-kernel-density estimation method to calculate each territorial male's utilization distribution. We then assessed the relationship between territory size and vegetation data collected in each territory and demographic variables measured for each nesting pair. Golden-winged warbler territory size varied predominantly with the percent cover of vines and the number of snags. The single demographic factor related to golden-winged warbler territory size was nest success; there was a greater rate of nest success in larger territories than smaller territories. A complete understanding of intraspecific territory size variation is important because of the relationship between territory size and population regulation. However, territory size is likely affected by numerous factors (i.e., food abundance, nest sites and materials, song perches, protective cover) and the relative importance of these factors are themselves influenced by their spatial distribution and abundance.

## Introduction

Territoriality is the competition for space as a resource (Gordon 1997) and all the divisible (food) and non-divisible (nest sites) resources therein (Both and Visser 2003). Because of the complex interactions between con-specifics and the often heterogeneous distribution of resources, territory size is likely related to both resource availability and demographic factors (e.g., male density, male age). Optimality models suggest that territory size is often determined simultaneously by two factors – resource availability and the density of neighboring competitors (Myers et al. 1979). Territories tend to be smaller as resources are more abundant and as competitors are more numerous, because of the apparent tradeoff between defense and foraging (Scheoner 1983, Adams 2001).

Territorial species often display density-dependent population regulation (Newton 1992), whereby the number of breeding territories is limited by the amount of available habitat and territory size varies inversely with population size or density (Nilsson 1987, Smith et al. 1991, Chamberlain and Fuller 1999, Sillett et al. 2004). However, many territorial songbirds are not spaced regularly across the landscape because of spatial heterogeneity in habitat and/or resources, such that there is wide variation in territory size regardless of population density. For example, some species have populations of tightly-packed individuals with little or no unoccupied space and many overlapping territory boundaries, whereas other species are distributed in loosely-packed populations where apparently suitable habitats are not fully utilized (Both and Visser 2003). Intra-specific variation in territory size can be significant and may be a function of habitat suitability in addition to population density (Weins et al. 1985).

Studies of resource availability and territory size often consider food abundance to be the resource of interest. Marshall and Cooper (2004) demonstrated that vegetation volume was highly correlated with food availability for red-eyed vireos (*Vireo olivaceous*), such that habitat factors related to vegetation structure may be considered a proximate resource for some songbirds. Habitat factors may be particularly related to territory size in species that occupy ephemeral habitats that are patchily distributed; patchily-distributed habitats may necessitate larger territories than consolidated habitats (Eason 1992, Matthysen 1999). Furthermore, species occupying ephemeral habitat patches often make use of a range of successional stages. It is unknown if there is a most favorable successional stage for these species, or if individual vegetation components present along this successional gradient are optimal, where territory size is consequently optimized. The relationship between songbird territory size and habitat structure/food resources is often hypothesized to be negative, such that higher quality territories with more resources tend to be smaller than resource-poor territories (Smith and Shugart 1987, Hunt 1996).

Territory size has also been demonstrated to vary with demographic factors such as male density (Both and Visser 2000, Sillett et al. 2004), male age (Lazano et al. 1996), and nesting success (Brooker and Rowley 1995). These and additional demographic factors may be related to territory size in socially monogamous species that have high rates of extra-pair paternity (EPP), a phenomenon known to occur in ~86% of passerine species (Griffith et al 2002). Specifically, males attempting to guard mates from neighboring males on extra-territorial forays may prefer smaller territories that are easier to patrol for these intruding males. The frequency of EPP is negatively related to red-winged blackbird (*Agelaius phoeniceus*) territory size and the probability of EPP by a nearby male increased with the proximity of a female's nest to the territory boundary (Westneat and Mays 2005). However, this relationship between territory size and EPP may simply be an indirect effect of male density because extra-pair fertilizations tend to be more common in years and populations with greater territory densities (Gowaty and Bridges 1991, Westneat and Sherman 1997, Richardson and Burke 2001, Estep et al. 2005, but see Ratti et al. 2001).

The golden-winged warbler (*Vermivora chrysoptera*), is a declining Nearctic-Neotropical migrant songbird that inhabits a range of early successional habitats from open shrublands with scattered patches of woody vegetation to mature woodlands with persistent herbaceous cover and scattered openings. How habitat quality varies along this successional gradient is unknown. Golden-winged warblers are highly territorial and participate in male-male and male-female aggressive interactions, particularly during the early breeding season when females are most fertile (L. Bulluck, personal observation). These behaviors are indicative of territoriality as well as EPP occurrence. Golden-winged warblers in Ontario displayed high rates of EPP with 30% of the nestlings and 55% of nests having extra-pair offspring (Vallender et. al., In Review). Previously published estimates of golden-winged warbler territory size are quite broad (~ 0.4 to 6.0 ha) and describe territories as having boundaries delineated by vegetation characteristics in addition to interactions with neighboring males (Confer 1992). This estimate was based solely on visual observation/estimation and not on an objective spatial territory analysis of numerous individuals. A more recent study in a North Carolina wetland described golden-winged warbler territories as ranging from 0.4 – 1.6 ha (Rossell et al. 2003). This estimate was based on the mapping of peripheral song perches for ten male golden-winged warbler territories and creating a polygon around these points.

Because golden-winged warblers occupy patchily-distributed, ephemeral habitats and display territorial aggression with high rates of EPP, they are an ideal species for comparing the influences of habitat and demographic factors on the variation in territory size. Our primary objectives were to (1) measure territory size variation for a population of golden-winged warblers in the Cumberland Mountains of Tennessee using statistically rigorous methods, and to (2) model the relationship between territory size and two sets of parameters; a suite of habitat-related parameters and a suite of demographic parameters.

We hypothesized that golden-winged warbler territory size variation will be partially explained by habitat factors, particularly those describing vegetation structure (percent cover of herbs, shrubs, saplings, trees and vines). We hypothesized a relationship between territory size and vegetation cover components because golden-winged warbler habitat is often a mixture of herbaceous and woody vegetation that spans a fairly wide successional range (Confer and Knapp 1981). Golden-winged warblers nest on the ground in herbaceous cover, yet their young immediately disperse into thick woody cover provided by shrubs and vines after fledging. Presumably, optimal conditions occur somewhere along the successional continuum for this species. We considered the percent cover of saplings both greater than and less than 1-m tall as well as sapling and shrub height to account for vegetation structural complexity/volume. We included these variables based on previous studies that have shown that increased vegetation volume is correlated with food availability, which in turn is correlated with territory size (Smith and Shugart 1987, Marshall and Cooper 2004, but see Keller et al. 2003). Golden-winged warblers also often use grapevine as a primary material in nest construction (42 of 47 nests collected in 2005 and 2006 [89%], L. Bulluck, unpublished data). We therefore assessed the relationship between territory size and percent vine cover. In addition to vegetation structural components, we modeled the relationship between territory size and the mean distance to the nearest forest edge because forest edges are often, but not always present within territories. Finally, we modeled territory size as a function of the number of snags because snags often provide song perches and singing is the primary means of territorial defense.

We also hypothesized that golden-winged territory size variation will be explained in part by demographic factors. Specifically, we considered the relationships between territory size and two productivity measures: clutch size and nest success. We explored whether male defense of a larger territory would allow for more resources to support larger and more successful clutches or if the time spent defending a larger area would lead to smaller and less successful clutches. We also considered the relationships between territory size and nest initiation date, and territory size and male age. Older and higher-quality individuals have been shown to arrive on the breeding grounds earlier than younger and poorer-quality individuals (Lazano et al. 1996). We hypothesized that the territory size of these same individuals may differ from later arriving and younger individuals. Lastly, we assessed whether territory size differed for males whose territories overlapped with or simply abutted a neighboring male’s territory; males with territory overlap may be more aggressive and defend larger areas than males that simply abut their neighbor’s territories.

## Methods

### *Study site*

The Cumberland Mountains comprise the southwestern portion of the Appalachian Mountains. The mean elevation is 580 m with the highest ridges > 1,000 m. More than 50,000 ha of this landscape is publicly owned by the Tennessee Wildlife Resources Agency (TWRA); our study sites are located within Sundquist Forest Wildlife

Management Area. The predominant landcover of the region was mixed-mesophytic forest and approximately 15% of the region was in early stages of succession because of the surface mining of coal and timber harvests. Golden-winged warblers occupy lands previously mined for coal in the Cumberland Mountains, and they ephemerally occupy timber harvests that have abundant herbaceous cover. This study was conducted on four reclaimed coal surface mines; two were reclaimed approximately 15 years before the study and the other two were reclaimed approximately 20-25 years before the study. Mine reclamation typically involved planting a thick herbaceous layer of grasses and forbs to prevent soil erosion as well as black locust (*Robinia pseudoacacia*) saplings. Since reclamation, maples (*Acer* spp), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus* spp), and thickets of blackberry (*Rubus* spp.) have become established. Periodic arson fires have maintained the thick herbaceous cover and created numerous snags at all sites.

The Cumberland Mountains are located near the southern extreme of the golden-winged warbler range. We estimated the 2005 Cumberland Mountains golden-winged warbler population to be approximately 369 (± 122) breeding pairs (Bulluck and Buehler, unpublished data). The four sites in this study supported approximately 85 breeding pairs, or 17-34% of the region's population.

### ***Field methods***

We monitored territorial males from 1 May to 15 June in 2005 and 2006. Male golden-winged warblers begin arriving on the study site around 15 April and most males were defending their territories and females were initiating nest construction by 1 May. By mid-June the majority of nests fledged and males no longer guarded their territory boundaries. We did not collect territory location data for males after nest fledging in a territory because of potential dispersal of the family group and lack of territoriality when feeding fledged young. We monitored male activity from 0600 to 1000 h using "burst" sampling (Barg et al. 2005). This method is advantageous for mapping bird territories because it enables the collection of a large sample size during the short territorial period exhibited by most single-brooded songbirds (25 days; Barg et al. 2005). We followed individual males during one 30-min visitation period per day and marked his location every 3 min for a total of ten potential locations per day. A male could easily traverse his territory during the 3-min interval; therefore we assumed but did not test for independence of locations (Lair 1987, Barg et al. 2005). Each male was visited five times from 1 May to 15 June, and at least once early and late in the morning to account for variation in behavior throughout the morning. Our goal was to collect 40-50 locations for each male across the breeding season because previous studies indicated that the territory size of an animal begins to asymptote at this sample size (Seaman et al 1999, Barg et al. 2005). If males made long flights outside of their territory (potentially for extra-territorial forays) in which we lost contact, we terminated a visit before 10 points were collected.

The majority (~90%) of territorial males used in this study were captured using target mist-netting techniques and marked with a unique color-band combination and a United States Fish and Wildlife Service (USFWS) aluminum band for easy field identification of individuals. We also aged all males as second-year or after second-year using the criteria described in Pyle (1997). The few unmarked individuals used in this study either had a unique song that distinguished it from neighboring males or all neighboring males were banded, such that it was the only unmarked individual in the area. Each territory location was confirmed by visual observation and more rarely by the auditory identification of the focal territorial male. We determined mating status for all studied males and located nests for many of the mated pairs.

We flagged locations of territorial males in the field, and returned to collect locational data with a Trimble GeoExplorer GeoXT GPS unit equipped with real-time differential correction and ~1-m accuracy. Most location data were collected only if the position dilution of precision (PDOP) was < 6 to assure accuracy. However, because of the rugged mountainous terrain in Tennessee, a few points had PDOP values ranging from 6 to 10.

We collected vegetation data within 11.3-m radius plots (0.04 ha) at four randomly selected locations in each territory (0.16 ha sampled per territory). Points were selected using a random point generator extension (Jenness 2005) in ArcView 3.2 (ESRI

1999). In each vegetation plot, we recorded number of snags (i.e., a dead tree/sapling with >5-cm diameter at breast height), estimated average shrub and sapling height (m), and measured percent cover of vines, forbs, grass, shrubs, small saplings (<1 m in height), large saplings (≥1 m in height), and tree canopy cover (trees defined as >10-cm diameter at breast height) using an ocular tube (James and Shugart 1970). Ocular tube readings for all cover types were taken at 20 points within the 11.3-m plot along four transects in the cardinal directions (5 readings per transect). Observers recorded the presence of each cover type when looking though the ocular tube downward from the line of site 45 degrees and straight up at each point. This method provided objective percent cover measures (# readings with cover type/20*100). We averaged vegetation data across the four plots to obtain a mean value in each territory used in analyses.

### ***Data analyses***

We tested the hypothesis that our field sites had different mean vegetation components, potentially related to their different elapsed times since reclamation, using Analysis of Variance (ANOVA). If an overall difference was detected, we then tested for individual differences between sites using Tukey's HSD, a multiple comparisons test that is conservative when sample sizes are different (Hayter 1984). These analyses were performed in JMP statistical software (JMP, Version 6. SAS Institute Inc., Cary, NC, 1989-2005).

We used the fixed-kernel-density estimation method to calculate each territorial male's utilization distribution. This method is considered superior to other methods because it is based on a probability density function (Worton 1989, 1995) that employs density isopleths to describe the relative amount of time an animal spends in any location (Seaman and Powell 1996). We used the least squares cross validation (LSCV) method to calculate the smoothing factor ($h$) that determines the distance over which a location point influences the territory contours. Smaller $h$ values lead to territories comprised of many discontinuous islands whereas larger $h$ values lead to one continuous island. The LSCV method is considered a reliable method to calculate the optimal value of $h$ (Seaman and Powell 1996). We calculated and displayed kernel territories using the

Animal Movement Analysis Program V1.1 (Hooge and Eichenlaub 1997) in Arc View 3.2 (ESRI 1999).

We modeled the relationship between territory size and several habitat variables based on a set of a priori hypotheses. We modeled territory size (ha) as a function of the mean percent cover of forbs, grass, saplings and shrub cover, sapling and shrub height, the distance to forest edge, and the number of snags. For a subset of mapped territories for which we found nests ($n = 27$), we modeled whether territory size was related to several demographic factors. We specifically modeled the effect of male age (second year or after second year), the occurrence of territory overlap with a neighboring male (0/1), clutch size, nest success (0/1), and nest initiation date (Julian date).

We ran these two sets of a priori models with habitat and demographic factors relating to territory size (Table 3.1) using multiple linear regression (JMP 2005) and $AIC_c$ as the model selection criteria (Burnham and Anderson 2002). Variables were first tested for normality and we assessed multi-colinearity of explanatory variables to be combined additively. No transformations were necessary as all variables met normality assumptions and none of the a priori models had combinations of variables that were collinear with values of $r > 0.5$.

## Results

The percent cover of shrubs, vines, tree canopy, and saplings ≥1-m tall differed across the four sites ($P < 0.01$, Table 3.2). In general, sites reclaimed more recently (Ash Log and Burge Mountains) had less canopy cover, more sapling cover, and taller saplings than sites reclaimed previously (Bootjack and Fork Mountains). Furthermore, Ash Log Mountain had significantly more shrubs than Bootjack Mountain and significantly fewer vines than Fork Mountain (Table 3.2).

We mapped the territories of 50 males across the four study sites over two years and documented a mean territory size of 0.922 ha ± 0.08 SE (range = 0.26 – 2.95 ha). Male territories exhibited two basic spatial patterns where the entire territory was contiguous or where there were discrete focal areas separated by unused space (Figure 3.1). We collected 40-55 locations per male (mean = 50 locations), and there was no relationship between the number of locations and territory size ($F = 0.494$, df = 49, $P = 0.486$), indicating a sufficient number of points per male to accurately estimate territory size. Male density was similar across the four sites (0.26 – 0.34 males/ha, Table 3.3), and there was an inverse relationship between territory size and male density (Figure 3.2). Mean territory size did not differ between years ($F = 1.17$, df = 1, $P = 0.285$), but differed across the four sites ($F = 4.67$, df = 3, $P = 0.006$). Ash Log Mountain had larger mean territories than Fork Mountain ($P < 0.05$). There was no relationship between territory size and time since reclamation (Table 3.3).

### *Habitat factors*

We used the $\log_{10}$ of territory size to account for its non-normal distribution (i.e., positively skewed; Shapiro Wilk GOF = 0.878, $P < 0.0001$); the log transformation corrected this problem (Shapiro Wilk GOF = 0.987, $P = 0.855$). Male territory size decreased as the percent cover of vines increased (Figure 3.3a). The parameter estimate from the best model for the effect of the percent cover of vines was $\hat{\beta} = -0.011$ (95% CL = -0.019, -0.003, $R^2 = 0.13$). The probability that the percent cover of vines represented the best model, given the data and the models evaluated was 0.574 (see AIC weights in Table 3.4), however, relatively little variation in the data was explained by this model. Territory size also varied as a function of the number of snags (Table 3.4); larger territories tended to have more snags (Figure 3.3b). The parameter estimate from the second best model for the effect of the number of snags was $\hat{\beta} = 0.016$ (95% CL = 0.002, 0.031, $R^2 = 0.09$). The probability that the number of snags represented the best model, given the data, was 0.225 (see AIC weights in Table 3.4). Again, little variation in the data was explained by this model. Lastly, territory size increased with mean distance to a forest edge (Figure 3.3c), but this model did not have strong support ($\Delta AIC > 3$). The parameter estimate from the third best model representing this relationship was $\hat{\beta} = 0.009$ (95% CL = -0.001, 0.019, $R^2 = 0.07$). The probability that the mean distance to a forest edge represented the best model, given the data, was 0.115 (see AIC weights in

Table 3.4). All other models had ΔAIC values > 7, suggesting that these models lacked support (Burnham and Anderson 2002).

### *Demographic factors*

Of the 50 territories we mapped, we found nests for 27 of these pairs. We used this subset of territories to assess whether territory size was related to the hypothesized demographic parameters (Table 3.1). We used the $\log_{10}$ of territory size for this subset for the same reason mentioned previously (Shapiro Wilk GOF pre-transformation = 0.869, P = 0.0029; post-transformation GOF = 0.984, P = 0.947). Nest success was related to male golden-winged warbler territory size. Territory size was larger for successful nests (1.31 ± 0.78 ha), compared with unsuccessful nests (0.79 ± 0.31 ha). The probability that nest success represented the best model given the model set compared was 0.697 (see AIC weights, Table 3.5). All other demographic variables had very little likelihood of being the best model (AIC $w_i \leq 0.1$).

## Discussion

### *Habitat factors*

Golden-winged warbler territory size varied predominantly with the percent cover of vines, and less so with the number of snags and the distance to the nearest forest edge. Vines not only provided the principal nesting material used by golden-wingeds in this region (L. Bulluck, unpublished data), but vines also provided dense, protective cover throughout the breeding season, especially during the vulnerable post-fledging period. Vines, therefore, may be an important resource that is defended by the territorial male and/or aid the female in selecting high-quality males/territories. Territory size increased with the number of snags, probably because snags provide preferred song perches and singing is a male’s primary method of territorial defense. Defending a larger area may be easier (i.e., less expensive) when more snags are available as they provide a space without dense vegetation for further song projection and a vantage point to observe intruding males. Whereas no other avian studies have documented this relationship, Eason and Stamps (1992) demonstrated a positive relationship between lizard visibility and territory size. Finally, territory size had a positive relationship with distance to forest edge; territories closer to a forest edge were smaller than those farther from a forest edge. However, the parameter estimate for this variable included zero and the model had little support in general.

Our initial hypotheses for assessing the relationship between territory size and habitat factors were twofold. First, we were interested in the possibility that territory size varied such that more structurally complex habitats had smaller territory sizes. Previous research correlated vegetation structural complexity with food availability, which is often inversely related to territory size (Smith and Shugart 1987, Marshall and Cooper 2004). The relationship between territory size and percent cover of vines may support this hypothesis as vines certainly add structural complexity, but vines also provide nesting materials and protective cover. Furthermore, sapling and shrub height and saplings cover (both > and < 1-m tall) were not related to territory size, suggesting that structural complexity was not a driving factor in territory size. Future studies are needed that directly measure food availability in golden-winged warbler territories and attempt to relate this to territory size as well as to productivity measures such as nest survival.

The second reason for assessing the relationship between territory size and habitat factors was to indirectly evaluate if there is an optimal successional stage within the early successional continuum for golden-wingeds. For example, if older successional areas were of higher quality, males should defend smaller territories with greater mean canopy cover and/or lower herbaceous cover. Such relationships were not detected and none of the variables in the highest-ranking models suggested that one successional sere was better than another. The importance of snags may indicate the need for repeated disturbance such that snags are always taller than the living vegetation, but snags were equally abundant across all sites, regardless of age. Moreover, the two oldest sites (Fork and Bootjack Mountains) did not have consistently larger or smaller territories than the two younger sites (Ash Log and Burge Mountains). Finally, the importance of the distance to the nearest forest edge suggested that smaller sites or those with greater edge to area ratios may be beneficial for golden-winged warblers; however, the relationship between territory size and distance to edge was weak, suggesting this focus on this relationship may not be an effective management strategy.

### ***Demographic factors***

Our goal for assessing the relationship between golden-winged warbler territory size and demographic factors was to indirectly examine current hypotheses relating to density dependence, male quality, and productivity. The single demographic factor related to golden-winged warbler territory size was nest success (a measure of productivity); birds with larger territories had a greater rate of nest success than smaller territories. Higher-quality males may defend larger areas and be better able to provision their young leading to greater nest success. At first, this may seem contrary to the theory of optimal territory size, but Hixon (1980) suggested that some animals are “area maximizers” and may defend the largest territory area for which benefits surpass costs.

We hypothesized that territory size would be related to male quality/age and the occurrence of territory overlap because of the highly aggressive, territorial behavior of golden-winged warblers coupled with their assumed high rates of EPP (based on EPP rates from Ontario). However, male age, nest initiation date, and the presence of territory overlap were not related to golden-winged warbler territory size. The lack of any relationship with these factors may be valid, or may reflect our relatively small sample size of mapped territories for which we found nests (n = 27). Future research that assesses the relationship between territory size and the actual rates of EPP by neighbors is certainly warranted.

### ***Study implications***

Our primary goal in assessing intra-specific variation in territory size was to assess the relative effects of habitat and demographic factors on territory size variation in the golden-winged warbler, a highly territorial migratory songbird that breeds in ephemeral habitats. In general, we found both habitat and demographic factors to be related to territory size. While our hypotheses regarding a relationship between territory size and successional stage were not supported, habitat factors were important in explaining some of the variation in territory size. The habitat factor that carried the most model weight, the percent cover of vines, suggests the importance of this resource as nesting material and dense cover for golden-winged warblers.

Surprisingly, of the entire suite of demographic parameters assessed, only nest success was related to territory size, especially considering the theoretical and empirical research that has demonstrated the importance of neighbor interactions in structuring territories and of male age and arrival date in determining territory quality (Lazano et al. 1996). We attribute the lack of a relationship with other demographic factors to four potential causes – (1) the small sample size for demographic models in this study, (2) additional factors may influence territory size that were not measured, (3) our sites were below carrying capacity such that high-quality territories were not limiting, and (4) numerous factors likely interact to determine territory size for a given individual.

An understanding of intraspecific territory size variation is important for several reasons, primarily because a definite and complex link between territory size and population regulation (Both and Visser 2003) has been recognized for decades (Fretwell and Lucas 1970). Territory quality is likely affected by numerous factors (i.e., food abundance, nest sites and materials, song perches, protective cover) and the relative importance of these factors are themselves influenced by their spatial distribution and population density. Spatially explicit, individual-based models of neighbor interactions may provide hypotheses for future empirical studies in addition to generalizations about the population consequences of such interactions (Gordon 1997, Mitchell and Powell 2004). Alternatively, empirical studies will provide the data necessary to develop sound theoretical models as well as insights into species-specific factors affecting territory size.

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# Appendix

**Table 3.1:** Habitat attributes and demographic factors hypothesized to have a relationship to golden-winged warbler (*Vermivora chrysoptera*) territory size and the model used to test each hypothesis, Cumberland Mountains, Tennessee, 2005-2006. SapsA and sapsB refer to the percent cover of saplings <1-m tall and $\geq$1 m tall, respectively.

| | **Model** | **Parameters** |
|---|---|---|
| **Habitat factors**<br>**n = 50 territories** | Mean herbaceous cover | grass + forbs |
| | Mean sapling cover | sapsA + sapsB |
| | Mean shrub cover | shrubs |
| | Mean canopy cover | canopy |
| | Mean vine cover | vines |
| | Mean height of saplings and shrubs | saphgt + shrubhgt |
| | Mean distance to forest edge | D_edge |
| | Number of snags | snags |
| **Demographic factors**<br>**n = 27 territories** | Clutch size | Clutch |
| | Nest survival (0/1) | N_surv |
| | Neighbor overlap (0/1) | overlap |
| | Nest initiation date | N_date |
| | Male age | M_age |

**Table 3.2:** Summary of habitat attributes on the four study sites in the Cumberland Mountains of Tennessee, 2005-2006. Values represent mean and standard errors (in parentheses) of all plots sampled within golden-winged warbler (*Vermivora chrysoptera*) territories.

| **Site** | ***Canopy cover (%)** | ***Sapling >1m cover (%)** | **Sapling <1m cover (%)** | ***Shrub cover (%)** | **Forb cover (%)** | **Grass cover (%)** | ***Vine cover (%)** | **Number of snags** | **Shrub hgt. (m)** | ***Sapling hgt. (m)** |
|---|---|---|---|---|---|---|---|---|---|---|
| Ash Log | 27.2 (3.9) | 58.7 (4.3) | 8.0 (1.3) | 45.6 (3.0) | 74.0 (2.6) | 57.8 (4.0) | 18.8 (3.6) | 21.6 (2.2) | 1.2 (0.1) | 2.7 (0.1) |
| Burge | 38.4 (5.9) | 54.8 (6.6) | 14.5 (2.0) | 47.1 (4.6) | 85.1 (3.9) | 60.4 (6.1) | 27.9 (5.4) | 22.2 (3.2) | 1.0 (0.1) | 2.5 (0.2) |
| Bootjack | 67.6 (7.6) | 12.4 (8.5) | 11.9 (2.5) | 27.6 (5.9) | 80.6 (5.1) | 78.6 (7.8) | 31.4 (7.0) | 14.5 (4.2) | 1.2 (0.2) | 1.7 (0.3) |
| Fork | 59.8 (5.6) | 26.3 (6.3) | 10.4 (1.9) | 32.7 (4.4) | 79.4 (3.8) | 63.3 (5.8) | 40.2 (5.2) | 15.1 (3.1) | 1.0 (0.1) | 1.8 (0.2) |
| All sites | 41.4 (3.4) | 45.2 (3.8) | 10.3 (0.9) | 40.9 (2.2) | 78.2 (1.8) | 62.0 (2.8) | 26.8 (2.6) | 19.4 (1.5) | 1.1 (0.05) | 2.4 (0.1) |

*Significant difference between mean vegetation components ($P \leq 0.01$) across the four sites

**Table 3.3:** The size, number of total males, and male density found on each study site as well as the number of territories mapped (n) and the mean territory size for golden-winged warblers (*Vermivora chrysoptera*), Cumberland Mountains, Tennessee, 2005-2006.  The number of years since reclamation was estimated based on vegetation succession and federal documents from the U. S. Office of Surface Mining.

| **Site** | **Size (ha)** | **Total males** | **Males /ha** | **N** | **Mean territory size (ha)** | **Year of reclamation** |
|---|---|---|---|---|---|---|
| Ash Log | 125 | 40 | 0.32 | 23 | 1.2 | ~1990 |
| Burge | 50 | 17 | 0.34 | 10 | 0.7 | ~1990 |
| Bootjack | 50 | 13 | 0.26 | 6 | 1.2 | ~1980 |
| Fork | 40 | 13 | 0.33 | 11 | 0.6 | ~1980 |
| All sites | 265 | 83 | 0.30 | 50 | 0.98 | - |

**Table 3.4:** Summary of model selection results for habitat-related factors association with territory size variation in golden-winged warblers (*Vermivora chrysoptera*), Cumberland Mountains, Tennessee, 2005-2006. K is the number of parameters in the model and $w_i$ is the model weight. The global model includes all variables from the other models (vines + snags + distance to edge + canopy + shrubs + sapsA + sapsB + grass + forbs + saphgt + shrubhgt).

| **Model** | **K** | **AICc** | **ΔAIC** | **$w_i$** |
|---|---|---|---|---|
| vines | 2 | -60.29 | 0.00 | 0.574 |
| snags | 2 | -58.42 | 1.87 | 0.225 |
| distance to edge | 2 | -57.08 | 3.21 | 0.115 |
| canopy | 2 | -54.60 | 5.69 | 0.033 |
| shrubs | 2 | -53.53 | 6.76 | 0.020 |
| sapsA + sapsB | 3 | -52.98 | 7.31 | 0.015 |
| grass + forbs | 3 | -52.24 | 8.05 | 0.010 |
| saphgt + shrubhgt | 3 | -51.59 | 8.70 | 0.007 |
| Global | 12 | -40.53 | 19.76 | 0.000 |

**Table 3.5:** Summary of model selection results for demographic factors associated with territory size variation in golden-winged warblers (*Vermivora chrysoptera*), Cumberland Mountains, Tennessee, 2005-2006. K is the number of parameters in the model and wi is the model weight. The global model includes all variables from the other models (nest survival + nest initiation + clutch size + male age + overlap with neighbor).

| **Model** | **K** | **AICc** | **ΔAIC** | **$w_i$** |
|---|---|---|---|---|
| nest survival | 3 | -26.64 | 0.00 | 0.697 |
| nest initiation | 2 | -22.05 | 4.59 | 0.070 |
| clutch size | 2 | -21.99 | 4.65 | 0.068 |
| Global | 6 | -21.26 | 5.38 | 0.047 |
| male age | 3 | -21.74 | 4.90 | 0.060 |
| overlap with neighbor | 3 | -21.65 | 4.99 | 0.057 |

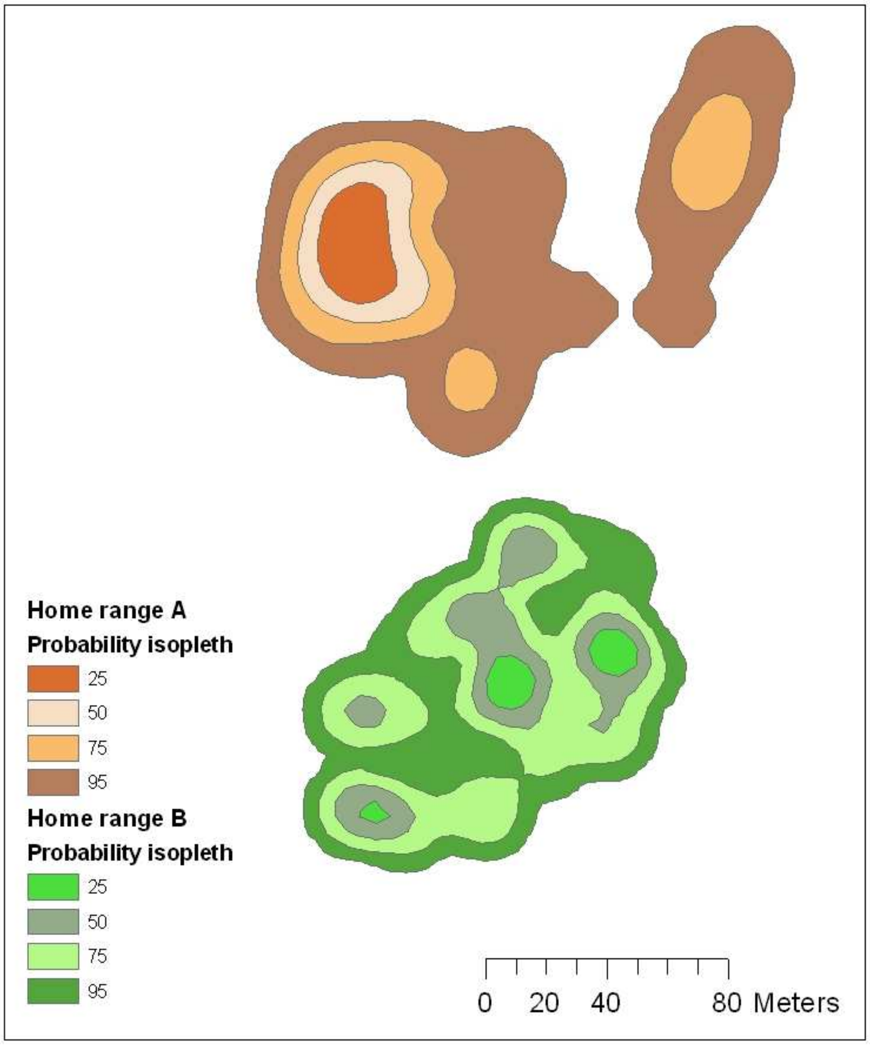

**Figure 3.1:** Examples of golden-winged warbler fixed-kernel territories in the Cumberland Mountains calculated using the Animal Movement Analysis Program V1.1 (Hooge and Eichenlaub 1997) in Arc View 3.2 (ESRI 1999). Territory A is comprised of one polygon whereas territory B is comprised of two separate polygons.

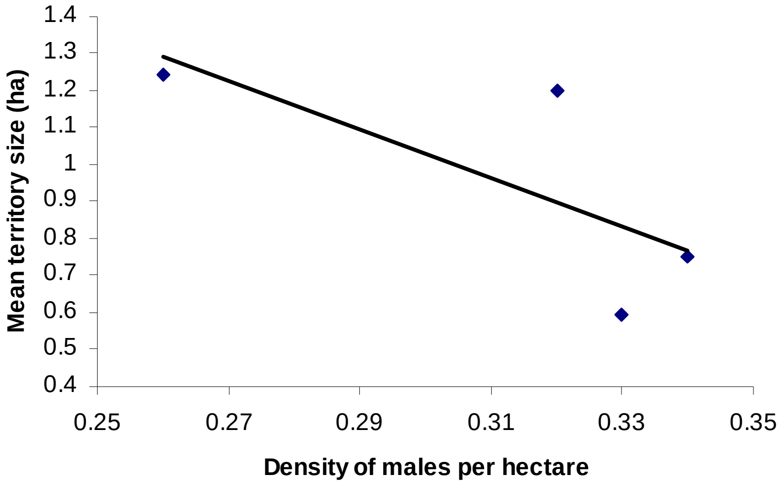

**Figure 3.2:** Relationship between golden-winged warbler territory size and male density across four study sites, Cumberland Mountains, Tennessee, 2005-2006.

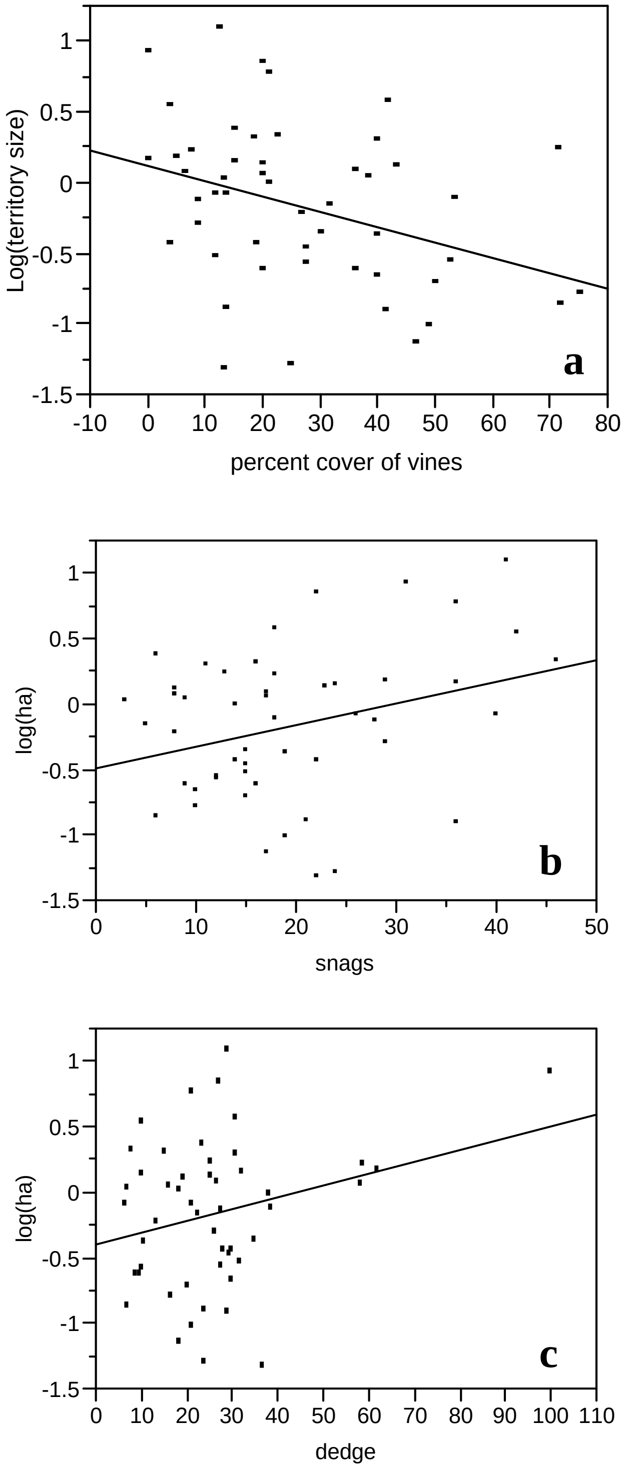

**Figure 3.3:** Relationship between golden-winged warbler territory size (ha) and the number of snags (a), the percent cover of vines (b), and distance to the nearest forest edge (c) in the Cumberland Mountains of Tennessee, 2005-2006.

# Part 4

# PART 4: GEOGRAPHIC VARIATION IN GOLDEN-WINGED WARBLER (*Vermivora chrysoptera*) DEMOGRAPHY

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manuscript refers to: L. P. Bulluck, D. A. Buehler, R.
Vallender, K. Fraser, and R. Robertson

## Abstract

Geographic life history variation is interesting theoretically, and it can also provide a framework within which to focus conservation efforts for declining species. The golden-winged warbler (*Vermivora chrysoptera*) is a Nearctic-Neotropical migratory songbird that uses early successional habitats and is experiencing steep population declines throughout its breeding range; causes of decline are thought to vary geographically. Contributing factors include the loss of habitat on both the breeding and wintering grounds, hybridization with the blue-winged warbler (*Vermivora pinus*), and climate change. In light of the numerous hypotheses regarding latitudinal differences in life history and golden-winged warbler population decline, our objective in this study was to compare demographic data from northern and southern extremes of this species range where we would expect to detect differences in life history strategies if any exist. We compared two multi-year demographic datasets for the golden-winged warbler, one from the Cumberland Mountains of Tennessee and the other from the Canadian Shield of Ontario. Specifically, we compared minimum estimates of annual adult survival rates, daily nest survival rates (DSR), population growth rates (lambda), and mean time to extinction from a stochastic simulation for both populations. Tennessee nest survival decreased as the daily minimum temperature increased over the nesting season, but the constant survival model was equally supported (model averaged DSR = 0.972 [0.01 SE]). Ontario nest survival also decreased with time throughout the nesting season, but not as a function of daily minimum temperature (model averaged DSR = 0.956 [0.02 SE]). Both Tennessee and Ontario adult survival differed for males and females (Tennessee male =

0.616 [0.11 SE], Tennessee female = 0.427 [0.12 SE], Ontario male = 0.618 [0.08 SE], and Ontario female = 0.477 [0.14 SE]). Lambda estimates from a two-stage Leslie matrix suggested that both populations were declining sharply ($\lambda = 0.756$ and 0.787 for Tennessee and Ontario, respectively) and project extirpation within the next 20-30 years without immigration. Adult survival and fecundity were similar for the two populations, such that predictions based on the theory of life history variation with latitude were not supported by our data. Minimum annual adult female survival estimates appear to be insufficient to sustain populations of golden-winged warblers. Increased knowledge of wintering ground ecology and demographics is critically needed to further our understanding of whether/how survival is limiting golden-winged warbler populations.

## Introduction

Latitudinal variation in species life history traits has been a phenomenon of interest in ecology for decades. Few studies consider such latitudinal differences for migratory songbirds, except in relation to clutch size. However, many of the same hypotheses for latitudinal differences in clutch size apply to other life history parameters. Organisms must balance reproduction and survival according to geographic differences in selective pressures. Indeed, annual fecundity and adult survival are often inversely related for birds (Martin 1995).

There are three main hypotheses for latitudinal variation in clutch size, which may also apply to other components of fecundity. Lack (1947) assumed food was limiting and hypothesized that increased day length at higher latitudes during the breeding season allowed more foraging time by parents and consequently larger clutches. Lack's hypothesis depends on latitudinal differences in seasonality and the associated availability of food. Higher latitudes have more marked seasonality and a stronger food pulse; as a result, these populations are often kept below carrying capacity (K) and are therefore selected to have a greater reproductive rate (i.e., a larger clutch). In contrast, populations at lower latitudes have a more stable environment with population size maintained closer to K, resulting in selection for adaptations promoting increased survival.

A second hypothesis states that food is most limiting during the non-breeding season, and this is most extreme in northern latitudes (Ashmole 1961). The result is lower overall densities and therefore less competition allowing for larger clutch sizes during the breeding season. While this mechanism cannot apply to Neotropical migratory species, the idea that factors outside the breeding season (i.e., during migration or the non-breeding season) may affect reproduction during the breeding season is becoming better understood for Nearctic-Neotropical migrant songbirds (Marra et al. 1998, Sillett et al. 2000, Bearhop et al 2004, Webster and Marra 2005, Newton 2006). For example, migration distance and the timing of molt (Hemborg et. al. 2001, O'Hara et. al. 2002, Hall and Tullberg 2004), as well as wintering ground habitat quality (Marra et al. 1998), can affect adult survival and arrival time on the breeding grounds, which in turn may affect reproduction (Smith and Moore 2005).

Lastly, Skutch (1949) considered nest predation the driving selective force behind latitudinal clutch size variation. Although his research focused on tropical species, he postulated that increased clutch sizes led to more parental visits to the nest that made it more obvious to predators, such that smaller clutch sizes were adaptive where predation rates were greater. Martin (1995) also provided evidence that nest predation is more correlated with fecundity and adult survival than is food limitation.

Cody (1966) hybridized the above two hypotheses of Lack and Skutch to consider the combined effects of environmental stability and predation rates. Indeed, it is a combination of factors that likely drives life history variation both within and between species. Because multiple factors affect the balance between survival and reproduction for any given species in a particular geographic location, evidence is contradictory and few generalizations have emerged. Notwithstanding the absence of consistent rules, life history studies continue to contribute to our understanding of species' adaptation and evolutionary theory.

In addition to contributing to ecological theory, an understanding of geographic variation in demography can provide a framework within which to focus conservation efforts for declining species. Many Nearctic-Neotropical migrant songbirds that breed in the eastern United States have large breeding ranges that extend from the southeastern United States into southeastern Canada. Some of these same species are experiencing population declines throughout their breeding range. Although the causes of the declines may vary geographically, conservation efforts are typically applied uniformly, range-wide. For these widely-distributed species, comparisons of demographics and limiting factors across the range provide an important basis for effective conservation. If northern breeding populations are in fact limited more by adult survival than fecundity compared to southern populations, conservation efforts would need to be focused to address region-specific limiting factors.

The golden-winged warbler (*Vermivora chrysoptera*) is a Nearctic-Neotropical migratory songbird that uses early successional habitat and is experiencing steep population declines throughout its breeding range (Sauer et al. 2005). Causes of decline may vary geographically, and are mostly related to two factors: (1) hybridization and competition with blue-winged warblers (*Vermivora pinus*) and (2) habitat loss associated with maturing forests and human development (Confer 1992, Buehler et al. In Press). Habitat loss is suggested to be the major cause of decline in the southern Appalachian portions of the golden-winged range (Buehler et al. In Press), where there is almost complete altitudinal separation from blue-winged warblers, which currently occupy relatively lower-elevation habitats. Hybridization is a bigger concern in the midwestern and northeastern United States and southern Canada, in addition to concerns about habitat loss.

There has been a general northward shift in the golden-winged breeding range over the last several decades (Hitch and Leberg 2007) that has been attributed to hybridization and competition with the expanding blue-winged warbler (Gill 1980). Another hypothesis for this northward range shift is global warming (Root et al. 2003, Matthews et al. 2004, Watkinson et al. 2004); the southern-most "remnant" populations of golden-wingeds are limited to high-elevation sites in the southern Appalachian Mountains. Although climate change could be a process driving the general northward shift, a loss of habitat in southern portions of the range cannot be ignored. Evidence that climate change is not the sole factor associated with the golden-winged warbler's northward shift is that prescribed fire management to increase habitat availability have been effective at increasing local populations in Georgia and Tennessee (Klaus 2004, L. Bulluck, personal observation).

To test hypotheses related to geographic variation in life history strategies and to identify limiting factors for conservation that may vary geographically, we compared two multi-year demographic datasets for the golden-winged warbler; one from the Cumberland Mountains of Tennessee (36° latitude) and the other from the Canadian Shield of southern Ontario (44° latitude). Specifically, we compared minimum annual survival estimates, daily nest survival rates, lambda estimates (an estimate of the finite rate of population growth), and mean time to extinction from a stochastic simulation for both populations. We hypothesized that the northern population in Ontario would have greater fecundity (i.e., clutch size, young per successful nest, and nesting success) than the Tennessee population based on hypotheses of increased predation (Skutch 1949) and a weaker food pulse at southern latitudes (Lack 1947). Additionally, we hypothesized that the southern population in Tennessee would have a greater annual survival rate because of a shorter migration distance.

## Methods

### *Study area Tennessee*

The Cumberland Mountains compose the southwestern portion of the Appalachian Mountains. The mean elevation is 580 m and the highest ridges reach 1,075 m. More than 50,500 ha of this landscape is publicly owned by the Tennessee Wildlife Resources Agency (TWRA); our study sites are located within the Sundquist Forest Wildlife Management Area. The predominant landcover of the region is mixed-mesophytic forest, and approximately 15% is in early stages of succession because of the surface mining of coal and timber harvests (Bulluck and Buehler, unpublished data). In this region, golden-winged warblers occupy reclaimed and abandoned coal surface mines, and sites after timber harvests (5-15 years post-harvest) until the herbaceous vegetation is lost because of succession.

This study was conducted on four reclaimed coal surface mines; two were reclaimed approximately 15 years before the study and the other two were reclaimed approximately 20-25 years before the study (Table 4.1). Mine reclamation on these sites typically involved planting a thick herbaceous layer of grasses and forbs to prevent soil erosion as well as black locust (*Robinia pseudoacacia*) saplings. Since reclamation, maples (*Acer* spp.), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), and thickets of blackberry (*Rubus* spp.) have become established. Periodic arson fires have maintained the thick herbaceous cover and created numerous snags in all sites. All study sites were at approximately the same elevation (mean = 850 m, range = 770-950 m). We selected these sites based on the relatively high concentration of breeding golden-winged pairs per site to efficiently focus our daily nest searching and monitoring efforts. Fewer than 10 pairs per site occur on most other known occupied sites in the region (L. Bulluck unpubl. data) and access was difficult to many potential sites because of poor roads and rugged terrain.

The Cumberland Mountains region is located near the southern extreme of the golden-winged warbler range (Figure 4.1). We estimated the Cumberland Mountains golden-winged warbler population to be approximately 369 (± 122) breeding pairs (Bulluck and Buehler, unpublished data). The four sites in this study supported approximately 85 breeding pairs, or 17-34% of the region's population (Table 4.1).

### ***Study area Ontario***

All Ontario study sites were in the area surrounding the Queen's University Biological Station (QUBS), near Chaffey's Lock, Ontario, Canada, ($44^0$30'N: $76^0$23'W) with a total area of > 2,000 hectares. This landscape was a patchy matrix of mature closed-canopy second-growth deciduous forest, interspersed with active and abandoned agricultural fields in varying stages of succession along with numerous small lakes and swamps. The southeastern extension of the Canadian Shield, known as the Frontenac Axis, creates the dominant geological feature of the area. The area is primarily comprised of rolling terrain with ridges of granite outcrops alternating with valleys every 500 m. Forests in the area are dominated by sugar maple (*Acer saccharum*), with other canopy species including American basswood (*Tilia heterophylla*), white ash (*Fraxinus americana*), bitternut hickory (*Carya aquatica*), shagbark hickory (*Carya ovata*), American elm (*Ulmus americana*), paper birch (*Betula papyrifera*), white oak (*Quercus alba*), and red oak (*Quercus rubra*). Understory tree species include ironwood (*Ostrya virginiana*) and blue beech (*Carpinus caroliniana*).

Most openings in the forest resulted from past anthropogenic land clearing however, natural clearings created by exposed bedrock outcrops and beaver ponds were also common. Species first colonizing abandoned fields and clearings in the area include common prickly ash (*Zanthoxylum americanum*), American elm, blue beech, gray dogwood (*Cornus racemosa*) and red raspberry (*Rubus ideus*; Demmons and Robertson, unpublished data). Abandoned agricultural fields of various sizes and successional stages can be found throughout this area, as well as numerous active agricultural fields, mostly hay fields. Study sites occupied by golden-winged warblers were chosen opportunistically throughout this landscape matrix – dictated by the patchy distribution of the species – and were primarily clustered in areas with accessible roads. These clusters of golden-winged warblers typically contained between 5 and 10 breeding pairs, but many isolated pairs (where habitat availability limited settlement to one pair) were also included in the study.

In addition to latitude, other factors differ between the Tennessee and Ontario study sites. The Tennessee sites are located within a mountainous region with extensive topographic relief whereas the Ontario study sites are located within a relatively flat region with gently rolling hills. The landcover in these two regions is also somewhat different. The Cumberland Mountains region is extensively forested with patches of early successional habitats from predominantly anthropogenic disturbances (mining and timber harvesting), whereas the Ontario landscape is less forested and the successional areas are a mixture of natural and anthropogenic disturbance (rock outcrops, wetlands and agriculture). These additional differences (beyond latitude) may influence the general demography of these two populations and should be considered when interpreting our results.

### ***Field methods***

From 20 April to 30 June 2003-2006 in Tennessee and from 1 May to 15 July 2001-2006 in Ontario, we visited each site every 2-3 d from sunrise (~0600 h) to mid afternoon. We spent the early morning hours (until 1000 h) observing behavior, mapping territories (2005 and 2006 only), and locating nests. To locate golden-winged warbler nests, we carefully observed male and female behavior, especially during nest building and nestling periods when visits to the nests were frequent. We located nests opportunistically during the laying and incubation periods while systematically walking through territories and while mapping male territory boundaries. In both Tennessee and Ontario, we found the majority of nests (~70%) during the nest-building stage.

We monitored all nests every 2-4 d until the nestlings fledged or the nest failed because of predation or some other event (i.e., abandonment or trampling by ungulates).

The golden-winged nesting cycle typically spans 25 d. The egg laying stage is 4 d; the average clutch size is 5 and incubation begins when the final egg is laid. Incubation is typically 10-11 d and the nestling stage is typically 9-10 d (Ehrlich et al. 1988, Confer 1992). If the exact age of a nest was known and the female's presence could be determined from a distance, we opted to not flush the female during incubation or brooding nest visits to minimize observer impacts on nest survival. Furthermore, vegetation was always moved with a natural object (e.g., a stick) rather than the observer's hands if necessary to observe nest contents and minimize nest disturbance.

During the late morning and early afternoons, we banded and color-marked adult male and female golden-winged warblers to allow for individual identification. We used target mist-netting techniques to capture and band adult males by erecting a mist net in an area surrounded by dense vegetation near the center of an active male territory. We then placed a decoy male golden-winged in a small tree or shrub near the net and played a male's type I and type II song (Highsmith 1989) to elicit an aggressive response by the territorial male. This method was effective for capturing territorial males, but our success was variable depending on the time of season, the nesting stage, and the male's pairing status. In general, we were successful at capturing ~60% of the males we attempted. To capture adult females, we flushed them into a mist net placed near the nest while the female was incubating eggs or, less commonly, while brooding young. We did not attempt to flush females from the nest until after at least 5 d of incubation to decrease chances of nest abandonment. Color-marked adult male and female golden-wingeds were re-sighted each year using binoculars during nest searching, territory mapping, and systematic surveys of all sites.

### ***Data analyses***

#### Nest survival

We first tested whether daily nest survival rates were different for the Ontario and Tennessee populations by combining the two datasets and modeling the effects of region, year, and time throughout the nesting season (linear time trend model). We then modeled the relationship between daily nest survival rate (DSR) and several variables based on a priori hypotheses for each population separately to obtain estimates of daily nest survival to use in regional calculations of fecundity. We used Akaike's Information Criterion ($AIC_c$) adjusted for small sample size for model selection (Burnham and Anderson 2002) in all analyses. For each population, we modeled daily nest survival as a function of year, daily precipitation, minimum daily temperature, time of season (both linear and quadratic models), nest age, nest stage, in addition to a global model containing all variables and a null model containing the intercept only (constant survival).

We expected annual variation in nest survival because of changes in regional weather patterns and/or annual fluctuations in predator abundance. For the Tennessee population, we had sufficient sample sizes to model nest survival in 2004 – 2006; for the Ontario population, we had sufficient data for 2003 – 2006. We hypothesized that temperature and/or precipitation could impact daily nest survival rate by forcing the female to incubate or brood less often, as has been demonstrated in previous studies for other species (Siikamaki 1996, Radford et al. 2001, but see Chase 2002). We obtained temperature and precipitation data from the National Oceanic and Atmospheric Association (NOAA) Climatic Data Center (station # 723246 KOQT Oak Ridge) for Tennessee and directly from a weather station located on the Queens University Biological Station (QUBS) for Ontario.

We used the nest survival module in Program MARK (White and Burnham 1999, Rotella et al. 2004) to run the above nest survival models and to obtain estimates of daily nest survival for both populations. With the logit link, daily survival rate of a nest on day *i* is modeled as:

$$DSR = \frac{\exp(\beta_0 + \sum_j \beta_j x_{ji})}{(1 + \exp \sum_j \beta_j x_{ji})}$$

where the $X_{ji}$ ($j$ = 1,2,…..,J) are values for $j$ covariates on the day $i$ and the $\beta_j$ are coefficients to be estimated from the data (Rotella et al. 2004). We assumed a 25-d nesting cycle for golden-winged warblers with 4 d for laying, 11 d for incubation and 10 d for brooding. Data structure and entry followed those of Dinsmore et al. (2002). As suggested by Dinsmore et al. (2002) and Rotella (2006), we did not standardize individual covariates.

## Adult survival

We first tested whether annual adult survival rate ($\Phi$) and recapture/re-sighting probabilities ($p$) were different for the Ontario and Tennessee populations by combining the two datasets and modeling the effects of region, year, and sex on these two parameters with the Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990, Lebreton et al. 1992) using Program MARK (White and Burnham 1999). We then modeled adult golden-winged warbler survival and recapture/re-sighting probabilities separately for each population to obtain survival estimates for each. We chose the set of candidate models a priori based on our knowledge of the species and the limitations of our data. For example, we were unable to assess differences in survival between hatch-year and after hatch-year birds because too few birds returned as second-year birds after being banded as nestlings in the previous breeding season (<10% in Tennessee and Ontario despite marking >100 nestlings each year). Likewise, we could not test for differences in survival between hybrids and phenotypically pure golden-wingeds because hybrids were rare in both populations. Model selection was based on $AIC_c$ (Burnham and Anderson 2002). We modeled $\Phi$ and $p$ as a function of sex, year, and sex*year interactions for both Tennessee and Ontario populations.

Differences in annual male and female survival were expected based on results from previous studies on other species (Liker and Szekely 2005). Similarly, annual variability in survival was expected because of weather events or annual fluctuations in food availability on the breeding and/or wintering grounds as well as during migration. Ideally, there were no difference in re-sighting probability between years indicating consistent field crew effort and no annual changes in bird behavior. However, differences in re-sighting probability were expected between males and females because of the inconspicuous behaviors associated with breeding females compared with males. To obtain final point estimates (and standard errors) for $\Phi$ and $p$, we used model averaging (Burnham and Anderson 2002) in Program MARK.

To determine if there was significant over-dispersion, we assessed model goodness of fit for our most parameterized model for each population using the median c-hat approach in Program MARK. Median c-hat estimates for the Ontario and Tennessee populations were 1.07 and 0.98, respectively, which were acceptable values that suggested good model fit (Lebreton et al. 1992).

### Population projections

We used the model-averaged estimates for adult female survival and daily nest survival rates to develop a single sex, two-stage Leslie population projection matrix. We assumed hatch-year female survival to be 50% of after hatch-year survival (Temple and Cary 1988, Donovan et al. 1995). We used PopTools (Hood 2006) to estimate lambda ($\lambda$), the finite rate of population growth, for both the Tennessee and Ontario populations. To calculate fecundity, we used the following equation:

$$F = C + (0.5)*(2p - p^2)$$

where C is the mean clutch size, 0.5 is the sex ratio, and p is the apparent nest success rate ($DSR^{25}$) where 25 is the number of days in the nesting cycle. The $2p-p^2$ term accounts for one re-nesting attempt after a failed nest (Giocomo 2005), which occurs often in golden-wingeds (Bulluck and Vallender, personal observation).

We also used PopTools to perform a stochastic population projection over 50 years for each population using Monte Carlo simulation. We performed 100 stochastic simulations to estimate population size. For each simulation, to obtain values of fecundity, we randomly sampled from a normal distribution and to obtain values of adult female survival, we randomly sampled from a beta distribution to ensure parameter values between 0.0 and 1.0. The mean and standard deviation of these distributions were based on our model-averaged estimates of nest survival and adult survival as well as our estimates of temporal process variance on adult survival. Total variance estimates for population parameters were comprised of both process and sampling variance; it is important to separate process from sampling variance when projecting population size over time (White 2000). We estimated temporal process variance using the variance components procedure in Program MARK (White et al. 2002). For both the Tennessee and Ontario populations, we used 500 breeding pairs as the starting population size in our simulations. Our estimate of the Cumberland Mountains golden-winged population was ~400 breeding pairs, but there are ≥ 100 other pairs that occur near our study area in both Tennessee and Kentucky that likely disperse into the focal population. No population estimate currently exists for the Ontario population because there have been no official surveys of the region, and BBS routes do not adequately cover the region. Approximately 200 breeding pairs occur within the Queens Biological Station, but the surrounding landscape is equally suitable and is occupied extensively by golden-wingeds.

## Results

For the Tennessee population, we monitored 102 golden-winged warbler nests during the 2004-2006 breeding seasons for a total of 1,613 exposure days across a 55-d nesting season. For the Ontario population, we monitored 86 golden-winged warbler nests during the 2003-2006 breeding seasons for a total of 1,234 exposure days across a 50-day nesting season. The raw nest success (number of successful nests/total number of nests*100) was 58.8% for the Tennessee population across the three years and 55.2% for the Ontario population. No evidence of double-brooding was observed in either population, but pairs were observed re-nesting if their first nest failed early in the season. Occasionally, female golden-wingeds disappeared after a predation event and we assumed they experienced mortality along with the clutch. The mean age of nests when found was 5.6 d (SE = 0.66) in Tennessee and 4.9 d (SE = 0.56) in Ontario. Mean clutch size for the Ontario population (4.95) was larger than the Tennessee population (4.30) ($t = 4.57$, $P < 0.001$). Likewise, the mean number of young fledged per successful nest in Ontario (4.84) was larger than in Tennessee (4.06) ($t = 3.87$, $P < 0.001$) (Table 4.2).

In Tennessee, we color-marked between 21 and 35 males per year between 2003 and 2005, respectively, and we marked 23 and 27 females in 2004 and 2005, respectively (Table 4.3). In Ontario, we color-marked between 22 and 45 males per year from 2001 to 2005 and between 15 and 33 females during these same years (Table 4.3). We did not explicitly measure pairing success in either study area, but we documented female activity on the majority of territories.

### *Nest survival*

When we combined the nest survival data for both populations, the linear time trend model was most supported (Table 4.4, $AIC_c$ weight = 0.55). The second most supported model was an additive model with linear time trend and region effect ($AIC_c$ weight = 0.34, $\Delta AIC_c = 0.94$). The evidence that golden-winged warbler nest survival varies between these two populations is limited; specifically, Ontario daily nest survival rates decrease throughout the nesting season at a slightly faster rate than Tennessee daily nest survival rates, but the confidence intervals for the DSR overlap considerably (Figure 4.2). All other models, including the global and null models, had $\Delta AIC_c$ values > 4 indicating that they had little support, given the data and the model suite considered (Table 4.4).

For the Tennessee population, the constant survival model was the most supported ($AIC_c$ weight = 0.21), indicating that golden-winged warbler daily nest survival may not vary significantly as a function of the modeled parameters. However, several other models (minimum temperature, year, daily precipitation, and linear and quadratic time) had $\Delta AIC_c$ values < 2, providing some evidence for nest survival variation with parameters of interest (Table 4.5). Our model selection results therefore provided limited evidence that daily nest survival rates decreased as daily minimum temperature increased (Figure 4.3a) and decreased over time in both a linear (Figure 4.3b) and quadratic manner (Figure 4.3c). Additionally, daily nest survival rates differed among years in Tennessee, however the 95% CI on the real parameter estimates overlapped considerably and the 95% CI for the year effect beta coefficients included zero. Daily nest survival rates in Tennessee also appeared to decrease slightly with daily precipitation (Figure 4.3d). Although these relationships may exist, the 95% confidence intervals for the parameter estimates for all covariates included zero and the constant survival model still performed best. The model-averaged estimate for golden-winged warbler daily nest survival rate in Tennessee was 0.9717 (SE = 0.011) and the overall nest success was 48.8%.

For the Ontario population, the linear time model had the most support given the data (AIC$_c$ weight = 0.64), with daily nest survival decreasing over time (Figure 4.4). The parameter estimate from the linear time model was $\hat{\beta}$ = -0.056 (95% CL = -0.086 to -0.025). The quadratic time model also had some support (AIC$_c$ weight = 0.24, $\Delta$AIC$_c$ = 2.01), but all remaining models had $\Delta$AIC$_c$ values > 5 (Table 4.5), indicating less support given the data (Burnham and Anderson 2002). The model-averaged estimate for golden-winged warbler daily nest survival rate in Ontario was 0.9564 (SE = 0.019) and the overall nest success was 32.8%.

### *Adult survival*

When we combined the adult survival data for both populations, the most supported models suggested that year and sex affect adult survival and re-sighting rate; no models with a region effect were supported (Table 4.6). The most supported model indicated a sex by year interaction effect on adult survival and a year effect on re-sighting rate (AIC$_c$ weight = 0.48) and the second most supported model suggested a year effect on survival and a sex by time interaction on re-sighting rate (AIC$_c$ weight = 0.21).

For the Tennessee population analyzed separately, the two most supported models indicated annual differences in male and female survival and recapture rate (Table 4.7). The most supported model provided evidence for annual differences in survival in addition to an interaction effect of sex and year on re-sighting rates (AIC$_c$ weight = 0.47); the second most supported model contained an interaction effect of year and sex on survival and annual differences in recapture rate (AIC$_c$ weight = 0.30). All other models had $\Delta$AIC$_c$ values > 2.8. The model-averaged estimates of Tennessee male and female apparent survival were 0.616 (SE = 0.111) and 0.427 (SE = 0.122), respectively. The model-averaged estimates of Tennessee male and female re-sighting rates were 0.846 (SE = 0.096) and 0.623 (SE = 0.283), respectively (Table 4.2). Temporal process variance for males and females was 0.0261 (95% CI: -0.0019 to 0.1.612).

For the Ontario population, no single model emerged as the best for adult survival. The top two models shared equal weight and the top five models all had $\Delta$AIC$_c$

values < 2 (Table 4.7), indicating these models all had some support (Burnham and Anderson 2002). The most supported model indicated annual differences in male and female survival and annual differences in re-sighting rate (Table 4.7, AIC$_c$ weight = 0.29). The second-most supported model provided evidence for differences in male and female survival, with re-sighting rates being constant between these two groups and with no annual differences in either parameter (AIC weight = 0.24). The top five models had variations of sex and year effects on adult survival (Table 4.7). The model-averaged estimates of Ontario male and female survival were 0.618 (SE = 0.084) and 0.477 (SE = 0.144), respectively. The model-averaged estimates of Ontario male and female re-sighting rates were 0.750 (SE = 0.085) and 0.664 (SE = 0.164), respectively (Table 4.2). Temporal process variance for males and females was 0.0160 (95% CI: 0.0034 to 0.0897).

### ***Population projections***

We estimated lambda for the Tennessee population as 0.7625 (95% CI: 0.497 to 1.03) and for the Ontario population as 0.8008 (95% CI: 0.506 to 1.10), suggesting that both populations were declining unless mortality and dispersal were being offset by immigration. For both the Tennessee and Ontario populations, after-second-year (ASY) survival had the greater elasticity values, but all four matrix elements had relatively similar values (Table 4.7). For both populations, second-year survival had the greatest sensitivity value, followed by ASY survival and second-year fecundity (Table 4.7). Overall, Tennessee and Ontario golden-wingeds appeared to have similar fecundity and annual survival estimates (Table 4.7). However, the Tennessee model-averaged daily nest survival rate and nest success rate appeared to be greater than that in Ontario (Table 4.2). The expected mean time to extinction based on Monte Carlo stochastic simulation was 22 years for the Tennessee population and 28 years for the Ontario population and the probability that both populations will fall below 25 breeding pairs increases steeply after five years (Figure 4.5).

## Discussion

Our predictions regarding demographic differences between Ontario and Tennessee golden-winged warbler populations were not supported. Despite the fact that the Tennessee and Ontario golden-winged warbler populations are located at the southern and northern extremes of this species range, respectively, we found very little difference in their basic demographics. Annual adult survival rates did not differ between the two populations (Table 4.4) and daily nest survival decreases over time within the nesting season for both populations with Ontario's possibly decreasing at a faster rate (Figure 4.2). One reason for the overall similarities between these two populations may be that the latitudes between these two locations were not significantly different enough to manifest any real biological differences in demography. Southern Ontario and northeastern Tennessee are separated by approximately 8 degrees of latitude (~1,000 km). However, other studies have found differences between populations occurring in similar latitudinal differences (Sanz 1998, Pearce et al. 2005, Cooper et al. 2006). Another explanation for the lack of a difference is that golden-wingeds occupy higher elevations in the southern extremes of their range (~400-500 m higher), and a 300-m rise in elevation is roughly equivalent to four to five degrees of latitude. Thus ecological differences between the two study sites might have been reduced because of the elevational differences; elevation and latitude have similar effects on avian life history traits (Sanz 1998, Fargallo 2004).

### *Nest survival*

Our prediction that the Ontario golden-winged warbler population would have a greater reproductive rate and greater nest survival than the Tennessee population was not supported. Our prediction was based on the hypotheses regarding the effects of predation (Skutch 1949) and food limitation (Lack 1947) on clutch size. While both the mean clutch size and young fledged per successful nest were significantly greater in Ontario, Tennessee daily nest survival rates, and therefore fecundity estimates, were somewhat greater than those in Ontario (Table 4.2). In both populations, the majority of nest failures were attributable to predation (>95%) as opposed other factors (e.g., weather or inadvertent trampling by deer or elk). In studies of numerous bird species, Ricklefs (1969) and Kulesza (1990) both demonstrated that predation rates decrease with increasing latitude, but our results do not seem to support this.

Despite the fact that the constant survival model was most supported, our model results provide some support for the fact that Tennessee daily nest survival rates were negatively related to daily minimum temperature and time throughout the nesting season. Ontario nest survival also decreased throughout the nesting season (Figure 4.4), but not as a function of temperature. Small mammals and snakes are very abundant on our study sites because of the dense cover of herbaceous vegetation, and snakes do not typically become active until later in the season (Stake et al. 2005, Bulluck and Vallender, personal observation), when temperatures are greater and more food is potentially available. Small mammals (Soderstrom et al. 1998) and snakes (Thompson and Burhans 2003, Weatherhead and Bloun-Demers 2004) make up the dominant nest predator community for ground-nesting birds such as golden-winged warblers. Our data suggest that daily nest survival rates decreased over time and as a function of minimum daily temperature in Tennessee; temporal variation in predation pressure may be the mechanism that drives this relationship.

### ***Adult survival***

Our prediction that the Tennessee population would have a greater adult survival rate because of a shorter migration distance was also not supported; Tennessee and Ontario male and female adult survival rates did not differ (Table 4.6). Accurate estimates of apparent survival are very important for understanding population dynamics and choosing the best strategy for maintaining populations of conservation concern (Knutson et al. 2006). However, survival estimates are rare as they require abundant resources of time and money to obtain. Furthermore, several confounding factors must be considered, including dispersal and lack of site fidelity (Marshall et al. 2004). A recent study of yellow warblers (*Dendroica petechia*) along a river corridor in Montana demonstrated that adult survival probabilities increased 6-22% when emigration was considered and that these dispersers typically moved less than 300 m from their original location (Cilimburg et al. 2002). Because our study sites were discrete patches and not a continuous river corridor, dispersal distances and frequencies were likely different for golden-winged warblers. We surveyed an additional 40 sites within 20 km of the focal study sites with potentially suitable habitat during 2005 and 2006 in Tennessee and recorded the location of all golden-winged males and whether or not they were banded. During these surveys, we documented very few dispersal events (n = 2 in 2005, n = 5 in 2006), and all were juvenile dispersals; if these were all of the dispersal events, our adult survival estimates would not have been affected. A small number of adult dispersal events were also recorded between core study sites (n = 1-3 individuals per year); overall site fidelity was very high. Separating dispersal from mortality is very difficult, especially when permanent emigration is known to occur, such that apparent survival rates underestimate true survival (Marshall et al 2004, Anders and Marshall 2005). This is especially true for females and returning juveniles because their site fidelity may be lower (Greenwood and Harvey 1982, Drilling and Thompson 1988, Clark et al. 1997, Hansson et al. 2002, Sillett and Holmes 2002); however, research has also demonstrated that these individuals may indeed have higher annual mortality (Woodrey and Moore 1997, Woodrey 2000, Marra and Holmes 2001, Latta and Faaborg 2002).

Apparent annual survival estimates for migratory songbirds encompass survival not only on the breeding grounds but also on the wintering grounds and throughout migration. Factors on the wintering grounds, where these birds spend ≥50% of their annual life cycle, likely affect annual survival rates. Our knowledge of golden-winged warbler non-breeding biology is very limited. The winter distribution of golden-wingeds is generally reported as being from northern Columbia to Guatemala (Confer 1992). Golden-wingeds occupy mid to high elevation woodlands and a variety of early successional habitats such as forest borders or gaps on the wintering grounds (Stiles and Skutch 1989). Beyond this, however, knowledge about wintering ecology is lacking. A recent study of American redstarts (*Setophago ruticilla*) during the non-breeding season documented differential habitat use by both age and gender (Marra 2000). Specifically, adult males occupied the highest-quality sites and young males and females occupied lower-quality sites (Marra 2000, Marra and Holmes 2001). Such studies would be extremely beneficial for golden-winged warblers throughout the winter range to determine if factors such as availability of high-quality habitat may be limiting populations and directly affecting adult annual survival rates. It is possible to estimate within-season survival rates to separate breeding from non-breeding survival rates, but we did not formally do this. Rather than allocating our daily field time to systematic surveys of each site required to estimate within-season survival, we focused on finding nests and mapping territories. However, we spent a great deal of time with most territorial males throughout the breeding season and noted very few individuals that disappeared (i.e., experienced a mortality event). In fact, all disappearances occurred early in the season and presumably were caused by competitive exclusion by another more dominant male. Studies on other warbler species have estimated very high *within* the breeding season adult survival (0.99 ±0.01, Sillett and Holmes 2002, 0.98 ±0.01, Jones et al. 2004); 85% of mortality events in black-throated blue warblers (*Dendroica caerulescens)* occurred during migration (Sillett and Holmes 2002).

Our results indicate that annual adult survival of golden-wingeds in Ontario and Tennessee are similar. This suggests that migration distance does not influence annual survival rates or that the migration distances for these two populations do not differ. We do not know the migration pattern of this species; golden-winged warblers may display a leapfrog migration pattern (Bell 1997) with northern breeders flying to Columbia and southern-breeders flying to northern Central America such that the Ontario population has a significantly longer migration distance. This pattern is fairly common among Neotropical migrants (Bell 1997, Kelly et al. 2002), but other patterns are possible, such that the Ontario and Tennessee populations may have similar migration distances. Until the migration pattern of golden-wingeds is known, we cannot determine if migration distance is directly affecting adult survival in the northern and southern extremes of their range. Similarly, we need to determine if golden-wingeds display migratory connectedness between the winter and summer distributions, as this may affect meta-population dynamics (Esler 2000). Migratory connectedness refers to the degree to which populations on the breeding grounds occupy the same regions during the non-breeding season (Webster et al. 2002). High connectedness would occur if, for example, all Ontario-breeding golden-winged warblers spent the non-breeding season in Columbia, whereas all Tennessee-breeding golden-winged warblers spent the non-breeding season in Costa Rica and Nicaragua. Low connectivity, on the other hand, would occur if Ontario and Tennessee-breeding golden-wingeds occupied a large portion of non-breeding season range with extensive overlap. Isotope studies are needed to establish these relationships. Knowledge of the level of connectedness and the degree of habitat destruction throughout the wintering range will lead to a better understanding of how winter habitat availability may be limiting golden-winged populations.

### ***Population projections***

Our estimates of lambda for both Ontario and Tennessee golden-wingeds (Table 4.2) suggested that these populations are declining at a rate of 20% and 24% per year, respectively. Breeding Bird Survey (BBS) data show these populations to be declining, but to a much lesser degree (Sauer et al. 2005). From 2000 to 2005, there were too few BBS routes with golden-winged occurrences in Tennessee to get a trend estimate, but golden-winged populations have declined 6.7% from 1966 to 2005 in Tennessee ($n = 5$ BBS routes, $P = 0.32$). Likewise, from 2000 to 2005, Ontario golden-winged populations have declined 12.9% ($n = 11$ BBS routes, $P = 0.06$). Our population data for the core study sites in Tennessee over the past 4 years also did not indicate a 25% annual decline; the number of breeding pairs on most sites remained stable. Our study sites represent high-quality habitat that likely receive immigrants on a regular basis. In fact, many un-banded individuals arrived on our sites each breeding season. We are unsure where these immigrants are dispersing from, but they are likely either juvenile dispersers hatched in the same region or individuals from nearby populations. Our use of 500 breeding pairs as the starting population size in Ontario may not be realistic because we know that the landscape surrounding Queens University Biological Station (where there are ~200 breeding pairs) has suitable habitat and is occupied by golden-wingeds. Until we estimate the regional population better, these results should be interpreted with caution.

In addition to immigration, the inconsistency between our lambda estimates and the apparent stability of these populations may be because our adult survival estimates were underestimated as a result of low female site fidelity as described above. Permanent emigration is occurring, yet it appears to be at low levels. Tennessee adult female survival would need to be 0.565, with known fecundity, to achieve a stable population ($\lambda = 1$). This is a difference of 0.14 or a 32.3% underestimate. Likewise, Ontario adult female survival would need to be 0.607, a difference of 0.13 or a 27.3% underestimate. Although such differences seem large, Marshall et al. (2004) demonstrated true survival for Prothonotary warblers (*Protonotaria citrrea*) was underestimated by 0.17 for males and 0.19 for females had dispersal events not been detected. The probability of dispersal and dispersal distance, therefore, are important demographic parameters that must be estimated explicitly for these populations if we are to obtain unbiased estimates of true survival. While we did not estimate the probability of dispersal explicitly, we did search potentially suitable habitat within a large area and found very little evidence of dispersal.

### ***Study implications***

The lack of significant differences in golden-winged warbler demographics at the northern and southern extremes of its breeding range has ecological and conservation implications. No studies to our knowledge have assessed latitudinal differences in intra-specific demography for a Neotropical migratory songbird. Our results suggest that differences may not exist (or may not be detectable) for these birds when studied only on the breeding grounds, especially annual adult survival rates. Factors throughout the entire annual life cycle affect these species demographically, and it appears that these factors may be similar for birds breeding in Ontario and Tennessee. Our results suggest that limiting factors on the wintering grounds are similar for Tennessee- and Ontario-breeding golden-wingeds and/or that migratory connectedness is weak; future studies of migratory connectedness are essential if we are to understand the demographic consequences of habitat loss on the wintering grounds (Rubenstein et al. 2002).

In contrast with annual adult survival, demographic differences in the breeding ecology of these two populations are not likely to be as affected by factors outside the breeding grounds (but see Marra et al. 1998 and Marra and Holmes 2001). We found significantly greater clutch sizes and number of young fledged per successful nest in the northern Ontario population that supports theoretical predictions. However, golden-winged nest success in Tennessee was greater than in Ontario, presumably because of differences in predation rates. In general though, daily nest survival rates differed only slightly among the two populations (Figure 4.2). Martin (1995) demonstrated in a multi-species meta-analysis that nest predation explains more variation in avian fecundity than food limitation. While we documented the majority of nest failures to be caused by predation, we did not explicitly assess the predator communities in the two study areas; such studies are needed for both populations.

Both the Ontario and Tennessee populations appear to be declining (based on our population projections and BBS data), and conservation strategies may need to be tailored for each region specifically. However, we did not find significant differences in annual adult survival or fecundity for the two populations suggesting that similar strategies in these two different regions may be sufficient, at least until we find differences in the nest predator community or migratory connectedness, for example. Annual adult survival is not typically affected by factors on the breeding grounds where monthly survival rates are >95% (Sillett and Holmes 2002, Jones et al. 2004). Likewise, our ability to influence daily nest survival rates may be currently limited by our knowledge of the predator communities and by the fact that golden-winged nest predation is a complex and dynamic process (Part 2). As a result, our best option for golden-winged conservation on the breeding grounds, considering the ephemeral nature of early successional shrublands, is the creation and maintenance of high-quality breeding habitat.

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# Appendix

**Table 4.1:** The size, number of total males, and male density of golden-winged warblers (*Vermivora chrysoptera*) found on each study site in the Cumberland Mountains of Tennessee, 2004-2006. The number of years since reclamation was estimated based on vegetation succession and federal documents from the Office of Surface Mining.

| **Site** | **Size (ha)** | **Total males** | **Male density** | **Years since reclamation** |
|---|---|---|---|---|
| Ash Log | 125 | 40 | 0.32 | ~15 |
| Burge | 50 | 17 | 0.34 | ~15 |
| Bootjack | 50 | 13 | 0.26 | ~25 |
| Fork | 40 | 13 | 0.33 | ~25 |
| Total | 265 | 83 | 0.30 | - |

**Table 4.2:** Summary of demographic information for the Tennessee and Ontario populations of golden-winged warblers (*Vermivora chrysoptera*) derived from field data and from data analyses. These data were used to develop a two stage Leslie Matrix. All values in parentheses are standard error values, except for the process variance and lambda estimates which are 95% confidence intervals.

| **Demographic parameter** | **Tennessee** | **Ontario** |
|---|---|---|
| Number of nests | 102 | 86 |
| Number of exposure days | 1613 | 1234 |
| Mean clutch size | 4.30 (0.09) | 4.95 (0.10) |
| Mean young fledged per successful nest | 4.06 (0.13) | 4.84 (0.15) |
| Fecundity ‡ | 1.57 | 1.35 |
| Daily nest survival rate (DSR) § | 0.9717 (0.011) | 0.9564 (0.019) |
| Nest success (DSR^25*100) | 48.8% | 32.8% |
| Raw nest success (number successful/total) | 58.8% | 55.2% |
| Adult male survival (Φ) § | 0.616 (0.111) | 0.618 (0.084) |
| Male recapture/re-sighting rate (p) § | 0.846 (0.096) | 0.750 (0.085) |
| Adult female survival (Φ) § | 0.427 (0.122) | 0.477 (0.144) |
| Female recapture/re-sighting rate (p) § | 0.623 (0.283) | 0.664 (0.164) |
| Process variance (temporal) – Φ | 0.0261<br>(-0.0019 – 1.612) | 0.0160<br>(0.0034 – 0.0897) |
| Lambda (λ) † | 0.7656<br>(0.497 – 1.03) | 0.8008<br>(0.506 – 1.10) |
| Years to extirpation † | 22 | 28 |

‡ Mean clutch size*sex ratio (0.5)*2p-p^2 where p = (DSR) ^25 and 2p-p^2 accounts for re-nesting after a failed clutch (Giocomo 2005)

§ Model averaged parameters estimates from Program MARK

† Parameter estimated using PopTools in Microsoft Excel (Hood 2006)

**Table 4.3:** Annual sample size for captured male and female golden-winged warblers (*Vermivora chrysoptera*) in the Tennessee (TN) and Ontario (ON) study sites by year.

| Year | TN Males | ON Males | TN Females | ON Females |
|---|---|---|---|---|
| 2001 | 0 | 45 | 0 | 16 |
| 2002 | 0 | 33 | 0 | 15 |
| 2003 | 21 | 55 | 1 | 33 |
| 2004 | 35 | 30 | 23 | 24 |
| 2005 | 35 | 22 | 27 | 19 |

**Table 4.4:** Summary of model selection results for golden-winged warbler (*Vermivora chrysoptera*) daily nest survival analyzed for Tennessee and Ontario data combined to assess regional effects. Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion ($AIC_c$), $AIC_c$ differences ($\Delta AIC_c$), and the relative likelihood of each model ($AIC_c$ model weights; $w_i$).

| **Model** | **K** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** |
|---|---|---|---|---|
| Linear time | 2 | 596.15 | 0.00 | 0.5491 |
| Linear time + region | 3 | 597.09 | 0.94 | 0.3429 |
| Linear time + year | 5 | 600.56 | 4.41 | 0.0605 |
| Linear time + region + year | 6 | 601.87 | 5.72 | 0.0315 |
| Null (intercept only) | 1 | 604.07 | 7.92 | 0.0105 |
| Region | 2 | 605.80 | 9.65 | 0.0044 |
| Year | 4 | 609.11 | 12.96 | 0.0008 |
| Region + year | 5 | 610.99 | 14.84 | 0.0003 |

**Table 4.5:** Summary of model selection results for golden-winged warbler (*Vermivora chrysoptera*) daily nest survival analyzed separately for the Cumberland Mountains of Tennessee, 2004-2006 and for the Canadian Shield in Ontario, 2003-2006. Columns provide model notation, the number of estimable parameters (K), second order Akaike Information Criterion (AIC$_c$), AIC$_c$ differences (ΔAIC$_c$), and the relative likelihood of each model (AIC$_c$ model weights; w$_i$).

| | **Model** | **K** | **AIC$_c$** | **ΔAIC$_c$** | **w$_i$** |
|---|---|---|---|---|---|
| **Tennessee** | Null (intercept only) | 1 | 318.35 | 0.00 | 0.2095 |
| | Minimum daily temperature | 2 | 318.43 | 0.09 | 0.2007 |
| | Linear time | 2 | 318.99 | 0.65 | 0.1516 |
| | Quadratic time | 3 | 319.52 | 1.17 | 0.1168 |
| | Year | 3 | 320.08 | 1.73 | 0.0883 |
| | Daily precipitation. | 2 | 320.10 | 1.76 | 0.0870 |
| | Nest age (linear) | 2 | 320.35 | 2.01 | 0.0769 |
| | Nest age (quadratic) | 3 | 321.93 | 3.59 | 0.0349 |
| | Nest stage | 3 | 321.99 | 3.65 | 0.0338 |
| | Global | 8 | 330.22 | 11.87 | 0.0006 |
| **Ontario** | Linear time | 2 | 277.03 | 0.00 | 0.6427 |
| | Quadratic time | 3 | 279.04 | 2.01 | 0.2354 |
| | Global | 8 | 282.32 | 5.29 | 0.0457 |
| | Year | 3 | 283.24 | 6.20 | 0.0289 |
| | Nest age (quadratic) | 3 | 284.27 | 7.24 | 0.0172 |
| | Daily precipitation | 2 | 284.70 | 7.67 | 0.0139 |
| | Nest age (linear) | 2 | 286.59 | 9.56 | 0.0054 |
| | Nest stage | 3 | 286.72 | 9.69 | 0.0050 |
| | Null (intercept only) | 1 | 287.40 | 10.37 | 0.0036 |
| | Minimum daily temperature | 2 | 288.40 | 11.37 | 0.0022 |

**Table 4.6:** Summary of model selection results for golden-winged warbler (*Vermivora chrysoptera*) annual adult survival (Φ) and re-sighting probability (p) using Tennessee and Ontario data combined to assess regional effects. Columns provide model notation, the number of estimable parameters (K), second order Aikaike Information Criterion ($AIC_c$), $AIC_c$ differences ($\Delta AIC_c$), and the relative likelihood of each model ($AIC_c$ model weights; $w_i$).

| **Model** | **K** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** |
|---|---|---|---|---|
| $\Phi_{sex*year}\ p_{year}$ | 14 | 1040.35 | 0.00 | 0.4759 |
| $\Phi_{year}\ p_{sex*year}$ | 14 | 1042.03 | 1.68 | 0.2058 |
| $\Phi_{sex*year}\ p_{sex}$ | 12 | 1042.38 | 2.03 | 0.1728 |
| $\Phi_{sex*year}\ p_{sex*year}$ | 18 | 1042.78 | 2.43 | 0.1415 |
| $\Phi_{sex}\ p_{sex}$ | 4 | 1051.99 | 11.63 | 0.0014 |
| $\Phi_{sex}\ p$ | 3 | 1052.96 | 12.61 | 0.0009 |
| $\Phi_{region*sex*year}\ p_{region*sex*year}$ | 28 | 1053.02 | 12.67 | 0.0008 |
| $\Phi_{region*sex}\ p_{sex}$ | 6 | 1054.37 | 14.01 | 0.0004 |
| $\Phi_{region*sex}\ p$ | 5 | 1054.78 | 14.43 | 0.0004 |
| $\Phi_{region*sex}\ p_{region*sex}$ | 8 | 1057.13 | 16.78 | 0.0001 |
| $\Phi_{year}\ p_{year}$ | 9 | 1059.59 | 19.24 | 0.0000 |
| $\Phi\ p$ | 2 | 1076.42 | 36.07 | 0.0000 |
| $\Phi_{region}\ p$ | 3 | 1077.09 | 36.74 | 0.0000 |

**Table 4.7:** Summary of model selection results for annual adult survival ($\Phi$) and re-sighting ($p$) probability for golden-winged warblers (*Vermivora chrysoptera*) in the Cumberland Mountains of Tennessee (2003-2006) and the Canadian Shield of Ontario (2001-2006). Columns provide model notation, the number of estimable parameters (K), second order Aikaike Information Criterion ($AIC_c$), $AIC_c$ differences ($\Delta AIC_c$), and the relative likelihood of each model ($AIC_c$ model weights; $w_i$).

| | **Model** | **K** | **$AIC_c$** | **$\Delta AIC_c$** | **$w_i$** |
|---|---|---|---|---|---|
| **Tennessee** | $\Phi_{year}\ p_{sex*year}$ | 8 | 256.32 | 0.00 | 0.4670 |
| | $\Phi_{sex*year}\ p_{year}$ | 8 | 257.18 | 0.86 | 0.3035 |
| | $\Phi_{sex*year}\ p_{sex*year}$ | 10 | 259.20 | 2.88 | 0.1109 |
| | $\Phi_{year}\ p_{year}$ | 5 | 260.81 | 4.49 | 0.0496 |
| | $\Phi\ p_{sex}$ | 3 | 261.53 | 5.21 | 0.0346 |
| | $\Phi_{sex}\ p$ | 3 | 263.38 | 7.05 | 0.0137 |
| | $\Phi_{sex}\ p_{sex}$ | 4 | 263.54 | 7.22 | 0.0126 |
| | $\Phi_{year}\ p$ | 4 | 264.45 | 8.13 | 0.0080 |
| | $\Phi\ p$ | 2 | 271.90 | 15.57 | 0.0002 |
| **Ontario** | $\Phi_{sex*year}\ p_{year}$ | 14 | 792.61 | 0.00 | 0.2863 |
| | $\Phi_{sex}\ p$ | 3 | 792.95 | 0.34 | 0.2410 |
| | $\Phi_{sex}\ p_{sex}$ | 4 | 793.68 | 1.07 | 0.1679 |
| | $\Phi_{sex*year}\ p_{sex*ear}$ | 18 | 794.01 | 1.40 | 0.1425 |
| | $\Phi_{year}\ p_{sex*year}$ | 14 | 794.39 | 1.78 | 0.1175 |
| | $\Phi\ p_{sex}$ | 3 | 796.82 | 4.21 | 0.0348 |
| | $\Phi_{year}\ p$ | 6 | 800.07 | 7.46 | 0.0069 |
| | $\Phi_{year}\ p_{year}$ | 9 | 801.76 | 9.15 | 0.0030 |
| | $\Phi\ p$ | 2 | 806.98 | 14.37 | 0.0002 |

**Table 4.8:** Parameter values for the two-stage Leslie matrices for Tennessee and Ontario golden-winged warbler (*Vermivora chrysoptera*) populations and the associated sensitivity and elasticity values for each matrix element. Annual ASY survival estimates (Φ) are for adult females estimated using Program MARK (see Table 4.4) and SY annual survival is assumed to be half of ASY survival. Fecundity estimates are those listed in Table 4.4 multiplied years the annual survival for SY and ASY birds.

| | **Parameter** | **Estimate** | **Sensitivity** | **Elasticity** |
|---|---|---|---|---|
| Tennessee | ASY Φ | 0.43 | 0.56 | 0.31 |
| | SY Φ ‡ | 0.21 | 0.88 | 0.25 |
| | ASY fecundity § | 0.67 | 0.28 | 0.25 |
| | SY fecundity † | 0.34 | 0.44 | 0.19 |
| Ontario | ASY Φ | 0.48 | 0.60 | 0.36 |
| | SY Φ ‡ | 0.24 | 0.80 | 0.24 |
| | ASY fecundity § | 0.64 | 0.30 | 0.24 |
| | SY fecundity † | 0.32 | 0.40 | 0.16 |

‡ Assumed to be half of ASY survival

§ ASY Φ multiplied by fecundity values from Table 4.5

† SY Φ multiplied by fecundity values from Table 4.5

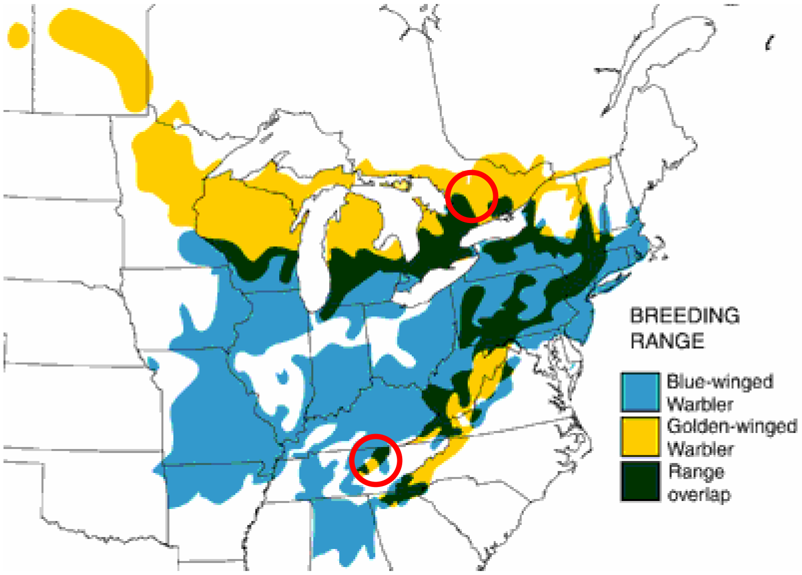

**Figure 4.1:** Map of golden-winged (*Vermivora chryspotera*) and blue-winged warbler (*V. pinus*) occurrence and areas where their ranges overlap produced by the Cornell Lab of Ornithology for the Golden-winged Warbler Atlas Project (GOWAP, unpublished data). Red circles show the location of the study areas for this research in Tennessee (south) and Ontario (north).

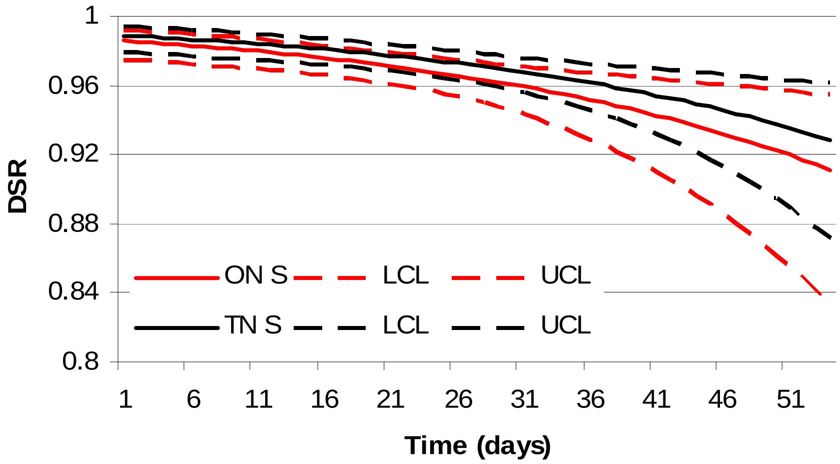

**Figure 4.2:** Linear time model for Ontario and Tennessee golden-winged warbler (*Vermivora chrysoptera*) daily nest survival rates (DSR) from the analysis using the combined datasets. Dashed lines represent standard errors.

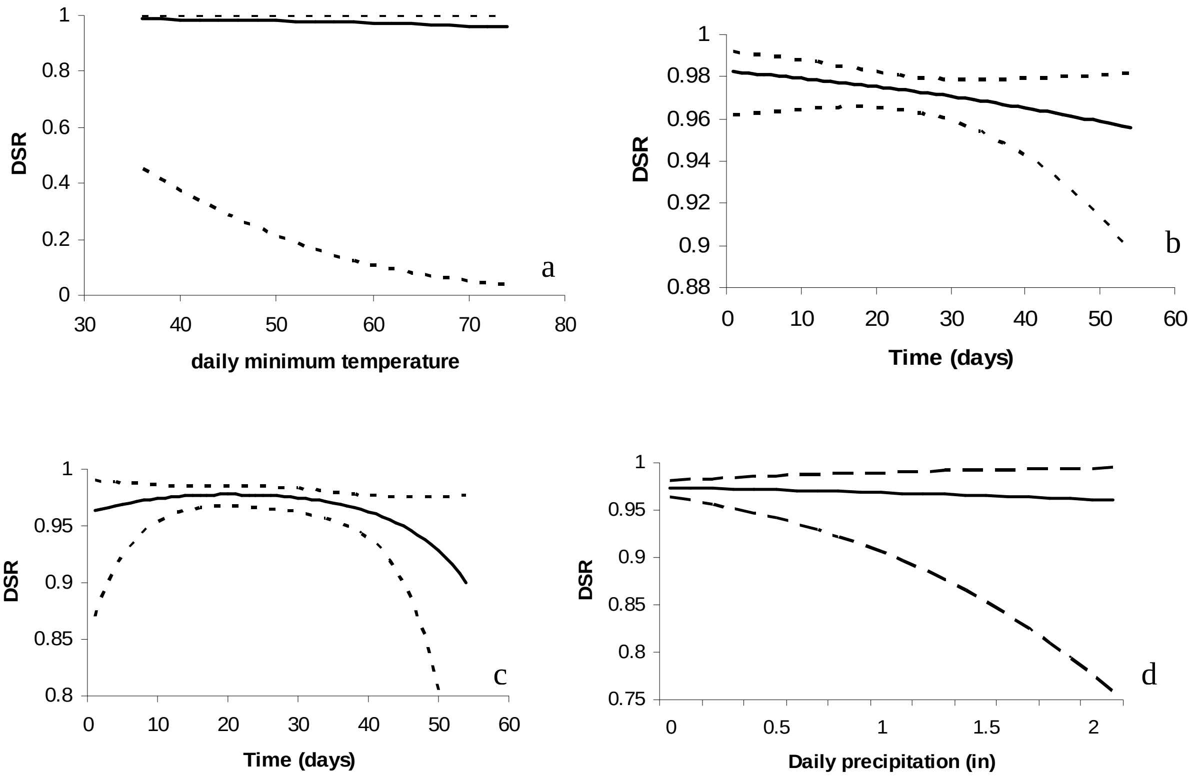

**Figure 4.3:** Daily nest survival rate for the Tennessee golden-winged warbler population as a function of daily minimum temperature (a), a linear time model (b), a quadratic model (c) and daily precipitation (d). Dashed lines represent standard errors.

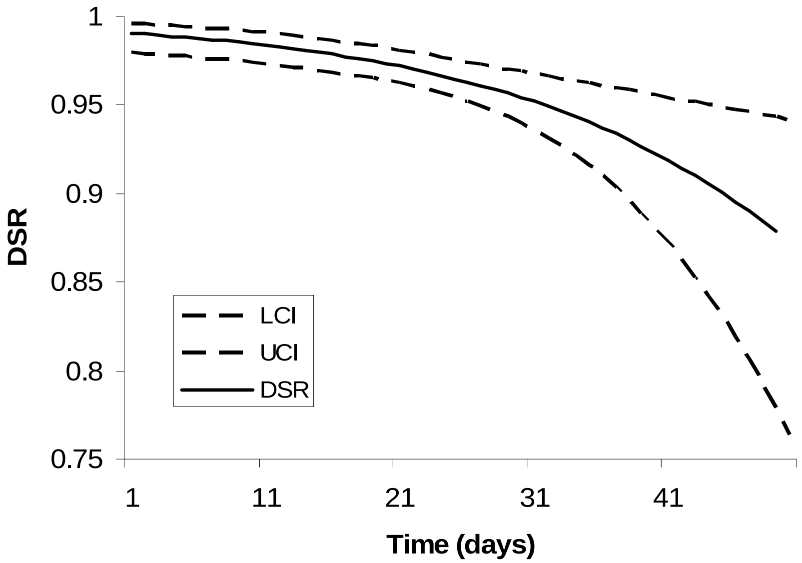

**Figure 4.4:** Linear time model for daily nest survival rates (DSR) of the Ontario golden-winged warbler population, 2003-2006. Dashed lines represent standard errors.

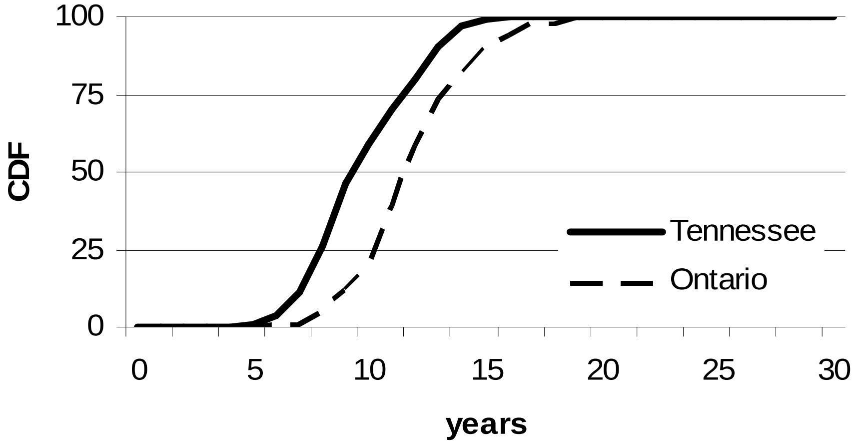

**Figure 4.5:** Cumulative distribution frequency (CDF) representing the probability that the Tennessee and Ontario golden-winged warbler populations will fall below 25 breeding pairs. The distribution is based on output from the stochastic simulation of population size.

# Part 5

# PART 5: MODELING ALTERNATIVE SCENARIOS FOR COAL MINING, MINE RECLAMATION, AND TIMBER HARVEST TO ASSESS THE IMPACTS ON GOLDEN-WNGED WARBLER (*Vermivora chrysoptera*) AND CERULEAN WARBLER (*Dendroica cerulea*) HABITAT AVAILABILITY

The following manuscript will likely be converted into two separate manuscripts for submission to peer reviewed journals. One manuscript will focus on the effects of future land use on habitat availability for golden-winged and cerulean warblers and the other manuscript will focus on the effects of future land use on interior forest loss. "We" throughout this manuscript refers to: L. P. Bulluck, R. Tankersley, and D. A. Buehler

## Abstract

Determining the effects of landscape-scale disturbances on the availability of habitat for species with conflicting habitat requirements is a daunting, yet increasingly important task. The Cumberland Mountains of Tennessee, with a combination of extensive habitat and intensive resource extraction, are an excellent test location for alternative scenario modeling. We examined two declining songbirds that occur in this region: the cerulean warbler (*Dendroica cerulea*), a forest-interior species; and the golden-winged warbler (*Vermivora chrysoptera*), a shrubland obligate. Our goal was to model different levels of resource extraction (expected mining and timber harvest versus limited mining and timber harvest) and two different types of reclamation (grassland reclamation and hybrid reclamation). We compared the availability of cerulean and golden-winged warbler habitat across the landscape and over time under each scenario. For ceruleans, habitat and number of breeding pairs declined significantly under all scenarios; under the best-case scenario, 5,260 ha of suitable habitat and >5,000 breeding pairs were lost after 10 years. For golden-wingeds, all scenarios using hybrid reclamation resulted in an increase in habitat; under the best-case scenario >1,200 ha of suitable habitat and 430 breeding pairs were added after 15 years. Our land use simulations were spatially explicit, which allowed us to compare the loss of interior forest to total forest loss. The percentage of

interior forest loss was 1.4-3.6 times greater than total mature forest loss under the base-case scenario (expected levels of disturbance); as we increased the edge-effect distance from 100 to 300 m, interior forest decreased.  In one sub-region of the Cumberland Mountains where the percentage of interior forest is currently high, 21-58% of interior forest was lost (depending on the edge effect modeled) under expected levels of disturbance.  Accounting for decreased cerulean densities in edge habitats, twice as many breeding territories were lost compared with when edge and interior forests were assumed to have equal densities.  None of the scenarios examined were sustainable alternatives for both cerulean and golden-winged warbler populations.  Our results suggested that none of the industry-planned scenarios adequately conserve habitat for these two priority warbler species.   To sustain cerulean warbler populations, our simulations indicate that new disturbance must be limited beyond that represented in the scenarios here.  To sustain golden-winged warbler populations, the early successional habitat currently on the landscape will need to be maintained and improved through time.  If songbird conservation is the goal, state-owned lands could provide a core of undisturbed habitat, especially considering the degree of disturbance expected on private lands.  At the same time, we must work with private landholders to identify the pattern and extent of disturbance that best conserves both species.

## Introduction

Spatially explicit models of alternative land use scenarios have become a valuable tool for conservation during the past decade following an increase in computer and software capabilities (Turner et al. 2001). The effects of human-induced disturbance on wildlife habitats are not easily predicted, especially at the landscape scale. Decisions regarding the best and most effective conservation strategy are not straightforward when land managers must consider more than one species of concern, and particularly when these species have conflicting habitat requirements. Despite the complexity of multi-species management, it is the approach promoted most often by state and federal wildlife agencies (Rahn et al. 2006) and is fundamental to the Partners in Flight (PIF, Pashley et al. 2000) philosophy. PIF is an organization made of public and private agency biologists, land managers, and researchers dedicated to landbird conservation.

Cerulean and golden-winged warblers are Nearctic-Neotropical migratory songbirds that are experiencing significant population declines throughout their breeding ranges, yet they inhabit very different habitats during the breeding season. The cerulean warbler (CERW) is a canopy-nesting songbird that requires large tracts of mature forests (Hamel 2000), and often prefers forests with structural complexity caused by small forest gaps (Weakland and Wood 2005). The golden-winged warbler (GWWA), on the other hand, is a ground-nesting songbird that requires early successional shrublands with dense herbaceous cover and scattered woody vegetation (Confer 1992). Although the micro-habitat of these two species is nearly opposite, they can be found within the same forested landscapes, such as in the Cumberland Mountains ecoregion in northeastern Tennessee. This rugged landscape has experienced a great deal of past disturbance from the clearing of land by settlers, and more recently by the surface mining of coal and by timber harvest. Despite these disturbances, the ecoregion is predominantly mature forest (~72%) with scattered patches of early successional habitats at various elevations. Because of the extensive nature of the forests in this region and because the core of the CERW breeding range exists here, some land managers suggest that CERW conservation should have precedence over GWWA conservation, the core of whose breeding range exists much farther north of Tennessee. On the other hand, because there are > 40,000 breeding pairs of CERW in the region and ≤ 500 breeding pairs of GWWAs, suggests that GWWA, and early successional species in general, deserve more conservation attention.

Coal mining and timber harvests are currently common disturbance types in the Cumberland Mountains region. Mines completed before the Surface Mining Control and Reclamation Act (SMCRA, 1977) and in those from the 1980s created narrow benches (15-50 m) along elevational contours. These mines were typically reclaimed with herbaceous and woody vegetation (mostly black locust – *Robinia pseudoacacia*); other woody species have since colonized (blackberries - *Rubus* spp, maples - *Acer* spp, yello poplar - *Liriodendron tulipifera*, etc.). Together with the steep mountain slopes, these mines create fairly small canopy gaps and a heterogeneous forest canopy. As a result, it is not uncommon for CERW to nest near the edges of these mines (L. Bulluck, personal observation). More recent surface coal mines are wider (≥50 m) because current technology and machinery allow for more efficient extraction of all coal in a given seam. The width of the mines, and the tendency to reclaim them solely with dense herbaceous cover, results in stronger edge effects thus affecting the adjacent forest. Indeed, research from West Virginia demonstrated that CERW abundance increased with distance from large (>1000 ha) reclaimed mines for up to 340 m into adjacent forest interiors (Wood et al. 2006).

Coal mining has been escalating throughout the Appalachian Mountains during the last few years because of increased coal prices and demand for coal as a source of energy (Department of Energy 2006). Coal power plants in the region are currently being equipped with improved scrubber technology (Tennessee Valley Authority news release: http://www.tva.gov/news/releases/octdec06/paradise.htm) that allow mining of high-sulfur content coal left behind from previous mining operations. With increased mining activity, there is much discussion about the best way to reclaim mine lands. The Surface Mining Control and Reclamation Act (SMCRA) requires the establishment of healthy and permanent vegetation cover on all areas affected by coal mining. Stabilizing the soil with permanent vegetation is of primary importance for minimizing erosion and reducing siltation and acidification of streams. Mining companies are required to plant vegetation that suits the pre-determined post-mining land use specified by the landowner. Post-mining land use refers to the desired condition of the mine site following reclamation and can be residential, agricultural, wildlife habitat, or golf course to name a few. In the Cumberland Mountains, the land being mined is often owned by someone other than the coal company, who may only own the mineral rights. Surface rights for Royal Blue and Sundquist Forest WMAs, for example, are owned by the Tennessee Wildlife Resources Agency (TWRA) who dictates a post-mining land use of wildlife habitat. This requires mining companies to plant a mix of herbaceous cover that will act as forage for white-tailed deer (*Odocoileus virginianus)*, elk (*Cervus elaphus*), and wild turkey (*Meleagris gallopavo)*. On the other hand, when the mining company owns the land and the mineral rights, they may be more inclined to plant the cheapest and most-easily established vegetation types to ensure a quick return of their bond money from the Office of Surface Mining (OSM).

Sites reclaimed solely with aggressive herbaceous cover, whether for forage or for quick release of bond money, may eventually be restored to native forest. However, the process of natural succession is likely to take a long time, possibly centuries (Angel et al. 2005). For this reason, a cooperative effort between university scientists in several Appalachian states and the OSM has developed the Appalachian Regional Reforestation Initiative. This effort was established to facilitate the reforestation of the region with native species and to establish forestry as the preferred post-mining land use (Angel et al. 2005). In the Cumberland Mountains, there is potential conflict regarding the most appropriate post-mining land use considering that OSM and forest bird conservationists would like to see predominantly reforestation and TWRA would like to see a portion of mines reclaimed to wildlife forage.

Timber harvesting in the region is also quite intensive, as several timber investment management companies own the timber rights on large tracts of land. Currently, industrial timber harvests disturb more land annually than coal mining (L. Bulluck, personal observation), but the effects are more ephemeral. The seed bank is not disturbed as it is with mining and a mature forest can be anticipated to re-grow within 50-80 years compared with centuries after mining.

The combined effects of coal mining and timber harvests in the Cumberland Mountains region has led to the initiation of a Habitat Conservation Plan (HCP) that will incorporate several taxa including CERW and possibly GWWA. In addition, there is a group of concerned avian ecologists that have developed population goals for both CERW and GWWA with hopes that land managers would attempt to meet them. These goals for bird conservation in the Cumberland Mountains are to sustain CERW populations with no net loss and to double the GWWA populations through limited creation of successional habitats and primarily through the maintenance and enhancement of already present early successional habitats. Whether or not such goals are feasible in light of expected levels of disturbance is not known. Landscapes where CERW and GWWA occur simultaneously present unique management challenges for the avian conservation community (Hamel et al. 2005), and the Cumberland Mountains region is no exception. We need to understand how conservation of these two species with conflicting needs can be concurrently managed for, and it is particularly important that we know the proper spatial distribution of disturbance on such a landscape that will support both species (Hamel et al. 2005) in addition to other species considered in the HCP.

Our objectives were to (1) simulate coal mining and timber harvesting scenarios of differing intensity (based on predictions of current land use and various limitations of this use), (2) assess the availability of CERW and GWWA habitat under these same scenarios, and (3) calculate the amount of interior forest loss compared to total forest loss under several scenarios. These scenarios are based on actual industry plans for the next decade, and are realistic models of future disturbance. By examining tradeoffs in habitat through the next 50 years as different scenarios of disturbance proceed through forest succession, we can evaluate whether any of the scenarios meet the population goals for cerulean and golden-winged warblers.

## Methods

### *Defining coal seams*

The majority of the coal seams that exist in the Cumberland Mountains of Tennessee were formed during the Pennsylvanian age approximately 290-323 million years before present (Geological Society of America (GSA) 1999 Geologic Timescale, GSA Website, 2006). There are few existing spatial data on the location of coal seams within the Cumberland Mountains region with the exception of isolated core samples taken for exploratory purposes before a potential mining operation (OSM staff, personal communication). Rather than simulating coal mining to occur randomly on the landscape, we derived a GIS layer of coal seams in the region from a map of geologic formations and published information on coal seam thickness for the region (Wilson et al. 1956, Barlow 1969). Within the Middle Pennsylvanian geologic age, there are six formations containing coal seams in the Cumberland Mountains, four of which have coal seams thick enough to be worthy of mining: Cross Mountain, Vowell Mountain, Redoak Mountain, and Graves Gap formations, all of which lie above 450 m elevation in the Cumberland Mountains (Luther 1959). The Grassy Springs, Pewee, Walnut Mountain, Windrock, Big Mary, and Jellico coal seams are the thickest in these formations (1-2 m), and therefore the most likely to be mined (Englund 1968).

All major coal seams in the region are located at the boundary of two geologic formations. For example, the Pewee, Walnut Mountain and Windrock seams are all located at the upper and lower boundaries of the Redoak Mountain geologic formation. Therefore, we created buffers at this geologic formation’s boundaries using the ArcGIS buffer wizard to encompass these coal seams. Buffering resulted in a spatially-explicit polygon layer of coal seams likely to be mined in this region, which we converted to a grid for use in our model (Figure 5.1). When we overlaid the coal mining permits from past and potential future mines on this coal seam layer, there was direct correspondence between them indicating that our representation of coal seams is adequate to use for modeling the location of future coal mines and certainly better than simulating mining randomly across the landscape.

### *Landcover classification*

We used ERDAS Imagine software to perform a supervised classification of SPOT satellite imagery (10-m resolution) collected in September 2006. We used a combination of “region-grow” techniques and manual polygon creation in known landcover types to create signatures for each landcover. We had extensive knowledge of the location of landcover types in many portions of the study area from numerous field excursions in addition to data on recent (2005-2006) and older (2001-2004) timber harvests from Fountain Forestry, Inc., a local timber consultant. After ten iterations of manually improving the signatures for each landcover type, we had classified the following landcover types: mature forest (undisturbed), older timber harvest (~5-10 yr post-harvest), recent timber harvest (<5 yr post-harvest), young forest (i.e., with some of type of disturbance but older than recent or older timber harvests), shrubland (mix of woody and herbaceous cover), grassland (all herbaceous cover), and urban/barren (developed lands or areas of bare ground immediately after disturbance).

We then performed an accuracy assessment in the Coal Creek watershed (9321 ha in the southeastern portion of the study area) where very high-resolution air photos were available (ARCADIS Inc., Knoxville, TN). We generated 25 random points in the young forest, mature forest, pasture, and urban/barren landcover types and assessed the air photos to see if our classification was correct. We used the region group command to extract all classified timber harvests that were >0.5 ha (n = 18 recent harvests and n = 14 older harvests). We did this rather than generating random points because there were scattered single pixels of these landcover classes throughout the landscape (representing small disturbances within the mature forests of unknown origin or noise/error in the classification). We were less concerned with the accuracy of single pixels than with our classification of actual timber harvests. Likewise, we generated 25 random points in the shrubland landcover class, but omitted 2 points that were placed in isolated pixels surrounded by mature forest pixels.

We decided a priori that if ≥75% of the test points were classified correctly for a given landcover type, it was sufficiently classified. Two of the seven landcover types had classification rates less than 75% (Table 5.1); grassland/pasture was sometimes misclassified as urban/barren, and older clearcuts were misclassified as shrubland. Because grassland and urban/barren cover types are not considered habitat for either species of interest, we did not adjust this classification or merge these classes. However, we did combine older clearcuts and shrubland cover types into one landcover class called shrubland. The resulting reclassified SPOT grid (Figure 5.2) was used as our base map upon which all future disturbances were modeled.

### *Meetings with stakeholders*

There are several large landowners in the Cumberland Mountains region (Figure 5.3) and most of the resource extraction occurs on these lands. We wanted to discuss our plans to spatially model land use in this region to gain insight from these stakeholders into how best to represent their activities. We chose to meet with the forestry and mining industries separately because of the very different processes and questions we would have for each group.

On November 17, 2006, we held a meeting on the campus of the University of Tennessee with forestry stakeholders to discuss our modeling plans. We had two main goals at this meeting: (1) to explain our modeling objectives to the foresters, and (2) to obtain specific input regarding how best to represent harvesting activities as realistically as possible. Before the meeting, we sent all forestry stakeholders an e-mail describing the types of questions we would be asking so they could come prepared with answers. We asked each forestry stakeholder for annual hectares harvested, average harvested stand size, places they would not harvest (i.e., steep slopes or riparian areas), the spatial arrangement of harvests (clumped or scattered), proportion of harvests that were clearcut versus shelterwood, average rotation length, and time span they expect to harvest timber on their given tract of land (short term or indefinitely).

The following foresters attended the November 17 meeting: E. Dennis from Fountain Forestry, J. Elkins from TWRA, and M. Schubert and M. Young from the University of Tennessee Forestry Experiment Station. The responses from these stakeholders are summarized in Table 5.2. We were not successful in obtaining any information from Coal Creek Mining and Manufacturing Company. We therefore assumed the same rate of harvest and spatial arrangement as Fountain Forestry since they both manage timber resources primarily based on profit motives and we have observed extensive timber harvesting on their lands. We obtained additional information for harvest rates on all other private lands from Forestry Inventory and Analysis (FIA) data from the US Forest Service (J. Turner, FIA data manager).

We established contacts with two coal-mining stakeholders; National Coal Corporation and the Tennessee Valley Authority (TVA), but we were not able to schedule official meetings with these groups. Instead, Bill Johnston from National Coal Corporation and Ruth Horton from TVA provided all information requested to the best of their knowledge in phone conversations and personal meetings. We also obtained information from the Office of Surface Mining, but we were unsuccessful in contacting other mining industries that own specific lands in the region (i.e., Coal Creek Mining and Manufacturing). We, therefore, assumed the same mining rates (adjusted for area in each ownership) applied to these areas as occurred on National Coal Corporation lands (see Table 5.2).

### *Simulation of disturbances*

We simulated disturbances across the landscape to represent the information provided by the above-mentioned stakeholders over a ten-year time period starting in 2006 (Figure 5.4). We identified disturbance described by these stakeholders as the 'base-case' scenario and also simulated alternative scenarios described below (see scenario section). We limited our simulation of disturbance to ten years because this is the time frame for which we had the most reliable information regarding expected disturbances (see model assumptions section).

#### Mining

#### Cross-ridge mining

Cross-ridge mining is similar to mountain-top removal, but there is one major difference. In mountain-top removal, the actual ridge is removed to access the underlying coal and the overburden is placed in the valley below (i.e., valley fill) resulting in a plateau where a mountain was previously (Office of Surface Mining website: http://www.osmre.gov/mountaintop.htm). This type of mining is common in West Virginia and Kentucky. Cross-ridge mining also removes the ridge to access the underlying coal, but instead of placing the overburden in the valley below, it is stored on a neighboring ridge and replaced to its "approximate original contour" once the coal has been extracted.

Neither mountain-top removal nor cross-ridge mining is common in the Cumberland Mountains of Tennessee as this region lacks thick coal seams near ridge tops. However, several cross-ridge mines are currently active or are planned for the future. Based on the rarity of this mining technique and on conversations with National Coal Corporation and the Tennessee Valley Authority, we made all cross-ridge mining occur at explicitly selected locations on the landscape for our modeling purposes. National Coal Corporation stated that Zeb Mountain mine would be the only cross-ridge mine they will operate in the near future, and TVA had locations of their potential cross-ridge mines already mapped. To simulate cross-ridge mining, we extended the current boundary of Zeb Mountain to make it twice its current size (~485 ha) based on permit information obtained from National Coal Corporation via J. Rizza (MS student in Department of Forestry, Wildlife and Fisheries conducting research on this mountain) and used the locations of two potential cross ridge mines already mapped by TVA. These two cross ridge mines are located in the Royal Blue WMA and are 895 and 461 acres.

### Contour mining

The majority of future surface mining is likely to be contour mining where coal is extracted from a seam that lies relatively close to the surface but significantly below the ridge. Typically these mines are active for 5 years or less and are linear because they follow elevational contours. Older contour mines (from 20-30 years ago) were fairly narrow (~15-50 m wide), whereas contemporary contour mines are wider (≥50 m wide) because of improved technology and ability to access more coal from a given seam. For this reason, and in addition to new technology in coal power plant scrubbers, coal that was previously not accessible or had too high of a sulfur content can now be mined.

Therefore, previously reclaimed mine sites can be re-mined, and we did not limit the location of potential future mines to areas that had not been previously mined.

From our conversations with National Coal Corporation and TVA, we learned that their specific future mining plans are unknown; however, they provided some basic guidelines to realistically simulate their mining. We used Arc Macro Language (AML) programming in Workstation ArcInfo to seed a random point within modeled coal seams, defined a cost-surface that limited mine growth to the seam, and iteratively grew mines until we had met desired number of mines and overall mined area. We randomly located seeds for future mines by generating a random grid of rows and columns, masking the random number grid by the coal seam layer, and randomly selecting a location from these. We then grew each mine to a randomly selected size from a uniform distribution between 60 and 100 ha, varying the width randomly between 30 and 70 m wide. We limited the area mined annually by land ownership (Table 5.2). We generated 810 ha of mines in the Sundquist Forest WMA (to represent mining by National Coal Corporation) over the next 10 years, 810 ha in Coal Creek property, 1,943 ha on Royal Blue (Koppers) to represent mining by TVA, and an additional 810 ha in the remaining landscape to represent mining by unknown landowners for a total of 4,371 ha in the Cumberland mountains ecoregion over the next 10 years for the base-case scenario.

### Deep mining

Deep mining allows access to coal resources not accessible through surface mining techniques (i.e., contour mining). A mine portal is established and a large amount of coal is excavated over a longer period of time (up to 10 years). Typically, ~12 ha of surface disturbance results from one deep mine. To simulate deep mines on the landscape, we generated random seeds within coal seams, as we did for contour mines, and grew each mine to 12 ha. Based on projections made by National Coal Corporation, we simulated ten deep mines per 5-yr time step (for an estimated two deep mines initiated per year) in the Sundquist Forest WMA for a total of 243 ha of surface disturbance. We assumed the same rate and number to be created in Coal Creek, Royal Blue, and elsewhere (private land and Brimstone) for a total of 728 ha/10-yr period in these areas.

Added to Sundquist, the surface area over the ten years to be disturbed by deep mining in the whole ecoregion is 971 ha (or 80, 12-ha mines) for the base-case scenario (see Scenario section below).

## Reclamation

### Grassland reclamation

Landowners are evaluated for successful reclamation after five years post-mining, which is not enough time for the natural succession of a hardwood forest (Holl 2002). Therefore, typical post-mine reclamation consists of planting a mixture of aggressive herbaceous plants, many of which are non-native and invasive, to ensure rapid establishment and to prevent erosion. For example, aggressive grasses (*Festuca* spp.) and legumes (*Lespedeza* spp.) are commonly planted on mines in the eastern U.S. To represent such reclamation practices, we assumed an entire simulated mine was planted with herbaceous cover and that succession was much slower (see succession section below) than the hybrid alternative.

### Hybrid reclamation

Zeb Mountain is currently being reclaimed with a mixture of herbaceous vegetation and native hardwoods as part of a research project through the University of Tennessee and National Coal Corporation. Foresters are in the process of learning what mixture of herbaceous and woody vegetation is best to maximize successful tree establishment. There is a tradeoff between preventing soil erosion and minimizing competition between these two vegetation types. To represent reforestation reclamation, we assumed 50% of all mines were planted with trees and the other 50% were planted with herbaceous cover as described above. The reforested half was simulated to occur around the perimeter of the mine site because these sites likely represent the steepest slopes and would buffer the edge effect on surrounding forests. We modeled reforestation by shrinking (an inverse buffer) each site until the desired area was reached. We made these decisions based on conversations with National Coal Corporation about their reclamation plans on Zeb Mountain and other future mines in the region.

## Timber Harvesting

### Industrial harvesting

We assumed there will be a difference in management approach on forest lands managed by timber management investment companies and by non-industrial private landowners. On industrial forest lands, we simulated the clumped nature of harvests within watersheds. We delineated sixth-order watersheds across the entire ecoregion because these watersheds most resembled the size of the watersheds currently being harvested by Fountain Forestry (as discerned from SPOT imagery) and projected to be harvested during the next five years (based on a GIS coverage provided by Fountain Forestry). We randomly selected watersheds within the Sundquist Forest, Brimstone, and Coal Creek property boundaries, and calculated the area of each selected watershed until the hectare goals for the ten-year period were met (Table 5.3). Harvests were clumped in selected watersheds and were the approximate sizes of those currently being harvested.

Fountain Forestry indicated that 25% of their harvests were shelterwoods, but we assumed all timber harvests were clear cuts on industry lands because of the residual basal area left by these industries. A typical silvicultural shelterwood harvest has 7.5-12.5 $m^2$/ha residual basal area and Fountain Forestry typically has 4-5 $m^2$/ha basal area (S. Reaves, Fountain Forestry Inc., personal communication).

### Harvesting by state agencies

TWRA owns the timber rights on one of their two WMAs in the region, the Royal Blue WMA. Based on our meetings with TWRA regarding their timber practices on this WMA (Table 5.2), we simulated 60 ha harvested per year in six 10-ha cuts scattered throughout the WMA. We classified 25% of these harvests as clearcuts and the other 75% as shelterwood. The University of Tennessee owns a small parcel of land in the southwest portion of the Cumberland Mountains ecoregion (Figure 5.3) where they conduct forestry research and harvest timber for financial gain. Based on our meetings with them regarding their timber practices (Table 5.2), we simulated 40 ha harvested per year in 4-30 ha cuts scattered throughout the property. We classified 100% of these harvests as clearcuts.

### Harvesting by private landowners

In addition to the above large landowners, there are a multitude of small, non-industrial private landowners (Figure 5.3), whose land use trends are difficult to simulate and/or predict as they occur more sporadically. We contacted the Forest Inventory and Analysis (FIA) researchers with the US Forest Service to obtain the annual area harvested across this region on non-industrial private lands. They estimated there were ~960 ha harvested annually between 1989 and 1999; more recent data were not available. We simulated individual harvests to vary randomly between 8 and 40 ha. FIA data also indicated a relatively high rate of partial harvests on private lands, so we assumed 50% of harvests were clearcuts and 50% were shelterwoods. We recognize that partial harvests on non-industrial private lands often entail diameter-limit harvests that differ from shelterwood harvests, but we assume that songbird response to these types of disturbances will be similar.

## ***Disturbance scenarios***

We developed twelve scenarios involving different amounts of timber harvesting and mining with two reclamation types (Table 5.3). We based these scenarios on land use in the region as projected by the landowners (i.e., base-case mining and/or timber) in addition to alternatives that seemed realistic from our discussions with these same landowners or desirable from a wildlife conservation perspective. We developed two alternative mining scenarios (limited A and limited B) that omitted all cross-ridge mines and either restricted the number of contour mines to none or one-half, respectively. We chose these scenarios specifically because “deep mines only” options are currently being considered by TVA in a recent draft Environmental Impact Statement for the Royal Blue area (R. Horton, personal communication). Deep mines provide the largest amount of coal with the least amount of surface disturbance to the landscape, making them less disruptive to natural resources compared with contour and cross-ridge mines. Alternative timber harvest scenarios did not change the amount of harvest on private lands as this would be difficult to implement, but had no harvest on Royal Blue and limited industrial harvest to half of their base-case area (Table 5.3). The following are the 12 combinations of scenarios:

1. Base-case mining/ base-case logging/herbaceous reclamation
2. Base-case mining/ base-case logging/hybrid reclamation
3. Base-case mining/limited logging/herbaceous reclamation
4. Base-case mining/limited logging/hybrid reclamation
5. Limited mining A/ base-case logging/herbaceous reclamation
6. Limited mining A/ base-case logging/hybrid reclamation
7. Limited mining A/limited logging/herbaceous reclamation
8. Limited mining A/limited logging/hybrid reclamation
9. Limited mining B/ base-case logging/herbaceous reclamation
10. Limited mining B/ base-case logging/hybrid reclamation
11. Limited mining B/limited logging/herbaceous reclamation
12. Limited mining B/limited logging/hybrid reclamation

### *Succession*

We designated five categories of successional habitat as a function of vegetation re-growth after certain disturbances and considering the different suitability of these habitats for ceruleans vs. golden-wingeds. Succession = 9 referred to areas that will not succeed over time, such as urban areas, utility right-of-ways, and pastures within 50 m of a main road; succession = 1 represented bare ground (post-harvest) or grassland (post-mining); succession = 2 represented shrubland; succession = 3 represented young forest; and succession = 4 represented mature forest. After timber harvest, the successional stage was assumed to depend on the harvest type (shelterwood; SW or clearcut; CC) and the time since harvest (Figure 5.5). Likewise, after mining, successional stage was assumed to depend on the reclamation procedure used and the time since mining. These decision rules resulted in 40 total successional classes using a three number coding system (Appendix B). The first number of the code represented the actual successional state (1-4 and 9 from above). The second number in the code represented the type of disturbance and/or reclamation (2 for mining, reclamation grass; 3 for mining, reclamation forest; 4 for clearcut; and 5 for shelterwood). The final number specified whether the disturbance occurred in the first five-year time step or the second five-year time step.

### *Avian habitat*

We defined high-quality golden-winged warbler habitat as being greater than 580 m elevation, in shrubland created from mining disturbance (Figure 5.6). We also considered shrubland created from timber harvests above this same elevation as suitable, but with lower densities (0.4 territories/10 ha) than the mined areas (3.2 territories/10 ha). These density estimates are based on data collected in the region (L. Bulluck, unpublished data, 2003-2006) during general surveys of early successional habitats. The high-quality habitat estimate is based on the density of GWWA found in our main study sites (see Part 3, Table 3.3) which were all located on surface coal mines reclaimed between 1980 and 1990; these are sites with the highest densities known to exist in the region. The low-quality habitat estimate is based on the density of GWWA found across other surveyed sites, including surface coal mines reclaimed before 1980 and timber harvests. We feel confident that these estimates are realistic, and if anything, may overestimate the true densities of GWWA in high- and low-quality habitats across the Cumberlands.

We defined high-quality cerulean warbler habitat as being greater than 580 m elevation, in mature deciduous forest that has experienced no disturbance or that had been disturbed by a shelterwood harvest 15 years earlier (Figure 5.6). We also assumed that mature forests (>40 years post-disturbance) that have succeeded from clearcuts or mines reclaimed with native trees had become suitable cerulean habitat. We know little about how cerulean warblers respond to different intensities of disturbance and when they will re-colonize areas post-disturbance. Research is currently being conducted to help us better understand cerulean response to timber harvests of differing intensities (Beachy and Buehler, personal communication). We do know that ceruleans in the Cumberland Mountains occur at lower densities (2.7 territorial males/10 ha) on study sites surrounded by more recent mining disturbance compared with sites surrounded by more mature forests (10.8 territorial males/10 ha, Beachy, unpublished data).

We calculated the total area of suitable habitat for both golden-winged and cerulean warblers at each 5-year time step for 50 years into the future. We also estimated the number of territories lost or gained at each time step based on the above-mentioned densities to rank the various scenarios from best to worst for each species.

### ***Interior forest loss***

It is unknown how the current rates of disturbance from forestry and mining may affect habitat quality for songbirds in the Cumberland Mountains. Previous studies have shown the effects of forest fragmentation penetrate into the remaining mature forests, such that the total loss of mature forest does not accurately depict the actual loss of habitat quantity and quality. In a study of the effects of mountain-top mining in Kentucky, Wickham et al. (2007) demonstrated that the loss of interior forests was 1.75 to 5.0 times greater than the direct loss of total forest from mining. The edge effects from disturbance can be far-reaching; CERW abundance is affected for up to 300 m from a large disturbance (Wood et al. 2006), negative effects on nest success for ground-nesting birds reach up to 340 m from a forest edge (Flashpoler et al. 2001), and forests within 100 m from an edge are considered sink habitats for ovenbirds (*Seiurus aurocapillus*) (Manolis et al. 2002). We modeled the loss of interior forest and compared this to the total loss of mature forest. We conducted a sliding window analysis with five different edge effect distances (50, 100, 150, 250, and 300 m; the window sizes were 1.10, 5.29, 10.89, 30.25 and 42.25 ha, respectively). The edge effect is approximately half the side length of a given window, and the window sizes selected represent the range of edge effects likely to affect breeding songbirds based on the literature (Flashpoler et al. 2001, Manolis et al. 2002, Wood et al. 2006).

We defined interior forest as an area within a window that was ≥90% forested. We used 90% rather than 100% to define interior forest because Wickham et al (2007) found similar results in their study of interior forest loss for these two thresholds and because we were interested in true edges and not in the effects of isolated 10-m pixels of non-forest scattered throughout a given window. In this analysis, a fixed-area window moved across the 2006 classified SPOT grid representing current landcover and across grids representing three scenarios 10 years post-disturbance. The window moved one pixel at a time and calculated the percent cover of forest within that window. If there was ≥90% forest in the window, the focal pixel was classified as interior forest. We conducted this window analysis for the base-case mining and timber harvest scenario, the base-case mining and limited timber harvest scenario, and the limited mining A and limited timber harvesting scenario. Additional scenarios were not evaluated because these were the best-case and worst-case scenarios for the species of interest.

We estimated the impact of interior-forest loss on CERW by assuming a 150-m edge effect distance. Research by Wood et al. (2006) suggests this effect can reach 340 m surrounding large mines in West Virginia, but we decided to use the 150-m edge effect distance because most mines in Tennessee are not expected to be as large as those in West Virginia. Therefore, our results for the effects of interior forest loss on CERW habitat are conservative and may be worse if CERW respond to future mining here as they have in West Virginia. We summarized the results of the 150-m forest interior window analysis for areas above 580 m elevation and estimated the area of interior and edge CERW habitat as well as the number of CERW territories with and without edge effects. Without edge effects assumed all mature forest has high density (10.8 territorial males/10 ha) and with edge effects assumed high density in mature forest and low density (2.7 territorial males/10 ha) in edge forest.

### *Model assumptions*

We assume that all disturbances occurred only within the first ten years. Although disturbance will continue through time, we had expert knowledge for the expected level and extent of disturbance to occur over the next decade, and our goal was to see how a series of realistic disturbance scenarios affected the tradeoff of habitat types over the next half century. Additionally, industry experts suggested that practices today may not be realistic in ten years because of anticipated changes in markets for timber and coal as well as land ownership. As an extension of our initial modeling, we performed an additional analysis for CERW that simulated continued disturbance, and extrapolated a decrease in high-quality habitat for 25 years under the six scenarios with hybrid reclamation while accounting for succession. To accomplish this, we subtracted the same area per year as a result of mining and timber harvest and added the same amount from succession as occurred in the first ten years. While these results were not spatially explicit, they are representative of the likely cumulative impact of these disturbances over time. Our initial modeling was designed to examine how a series of disturbances will succeed through time and create habitats of different quality; this extension of our modeling begins to examine habitat tradeoffs in the context of additional disturbance through time. We isolated the initial 10 years of disturbance because examining the spatial distribution of succeeding landscapes for a discrete disturbance event yields important insights about how individual disturbances will impact habitat quality over decades. This assumption leads to conservative results considering that disturbance will undoubtedly continue beyond ten years.

Similarly, we assumed no change in mining technology or in the public's demand for coal over the next ten years. Advances in coal mining technology is likely over the next several decades as fossil fuels become scarcer and demand increases. However, for ease of modeling, we assumed no significant advances in technology will occur in the next ten years. Likewise, economic predictions for North America's use of coal as an energy source indicate that consumption will likely remain high in future decades (Department of Energy 2006). Recent advances in mining technology (i.e. larger equipment) during the past 20 years have generally led to larger mines. Therefore, these assumptions likely cause our results to be conservative in terms of relative impacts on the Cumberland landscape.

We assumed that land ownership patterns will not change significantly in terms of the relative proportion of land owned and managed intensively for timber resources compared to land owned by non-industrial private landowners. A relatively great proportion of the Cumberlands is currently owned by a relatively few landowners. Some of these parcels may be divided in the next 50 years or will likely change ownership and therefore the management of these lands could change dramatically. Because this is difficult to predict, we assumed that the wide variety of land use scenarios modeled here will encompass the likely alternatives of changing land ownership and may even guide management in such a situation. This assumption likely leads to our results being conservative considering that land ownership changes would lead to the creation of more and smaller parcels and more residential and commercial development.

We assumed that no additional disturbance/land uses other than mining and timber harvests will change the current configuration of the landscape. Additional disturbances might include both natural disturbance, such as landslides and insect outbreaks, and human-induced disturbances such as arson fire, prescribed fire, installation of gas wells, and residential/commercial development. Each of these disturbance types occurs in the Cumberland Mountains landscape, but modeling these additional disturbance types would make the modeling extremely complex. As a result, our model ouput should be interpreted as a conservative estimate of disturbance and forest fragmentation considering that these other disturbances are likely to continue in addition to mining and timber harvests.

We assumed our estimates of succession rate for each disturbance and reclamation type were accurate (Figure 5.6). We based our estimates, when available, on results published in the primary literature (e.g., Holl 2002) and/or on our observation of vegetation in areas of known disturbance type and time since disturbance. However, in some instances, such as reforestation/hybrid reclamation of mines that has not been specifically observed in the past, we based our predictions of succession rates on research published on data from mines reclaimed with woody vegetation, such as white pine (*Pinus strobus*) and black locusts (Holl and Cairns 1994, Holl 2002). We assumed that after 40 years, a mine site reclaimed with hardwoods would be in a mature forest state. This is the same rate as is assumed to occur on clearcuts, but the shrub stage is elongated on mines reclaimed with hardwoods because they also plant herbaceous cover that is not often present after timber harvests. (Note: Although we classify these areas as mature forests after 40 years, clearcuts and mined lands are assumed to be low-quality habitat for ceruleans during the last 10 years of the 50-year time period of this model [Figure 5.7]). We cannot be sure how this assumption may affect our results. We plan to conduct a sensitivity analysis where we vary how fast succession occurs following different disturbance types to determine how sensitive our results are to our succession scheme.

We also assumed that current young forest (i.e., classified in the SPOT imagery) did not succeed into mature forest during the 50-year time frame of our model. This is not unrealistic for some of the young forest that originated as reclaimed mine on poor, rocky soils. However, this is not a valid assumption for young forest that originated as timber harvest, although these areas are not likely to succeed all at once. Currently, there are 22,258 ha of young forest across the Cumberland landscape. Of these 22,258 ha, only 5,073 (22.8%) are above 580 m elevation where they may become suitable for CERW habitat if modeled to succeed into mature forest. Of these 5,073 ha, 774 (15.4%) originated as mines that would not succeed into mature forest during the 50 year timeframe of our model. This leaves 4,292 ha (19.3% of total 22,258) that theoretically should succeed into mature forest suitable for CERW. Furthermore, this young forest would not succeed into suitable habitat for at least 15+ years and so this assumption does not affect our ranking of scenarios or the interior forest analysis as these were based on the first ten years of simulation only.

Lastly, we assumed there are only high and low-quality habitats for both species with two pre-defined densities. In reality there is likely a continuum of habitat quality across the landscape with varying densities. For CERW, we started the simulation assuming that all mature forest habitats over 580 m elevation were high-quality and that low-quality habitat does not occur on the landscape until after our simulated disturbances become mature forest (i.e., at 50 years). However, we know that there are currently high and low density patches of CERW habitat throughout the Cumberlands and that this is therefore not strictly true. Besides proximity to edge (Wood et al. 2006), we are not sure what other factors may drive these differences in density. This assumption likely leads to our estimates of CERW and GWWA populations in the Cumberlands to be greater than they actually are because there are certainly additional factors that reduce the densities of these species.

## Results

Classification of 2006 SPOT imagery determined the current/baseline landscape conditions (Table 5.4) prior to simulating any disturbance. Sundquist Forest WMA had similar landcover percentages as the entire Cumberland Mountain landscape, whereas Royal Blue had greater mature forest cover and lesser successional cover. As a result, Royal Blue has a greater percentage of high-quality CERW habitat (51%) than Sundquist (37%) or the Cumberland Mountains (29%) (Table 5.4). Sundquist, on the other hand, has a greater percentage of high-quality GWWA habitat (4%) than Royal Blue (1.8%) or the Cumberland Mountains landscape as a whole (2.5%).

For all scenarios, shrub cover increased markedly from the current 16,368 ha to a peak >32,000 ha after 15 years and then decreased to nearly zero after 25 years as it succeeded into young forest (Figure 5.7a). There was a second spike of shrub cover from 25-40 years from mines that were reclaimed as grass (or the portions of mines reclaimed as grass for the hybrid reclamation scenarios). For all scenarios, mature forest cover decreased from the current ~150,000 ha to a low after 10-15 years and then increased slightly from the succession of shelterwood harvests (Figure 5.7b). After forty years mature forest increased to greater than current levels following succession of clear cuts and mines reclaimed with trees (Figure 5.7b), assuming no more disturbance occurred after the first ten years. The sharp rise and fall of these landcover types, as well as the habitat types (see next two sections), is caused by our five year time-step. If we had used a one year time-step, these changes would be smoother, but the net effect would be similar.

### *Cerulean warbler habitat availability*

Across the Cumberland Mountains landscape, high-quality CERW habitat decreased markedly with the simulation of disturbances during the first 10 years and then increased slightly as young forest and shelterwood harvests grew into mature forests (Figure 5.8a). We only showed six scenarios for CERW (Figure 5.8a) because reclamation type did not affect CERW habitat during the 50-year timeframe used in these simulations (i.e., neither grass nor hybrid reclamation will become mature forest during this time). The limited mining A and limited timber harvesting scenario was considered the best for CERW because it maintained the greatest amount of high-quality CERW habitat and resulted in the loss of the fewest territorial males (Table 5.5). Currently, 28.6% of the landscape is considered high-quality CERW habitat and the best-case scenario caused this to decrease to 26%, resulting in a loss of >5500 territories in 10 years (about 10% of the cerulean population), whereas the worst-case scenario (base-case mining and timber harvesting) decreased CERW habitat to 24.5% (Figure 5.8b), resulting in a loss of >9000 territories, or about 15% of the population (Table 5.5).

Scenarios that limited the amount of mining and timber harvesting were better than the base-case scenarios for CERW (Table 5.5), and the limited mining A scenario (deep mines only) was better than the limited mining B scenario (see Table 5.3 for scenario descriptions). We repeated this ranking process for Sundquist Forest and Royal Blue WMAs; the ranking did not change for Sundquist, but did for Royal Blue compared with the entire Cumberland landscape. The best and worst case scenarios did not change for Royal Blue, but the intermediate scenarios were ranked differently (Table 5.5). The best-case scenario for CERW is the limited mining A and limited timber harvesting scenario where there is no timber harvesting on Royal Blue and only deep mines for coal extraction. Because there is no harvest in Royal Blue WMA under limited timber scenarios, there is minimal recovery of CERW habitat compared with the base-case scenarios in this same WMA (Figure 5.9). In Sundquist Forest, where limited timber harvesting is represented by half the current area, this recovery does not occur (Figure 5.10).

When extrapolated out 25 years across the Cumberland Mountains landscape, high-quality CERW habitat declined from 28.6% of the current landscape to 18.8% in the worst-case scenario and to 22.8% in the best-case scenario (Figure 5.11a). Within the Royal Blue WMA, high-quality CERW habitat declined from 51.3% of the current landscape to 35.1% in the worst-case scenario and declined to 45.0% in the best-case scenario (Figure 5.11b). Within the Sundquist Forest WMA, high-quality CERW habitat declined from 37.0% of the current landscape to 23.7% in the worst-case scenario and declined to 31.8% in the best-case scenario (Figure 5.11c).

### ***Golden-winged warbler habitat availability***

Across the Cumberland Mountains landscape, high-quality GWWA habitat increased markedly for hybrid reclamation scenarios during the first 10 to 15 years and decreased with grassland reclamation scenarios (Figure 5.12). After 20 years and across all scenarios, high-quality GWWA habitat decreased drastically and then increased temporarily as the mines reclaimed as grassland succeeded to shrubland and then young forest (Figure 5.13). The same trend existed for high-quality GWWA habitat in the Royal Blue and Sundquist Forest WMAs, but with some noticeable differences for Royal Blue specifically. More mining than timber harvest was projected to occur in the Royal Blue WMA, resulting in a more marked increase in habitat followed by a relatively smaller decline after 20 years (Figure 5.14). The Sundquist Forest WMA was similar to the landscape as a whole, where both timber harvests and mining were projected to occur at high levels. As a result, the availability of high-quality GWWA habitat followed a similar trend with a relatively small increase initially followed by a drastic decrease after 25 years (Figure 5.15).

We ranked the scenarios based on the availability of high-quality GWWA habitat as well as the combination of high- and low-quality GWWA habitats. Under all hybrid reclamation scenarios, high-quality GWWA habitat increased in the short term; these scenarios therefore ranked higher than the grassland scenarios under which high-quality GWWA habitat decreased (Table 5.6). The base-case mining and limited timber harvesting scenario with hybrid reclamation represented the best case for this species and resulted in an increase of 439 breeding territories (~100% increase) after 15 years. The base-case mining and timber harvesting scenario with grassland reclamation was the worst scenario for golden-wingeds and caused a loss of 170 breeding territories (~40% decrease) after 15 years. The scenario rankings did not change for the Royal Blue and Sundquist Forest WMAs compared to the landscape as a whole based on the availability of GWWA high-quality habitat.

When we considered the availability of both high- and low-quality habitats for GWWA, the worst-case scenario was still the base-case model, but the rankings for the other scenarios changed slightly. Scenarios with base-case timber harvesting moved up in rank over the limited timber harvest scenarios. However, there is very little difference in the actual number of territories gained from the base-case timber harvesting compared with the limited timber harvesting (Table 5.7), because of the low densities of GWWA found on sites following timber harvests.

### *Interior forest loss*

Currently, 72.6% of the Cumberland Mountains landscape is mature forest (Table 5.4) and 35-59% is interior forest, depending on the scale of the analysis (i.e., 50-300 m edge effect, Figure 5.16). The twenty largest patches of interior forest are located on both public and private lands with the largest patch and four of the top twenty patches located in the Royal Blue WMA (Figure 5.17). Under the base-case scenarios, 11.6% of mature forest cover was lost to mining and timber harvesting over a ten-year period. Assuming 50-300 m edge effects, the estimated loss of interior forest under this same scenario ranged from 16.6% to 41.3%, respectively (Table 5.8). Percentage of interior-forest loss was 1.4-3.6 times greater than total mature-forest loss; this ratio increased with the size of the edge-effect window (Table 5.8, Figures 5.18 and 5.19). The percentage of interior forest loss was similar for the base-case mining and limited timber-harvesting scenario (14.8% to 37.4% lost and 1.5-3.7 times greater than total forest loss) and smaller for the limited mining A and limited timber harvest scenario (11.5% to 26.8% lost and 1.3-3.1 times greater than total forest loss).

When we limited the results from the window analysis to the Royal Blue WMA, the total mature forest loss was similar to the landscape as a whole (11.8%), but the percentage of interior forest loss was much greater and ranged from 20.8% to 58.0% or 1.7-4.9 times greater than total forest loss under the base-case scenario (Table 5.9, Figure 5.19). The loss of interior forest was also dramatically greater than total forest loss in the Royal Blue WMA under the base-case mining and limited timber-harvesting scenario (16.5% to 47.0%). When both mining and timber harvesting were limited such that deep mines were the only disturbance in the Royal Blue WMA, the total mature forest loss decreased to 3.9% and the percentage of interior forest loss ranged from 5.9% to 16.9%, depending on the scale of the analysis (Table 5.9). Results from the window analysis for

Sundquist Forest WMA were not very different from the Cumberlands landscape as a whole (Table 5.10). Regardless of the scale of analysis or ownership, mining had a greater impact on the loss of interior forest compared with timber harvesting, because of the linear nature of contour mines and the amount of edge created as a result. This phenomenon was apparent when comparing interior-forest loss between the base-case mining and limited timber harvest scenario with the limited mining A and limited timber harvesting scenario (scenarios B and C in Tables 5.8-5.10).

Forty-three percent of CERW habitat is currently within 150 m or less of an edge; under the base-case scenario, this proportion increased to 55% (Table 5.11, Figure 5.20). Not accounting for edge effects on CERW density, there was a 14.6% decline in the number of territories potentially supported under the base-case scenario. Accounting for edge effects, there was a 26% decline in the number of CERW territories (Table 5.11). Likewise, the number of CERW territories lost under the other two scenarios was nearly twice as great when edge effects were included (Table 5.11).

## Discussion

### *Cerulean Warbler Habitat Availability*

Cerulean warblers were negatively affected by all modeled land use scenarios. This species showed slight increases after 20 years under some scenarios; suggesting that current populations can recover if future resource extraction is limited. However, this increase disappeared in the face of continuing disturbance beyond our ten-year timeframe. When we extrapolated disturbance beyond the first ten years assuming the same rates of mining and timber harvest, CERW populations continued to decline dramatically under all potential scenarios out to 50 years. The best-case scenario for CERW was the one with the least amount of disturbance – limited mining A (deep mines only) and limited timber harvesting – yet this scenario still resulted in a predicted loss of ~5000 breeding territories during ten years (and > 6000 territories lost if edge effects were considered, Table 5.11). Therefore, none of the modeled scenarios sustained this species. Continued disturbance at base-case levels will have significant effects on

Cumberland Mountains CERW population, which represents a significant portion of the global breeding population.

Our modeling cannot show whether there is a threshold of habitat availability that is reached before all mature forest is lost, below which CERW may disappear from the landscape. Such an ‘extirpation threshold’ refers to the minimum proportion of suitable habitat necessary for population persistence (Lande 1987, Bascompte and Sole 1996). As the proportion of suitable habitat declines, the landscape-level mortality rate increases and the landscape-level reproductive rate decreases (Fahrig 2002). Similar thresholds have been described at the system level when normal cycles of disturbance and recovery are replaced by compounded disturbances (Paine et al. 1998) or when more frequent, more intense, or larger perturbations occur than the system is accustomed (Romme et al. 1998). Percolation theory is also relevant as it is based on the concept of a fundamental critical threshold of cluster size and number in random grids, and has increased our theoretical understanding of habitat fragmentation (Turner et al. 2001). Forests are contiguous and ‘percolate’ across a landscape when there is little or no fragmentation; however, as forest area is lost, there is a point where connectivity is so low that the percolating cluster is disconnected, and this process is typically non-linear (Turner et al. 2001). Percolation theory is based on randomly generated maps where this threshold response occurs around 0.6 (i.e., when forest area is less than 60% of the landscape). The level of disturbance expected to occur in the coming decade from the combined effects of mining and timber harvesting may be within the realm of causing this type of threshold response; there is currently ~72% forest cover and under the base-case scenario we predict a total forest loss of 11%. Predicting the level of habitat loss where such a threshold response is likely on a real landscape with real populations is not trivial and requires incorporation of animal movement rates, matrix quality, as well as birth and death rates (Fahrig 2001). Nevertheless, in simplistic terms, the Cumberlands landscape will be at approximately 60% forest cover in ten years given the base-case scenario. This result may suggest serious potential problems with the integrity of this forest landscape in the near future for mature-forest songbirds.

### *Golden-winged warbler habitat availability*

Golden-winged warblers were positively affected by some scenarios in the short term and negatively affected by others. Scenarios in which mines were reclaimed with a mix of herbaceous and woody vegetation all resulted in increases in the GWWA population whereas herbaceous-only reclamation scenarios all resulted in a decrease. Mines reclaimed to grassland eventually become suitable for GWWA in our simulations, but not before a dramatic decrease where there was little remaining suitable habitat on the landscape (Figure 5.12). Again, this pattern assumed disturbance only occurred in the first ten years; if mining continued for another decade, the amount of GWWA habitat would likely stabilize or slightly increase as grassland succeeded to shrubland and shrubland to young forest. Base-case mining with hybrid reclamation and limited timber harvesting represented the best-case scenario for GWWA; it created 438 high-quality territories, doubling the current Cumberland population estimated to be approximately 400 breeding pairs (Bulluck and Buehler, unpublished data).

When we considered both high- and low-quality habitats for GWWA, reclaimed mines and timber harvests, respectively, the ranking of scenarios changed (Table 5.7). Scenarios with base-case timber harvesting were ranked higher than those with limited timber harvesting, because of additional low-quality habitat. However, the actual number of territories added under the base-case timber-harvesting scenario was minimal compared to the limited timber harvesting scenarios (Table 5.7). Viewed in light of the conservation goals at hand, the benefit of the tens of GWWA territories added over the Cumberland landscape probably does not compensate for the thousands of CERW territories lost in these same scenarios (Table 5.5).

### *Interior forest loss*

The loss of interior forests is much greater than the total loss of forests from mining and timber harvesting in the Cumberland Mountains region. This effect increased with the spatial extent of the analysis and with the intensity of disturbance (Figure 5.18). Comparable ratios of interior and total forest loss were found for the region as a whole and Sundquist Forest WMA, but the loss of interior forests was much more dramatic in the Royal Blue WMA. Currently, 56-74% of the mature forest in Royal Blue WMA is interior (depending on the scale of the window analysis), compared to only 24-55% in the Sundquist Forest WMA and 32-59% in the Cumberland Mountains region as a whole. Therefore, every hectare of mature forest lost to disturbance in Royal Blue is more likely to be interior forest than in Sundquist Forest WMA or the entire region. This is also demonstrated well by the fact that the largest patch of interior forest comprises almost the entire southern half of Royal Blue WMA (Figure 5.17). The scenario with the most limited amount of disturbance (limited mining A and limited timber harvest) was undoubtedly the best alternative for minimizing loss of interior forests on Royal Blue with a loss of only 3.9% of total forest and a loss of 6-14.8% of interior forest (Table 5.9). In Royal Blue, this scenario represented no timber harvesting by TWRA and deep mines as the only method of coal extraction. If CERW conservation is a priority, limiting disturbance in forests that are currently spatially contiguous and intact may be the most effective strategy for limiting impacts on CERW populations. This is especially true considering the degree of disturbance slated to occur in the remainder of the region.

Mining and timber harvesting have unique impacts on forest loss. Timber harvesting removes more total area of mature forest from the Cumberland Mountains landscape (Table 5.3) because industrial harvests are spatially more extensive than the contour mines that are ubiquitous in this region. This may not be the case in Kentucky and/or West Virginia where mountain-top removal and cross-ridge mining are more prevalent. Both mining and timber harvesting cause considerable declines in interior forest relative to total forest loss, but mining appears to have a larger per-hectare impact on interior forests. For every hectare of forest removed from mining activities, there is a greater loss of interior forest than with the same area of forest lost from timber harvesting. This result is likely a reflection of the linear nature of contour mines and therefore the greater amount of edge created compared to timber harvests.

Interior-forest loss is not a loss of forest area per se, but the conversion of interior forest to edge forest (Wickham et al. 2007). Edge forests are different from interior forests in their microclimate, species abundance and community assemblage, and ecological processes such as biomass accumulation (Saunders et al. 1991). Furthermore, edges can negatively affect forest songbird abundance (Boulinier et al. 1998, Wood et al. 2006) and productivity (Brittingham and Temple 1983, Robinson et al. 1995, Flashpoler et al. 2001, Manolis et al. 2002). For this reason, we assessed the impact of interior-forest loss on CERW habitat and the resulting number of breeding territories compared with the loss of total forest. The loss of breeding territories was nearly twice as great when accounting for the lower density of breeding territories in edge forest (Table 5.11).

### *Study implications*

The Cumberland Mountains landscape, occupied by two declining songbirds with conflicting habitat needs, presents a unique challenge to conservation biologists. None of the land use scenarios modeled in this study represented a sustainable option for both golden-winged and cerulean warbler populations in the Cumberland Mountains. The goal of no net loss for ceruleans was not met under any of the scenarios (Table 5.5); the best-case scenario for ceruleans resulted in a loss of >5,000 breeding pairs in only ten years (~10% of the total population). This same scenario would increase the golden-winged population by ~100 breeding pairs. The best-case scenario for golden-wingeds resulted in a loss of >8000 cerulean warbler breeding territories. The goal of doubling the golden-winged population was met under the base-case mining and limited timber harvest scenario, but this increase was ephemeral (Figures 5.12-15). If disturbance continued beyond ten years, shrubland habitat would likely be more ubiquitous over time and golden-winged warbler populations may be sustained, but this disturbance would inevitably lead to the loss of additional cerulean habitat.

Despite the fact that none of the scenarios we assessed here were sustainable alternatives for either GWWA or CERW, more sustainable alternatives are possible. Our scenarios represented the expected rates of timber harvesting and mining as described by current landowners in the region. To sustain cerulean warbler populations, new disturbance must be much more limited than that represented in the scenarios here and preferably should be limited most in the largest patches of existing interior forest (Figure 5.17). This may be most achievable on state-owned lands if both the timber and mineral rights are publicly-owned; making these lands refugia in a highly-disturbed landscape in the near future. To sustain golden-winged warbler populations, the early successional habitat currently on the landscape could be maintained and improved through time rather than depending on new disturbance to sustain this species. If songbird conservation is the goal, it imperative that state-owned lands provide a core of undisturbed habitat for ceruleans and a core of quality, early successional habitat for golden-wingeds, especially considering the degree of disturbance expected on private lands. At the same time, we must work with private landholders to identify the pattern and extent of disturbance that best conserves both species.

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# Appendices

## Appendix A: Tables and Figures

**Table 5.1:** Accuracy assessment for the Cumberland Mountains landcover classification of SPOT imagery from September, 2006.

| | | ACTUAL | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mature forest | Grassland/ pasture | Young forest | OlderCC | RecentCC | Urban/ barren | Shrubland | Total | % classified correctly |
| **PREDICTED** | Mature forest | 23 | 1 | | | | | 1 | 25 | 0.920 |
| | Grassland/pasture | 1 | 17 | | | | 6 | 1 | 25 | 0.680 |
| | Young forest | | | 20 | | | 1 | 4 | 25 | 0.800 |
| | OlderCC | | | 1 | 9 | | | 4 | 14 | 0.643 |
| | RecentCC | | | | | 17 | | 1 | 18 | 0.944 |
| | Urban/bare | | 2 | 2 | | | 21 | | 25 | 0.840 |
| | Shrubland | 1 | 1 | 4 | | | | 18 | 23 | 0.783 |
| | Total | 25 | 21 | 27 | 9 | 17 | 28 | 29 | 155 | |

**Table 5.2:** Description of stakeholder land ownership and land use in the Cumberland Mountains obtained from meetings and individual conversations with each.

| | Landowner | | | | |
|---|---|---|---|---|---|
| | **Coal Creek** | **Fountain Forestry and National Coal** | **TWRA and TVA** | **University of Tennessee** | **All other private lands** |
| Area managed (ha) | 16,363 | 51,668 | 21,611 | ~4,452 | 111,910 |
| Property | Coal Creek | Sundquist WMA and Brimstone** | Royal Blue WMA | UT property | NA |
| Hectares harvested /year | 445* | 931 | 61 | 41 | 971 |
| Hectares/harvest | 28-49* | 28-49 | 10 | 4-32 | 8-41 |
| Harvest arrangement | Clumped in watersheds | Clumped in watersheds | Scattered | Scattered | Scattered |
| Proportion CC:SW | 1:0* | 1:0 | 1:3 | 1:0 | 1:1 |
| Rotation length | 80* | 80 | 100 | 100 | NA |
| Management expectation | Indefinite | Indefinite | Indefinite | Indefinite | NA |
| Annual contour mining (ha) | 81* | 81 | 194 | 0 | 81* |
| Annual deep mine (ha) | 24* | 24 | 24 | 0 | 24* |

*Information assumed based on other landowner estimates because we were unable to get the information directly from the actual landowner

**Brimstone is managed by Fountain Forestry, but not by National Coal

**Table 5.3:** Descriptions of land use scenarios in the Cumberland Mountains and the total area associated with each disturbance during the ten-year time frame for this model.

| Scenario | Description | Total Hectares |
|---|---|---|
| Base-case mining (BCM) | Mining as described to occur by stakeholders | 4,695 contour, 971 deep, and 486 from Zeb = **6,152** |
| Base-case timber (BCT) | Logging as described to occur by stakeholders | 18,212 industrial, 607 TWRA, 405 UT, and 6,475 private = **25,699** |
| Limited mining A (LIMa) | Deep mines and Zeb only | 1,457 |
| Limited mining B (LIMb) | Deep mines plus half of the number of contour mines | 3,804 |
| Limited timber (LIM) | Half the area on industrial land, none on public lands, and no change on private | 15,581 |
| Herbaceous reclamation | Current standard procedure with thick plantings of non-native grasses and forbs with no woody vegetation | NA |
| Hybrid reclamation | Planting of native hardwoods on half of the mine and herbaceous cover on the other half | NA |

**Table 5.4:** Summary of baseline conditions across the Cumberland Mountains ecoregion and in the Royal Blue and Sunquist Forest WMAs. Numbers are percentages. High-quality CERW and GWWA habitat are defined in Figure 5.8.

| | **Ecoregion** | **Royal Blue** | **Sundquist** |
|---|---|---|---|
| Mature forest cover | 72.6 | 86.0 | 72.8 |
| Young forest cover | 10.8 | 8.3 | 10.8 |
| Recent clearcut | 4.4 | 1.6 | 4.7 |
| Shrub cover | 4.2 | 2.7 | 8.6 |
| High-quality CERW habitat | 28.6 | 51.3 | 37.0 |
| High-quality GWWA habitat | 2.5 | 1.8 | 4.0 |

**Table 5.5:** Ranked scenarios for CERW based on the area of high-quality habitat lost and the number of territorial males lost under each for the Cumberland Mountains landscape. The two numbers in the first column represent the ranking of scenarios for the entire Cumberland Mountains ecoregion and for the Royal Blue WMA, respectively. The number of territories is estimated from the number of hectares assuming 10.8 territorial males/10 hectares.

| **Rank** | **Scenario** | **Hectares lost in 10 years** | **Territories lost** |
|---|---|---|---|
| 1,1 | Limited mining A, limited timber | -5,234 | -5652 |
| 2,3 | Limited mining B, limited timber | -6,376 | -6885 |
| 3,2 | Limited mining A, base-case timber | -6,679 | -7212 |
| 4,5 | Base-case mining, limited timber | -7,251 | -7830 |
| 5,4 | Limited mining B, base-case timber | -7,784 | -8405 |
| 6,6 | Base-case mining and timber | -8,616 | -9303 |

**Table 5.6:** Ranked scenarios for GWWA based on the area of high-quality habitat gained or lost after 15 years and the number of territorial males lost or gained under each for the Cumberland Mountains landscape. The number of territories is estimated from the number of hectares assuming 3.2 territorial males/10 ha.

| **Rank** | **Scenario** | **Hectares gained or lost** | **Territories lost or gained** |
|---|---|---|---|
| 1 | Base-case mining, Limited timber, hybrid | 1366 | 439 |
| 2 | Base-case mining and timber, hybrid | 1160 | 373 |
| 3 | Limited mining B, Limited timber, hybrid | 930 | 299 |
| 4 | Limited mining B, base-case timber, hybrid | 717 | 230 |
| 5 | Limited mining A, Limited timber, hybrid | 338 | 109 |
| 6 | Limited mining A, base-case timber, hybrid | 129 | 41 |
| 7 | Base-case mining, Limited timber, grass | -131 | -42 |
| 8 | Limited mining A, Limited timber, grass | -234 | -75 |
| 9 | Limited mining B, Limited timber, grass | -295 | -95 |
| 10 | Limited mining A, base-case timber, grass | -437 | -141 |
| 11 | Limited mining B, base-case timber, grass | -491 | -158 |
| 12 | Base-case mining and timber, grass | -529 | -170 |

**Table 5.7:** Ranked scenarios for GWWA based on the number of territories gained from the addition of both high and low-quality habitat after 15 years for the Cumberland Mountains landscape. The number of territories is estimated from the number of hectares assuming3.2 males/10 ha on high-quality habitat and 0.4 males/10 ha on low-quality habitat.

| Rank | Scenario | Territories gained |
|---|---|---|
| 1 | Base-case mining and timber, hybrid | 649 |
| 2 | Base-case mining, Limited timber, hybrid | 641 |
| 3 | Limited mining B, base-case timber, hybrid | 513 |
| 4 | Limited mining B, Limited timber, hybrid | 505 |
| 5 | Limited mining A, base-case timber, hybrid | 328 |
| 6 | Limited mining A, Limited timber, hybrid | 317 |
| 7 | Base-case mining, Limited timber, grass | 178 |
| 8 | Limited mining A, base-case timber, grass | 146 |
| 9 | Limited mining A, Limited timber, grass | 134 |
| 10 | Limited mining B, base-case timber, grass | 125 |
| 11 | Limited mining B, Limited timber, grass | 111 |
| 12 | Base-case mining, base-case timber, grass | 107 |

**Table 5.8:** Current (2006) and projected (2016) interior forest loss (ha) over a ten-year period for three different land use scenarios (A-C) and with four different edge effects represented by various window sizes (see text). The percentage loss is relative to the current amount of interior forest (in 2006). Ratio equals the percentage loss divided by the total forest loss (e.g., 16.58/11.6 = 1.43).

| **Edge effect (window size)** | **Interior forest (2006)** | **Interior forest (2016)** | **Percentage loss** | **Ratio** |
|---|---|---|---|---|
| *A. Base-case mining and timber harvesting, Total forest loss = 11.6%* | | | | |
| 50 m (1.2 ha) | 87,968 | 73,380 | 16.58 | 1.43 |
| 100 m (5.29 ha) | 73,053 | 56,202 | 23.07 | 2.00 |
| 150 m (10.89 ha) | 64,744 | 47,371 | 26.83 | 2.32 |
| 250 m (30.25 ha) | 52,961 | 33,444 | 36.85 | 3.19 |
| 300 m (42.25 ha) | 48,554 | 28,509 | 41.28 | 3.57 |
| *B. Base-case mining and limited timber harvesting, Total forest loss = 10.1%* | | | | |
| 50 m (1.2 ha) | 87,968 | 74,950 | 14.80 | 1.46 |
| 100 m (5.29 ha) | 73,053 | 57,763 | 20.93 | 2.07 |
| 150 m (10.89 ha) | 64,744 | 49,019 | 24.29 | 2.40 |
| 250 m (30.25 ha) | 52,961 | 35,263 | 33.42 | 3.30 |
| 300 m (42.25 ha) | 48,554 | 30,408 | 37.37 | 3.69 |
| *C. Limited mining A and limited timber harvesting, Total forest loss = 8.6%* | | | | |
| 50 m (1.2 ha) | 87,968 | 77,895 | 11.45 | 1.32 |
| 100 m (5.29 ha) | 73,053 | 61,522 | 15.78 | 1.83 |
| 150 m (10.89 ha) | 64,744 | 53,261 | 17.74 | 2.05 |
| 250 m (30.25 ha) | 52,961 | 40,260 | 23.98 | 2.77 |
| 300 m (42.25 ha) | 48,554 | 35,522 | 26.84 | 3.10 |

**Table 5.9:** Current (2006) and projected (2016) interior forest loss (ha) in the Royal Blue WMA over a ten-year period for three different land use scenarios (A-C) and with four different edge effects represented by various window sizes (see text). The percentage loss is relative to the current amount of interior forest (in 2006).

| **Edge effect (window size)** | **Interior forest (2006)** | **Interior forest (2016)** | **Percentage loss** | **Ratio** |
|---|---|---|---|---|
| *A. Base-case mining and timber harvesting, Total forest loss = 11.8%* | | | | |
| 50 m (1.1 ha) | 13,795 | 10,922 | 20.83 | 1.76 |
| 100 m (5.29 ha) | 12,647 | 8,722 | 31.03 | 2.62 |
| 150 m (10.89 ha) | 11,953 | 7,466 | 37.54 | 3.17 |
| 250 m (30.25 ha) | 10,884 | 5,230 | 51.94 | 4.39 |
| 300 m (42.25 ha) | 10,483 | 4,408 | 57.95 | 4.89 |
| *B. Base-case mining and limited timber harvesting, total forest loss = 9.1%* | | | | |
| 50 m (1.1 ha) | 13,795 | 11,513 | 16.54 | 1.82 |
| 100 m (5.29 ha) | 12,647 | 9,460 | 25.19 | 2.76 |
| 150 m (10.89 ha) | 11,953 | 8,337 | 30.25 | 3.32 |
| 250 m (30.25 ha) | 10,884 | 6,293 | 42.18 | 4.63 |
| 300 m (42.25 ha) | 10,483 | 5,553 | 47.03 | 5.16 |
| *C. Limited mining A and limited timber harvesting, Total forest loss = 3.9%* | | | | |
| 50 m (1.1 ha) | 13,795 | 12,974 | 5.95 | 1.49 |
| 100 m (5.29 ha) | 12,647 | 11,456 | 9.42 | 2.36 |
| 150 m (10.89 ha) | 11,953 | 10,674 | 10.70 | 2.68 |
| 250 m (30.25 ha) | 10,884 | 9,273 | 14.80 | 3.71 |
| 300 m (42.25 ha) | 10,483 | 8,709 | 16.92 | 4.24 |

**Table 5.10:** Current (2006) and projected (2016) interior forest loss (ha) in the Sundquist WMA over a ten-year period for three different land use scenarios (A-C) and with four different edge effects represented by various window sizes (see text). The percentage loss is relative to the current amount of interior forest (in 2006).

| **Edge effect (window size)** | **Interior forest (2006)** | **Interior forest (2016)** | **Percentage loss** | **Ratio** |
|---|---|---|---|---|
| *A. Base-case mining and timber harvesting, Total forest loss = 11.5%* | | | | |
| 50 m (1.1 ha) | 13,785 | 11,558 | 16.15 | 1.40 |
| 100 m (5.29 ha) | 10,874 | 8,415 | 22.61 | 1.96 |
| 150 m (10.89 ha) | 9,197 | 6,807 | 25.99 | 2.25 |
| 250 m (30.25 ha) | 6,904 | 4,448 | 35.57 | 3.08 |
| 300 m (42.25 ha) | 6,047 | 3,667 | 39.36 | 3.41 |
| *B. Base-case mining and limited timber harvesting, total forest loss = 8.9%* | | | | |
| 50 m (1.1 ha) | 13,785 | 11,890 | 13.74 | 1.53 |
| 100 m (5.29 ha) | 10,874 | 8,669 | 20.28 | 2.26 |
| 150 m (10.89 ha) | 9,197 | 7,033 | 23.53 | 2.63 |
| 250 m (30.25 ha) | 6,904 | 4,651 | 32.64 | 3.64 |
| 300 m (42.25 ha) | 6,047 | 3,858 | 36.20 | 4.04 |
| *C. Limited mining A and limited timber harvesting, Total forest loss = 6.9%* | | | | |
| 50 m (1.1 ha) | 13,785 | 12,512 | 9.23 | 1.34 |
| 100 m (5.29 ha) | 10,874 | 9,449 | 13.10 | 1.90 |
| 150 m (10.89 ha) | 9,197 | 7,898 | 14.12 | 2.05 |
| 250 m (30.25 ha) | 6,904 | 5,610 | 18.75 | 2.72 |
| 300 m (42.25 ha) | 6,047 | 4,778 | 20.98 | 3.05 |

**Table 5.11:** Hectares of CERW habitat (mature forest > 580 m), interior forest habitat, edge habitat (defined by the 150-m edge effect window), and the proportion of CERW habitat that is edge (edge/mature [total]) both currently and for three different land use scenarios. The estimated number of CERW territories and the percent decrease in territories for three different scenarios both with and without edge effects. Without edge effects assumes high densities in both edge and interior habitats (10.8/10 ha) and with edge effects assumes high density (10.8/10 ha) for interior habitats and low density (2.7/10 ha) for edge habitats.

| | **Current 2006** | **Base-case 2016** | **Base-case/LIM 2016** | **LIMa/LIM 2016** |
|---|---|---|---|---|
| Mature habitat (total) | 58,930 | 50,314 | 51,679 | 53,696 |
| Interior habitat | 33,446 | 22,517 | 23,618 | 27,376 |
| Edge habitat | 25,484 | 27,797 | 28,060 | 26,320 |
| Proportion in edge | 0.43 | 0.55 | 0.54 | 0.49 |
| # territories (no edge effect) | 64071 | 54703 | 56186 | 58379 |
| % decrease in territories | | 14.6 | 12.3 | 8.9 |
| # territories (with edge effect) | 43290 | 32037 | 33305 | 36918 |
| % decrease in territories | | 26.0 | 23.1 | 14.7 |

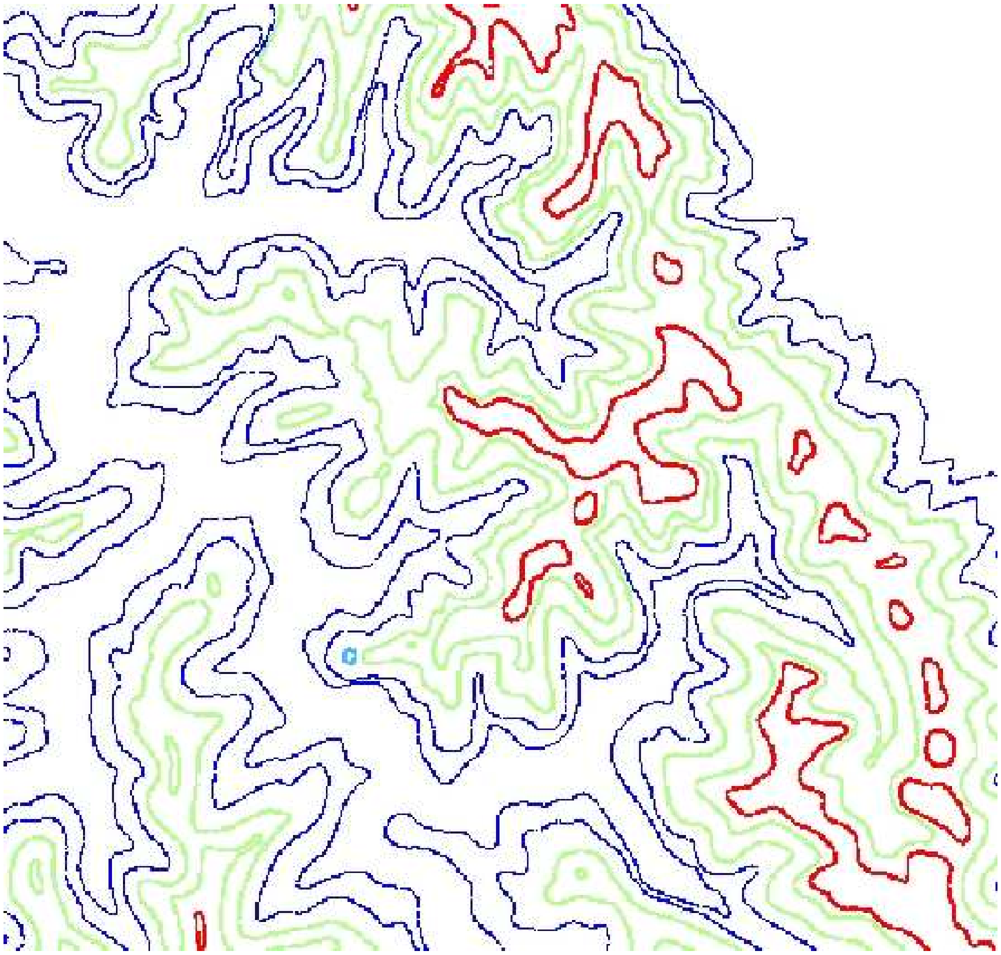


**Figure 5.1:** Portion of the derived coal seam layer for the Cumberland Mountains of Tennessee. Each line represents an individual coal seam. During our modeling of land use, all simulated coal mining originated on these coal seams.

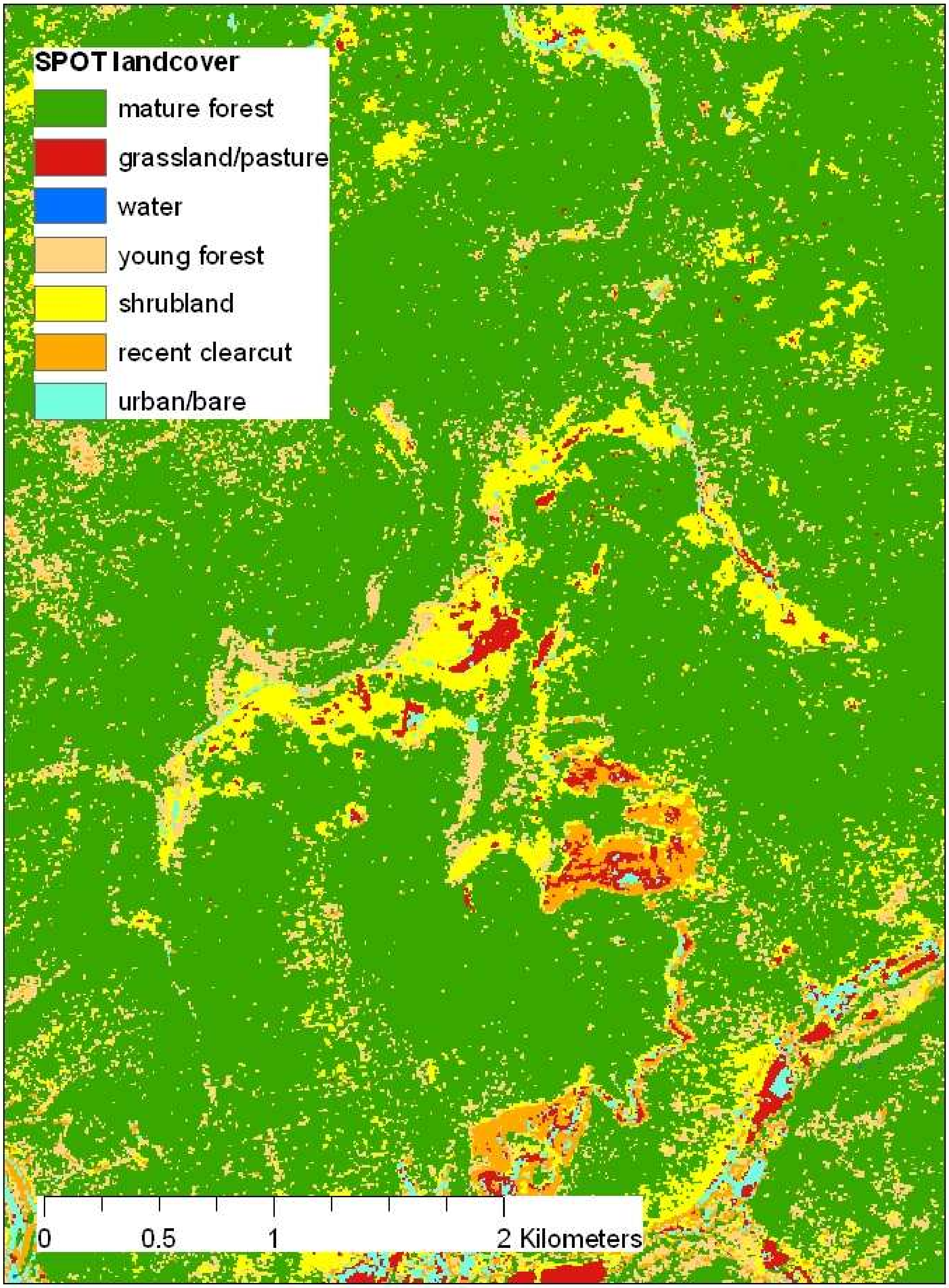


**Figure 5.2:** Example from final SPOT landcover classification centered on Ash Log Mountain, one of our main study sites in the Sundquist Forest WMA.

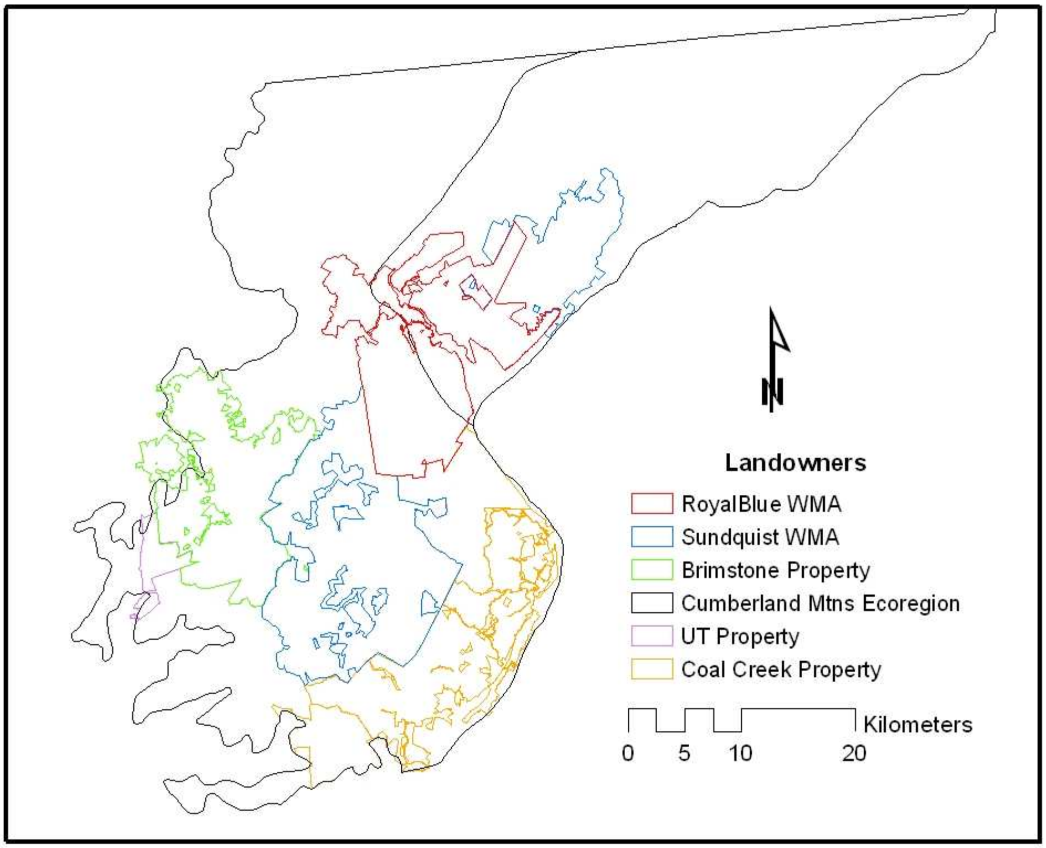


**Figure 5.3:** Large landowner boundaries in the Cumberland Mountains ecoregion of Tennessee. Royal Blue and Sunquist Forest WMAs are owned by TWRA, but the timber rights on Sundquist are owned by Fountain Forestry along with Brimstone property. The mineral rights on Royal Blue are owned by TVA and the mineral rights on Sundquist are owned by National Coal Corporation. Coal Creek Property is owned by Coal Creek Mining and Manufacturing who own both the mineral and timber rights on these lands. All other areas are assumed to be private landowners.

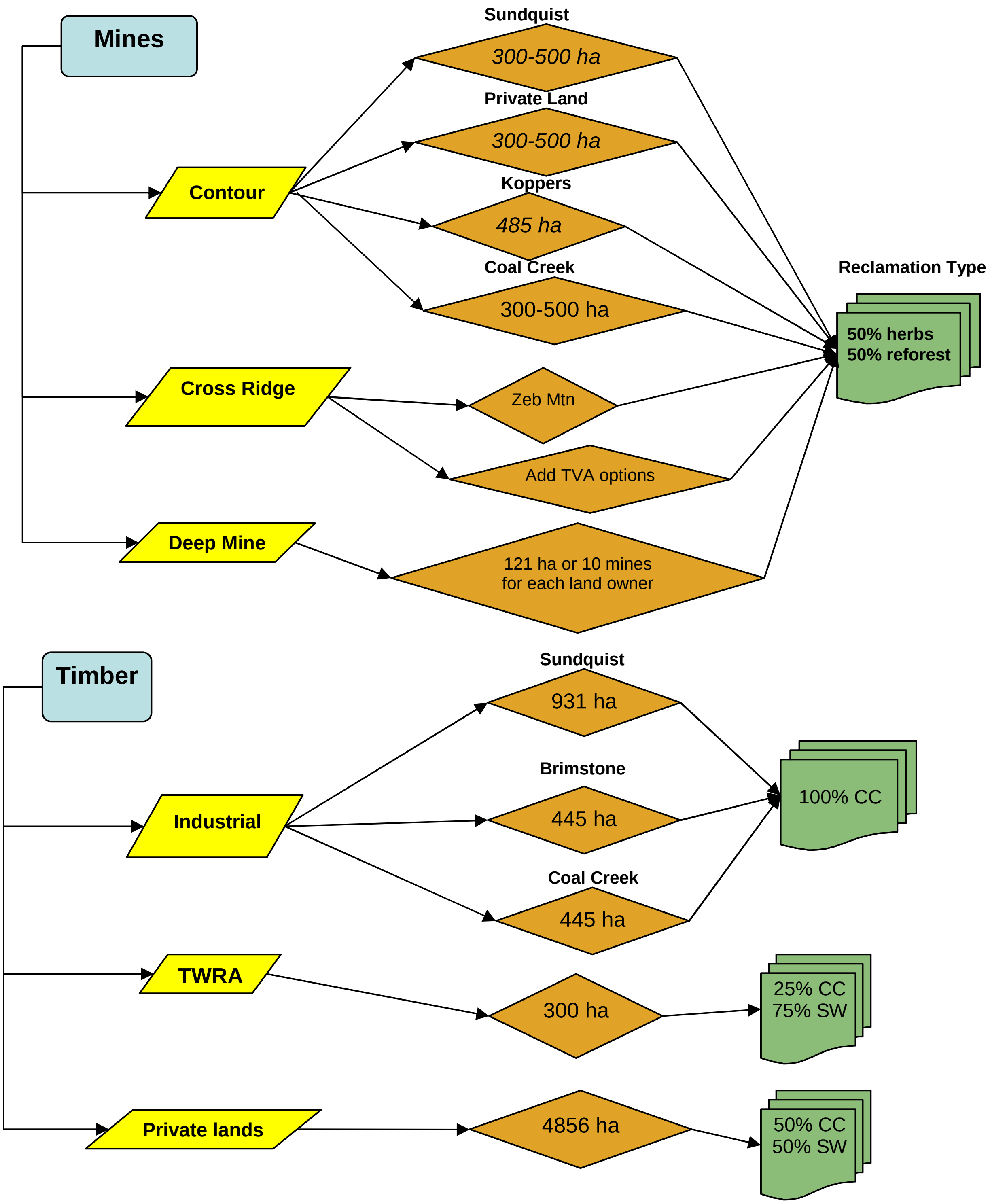


**Figure 5.4:** Framework for disturbance models. This framework represents base-case timber harvests, base-case mining, and hybrid reclamation of mines. Hectares are for the first 5 years of disturbance.

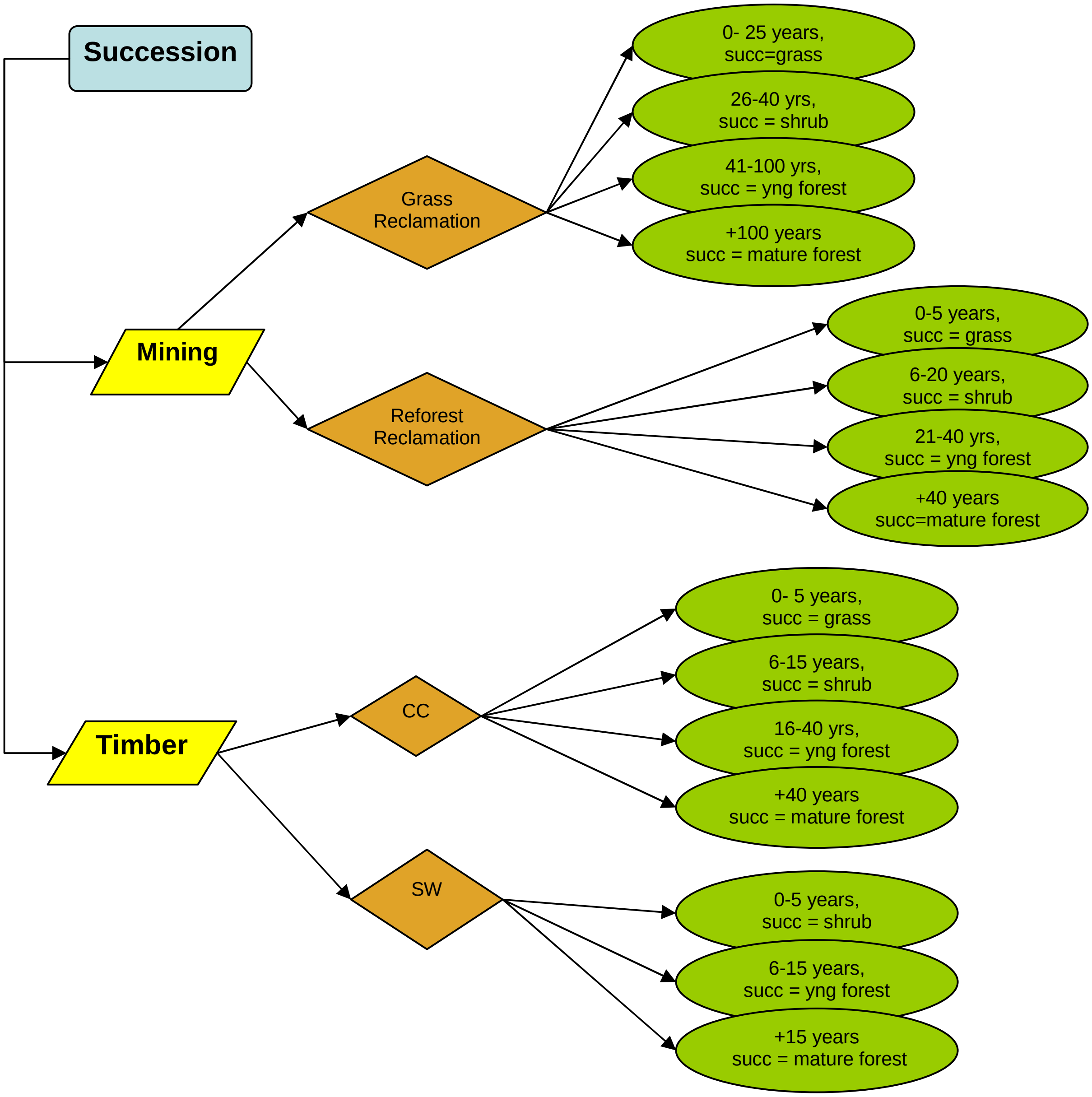


**Figure 5.5:** Description of succession rules following mining with two types of reclamation and following two types of timber harvest.

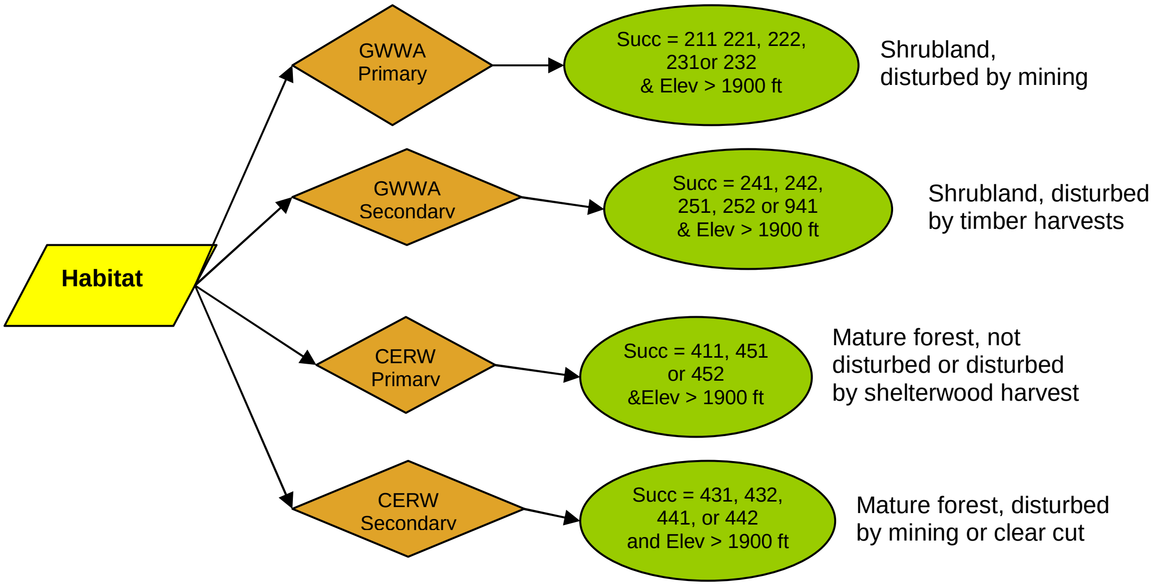


**Figure 5.6:** Framework for habitat classification for golden-winged and cerulean warblers. The total area of suitable habitat is output at each time step and for each model scenario. Primary habitat for a species is assumed to be high-quality and have a higher density of breeding males than secondary habitat (see text).

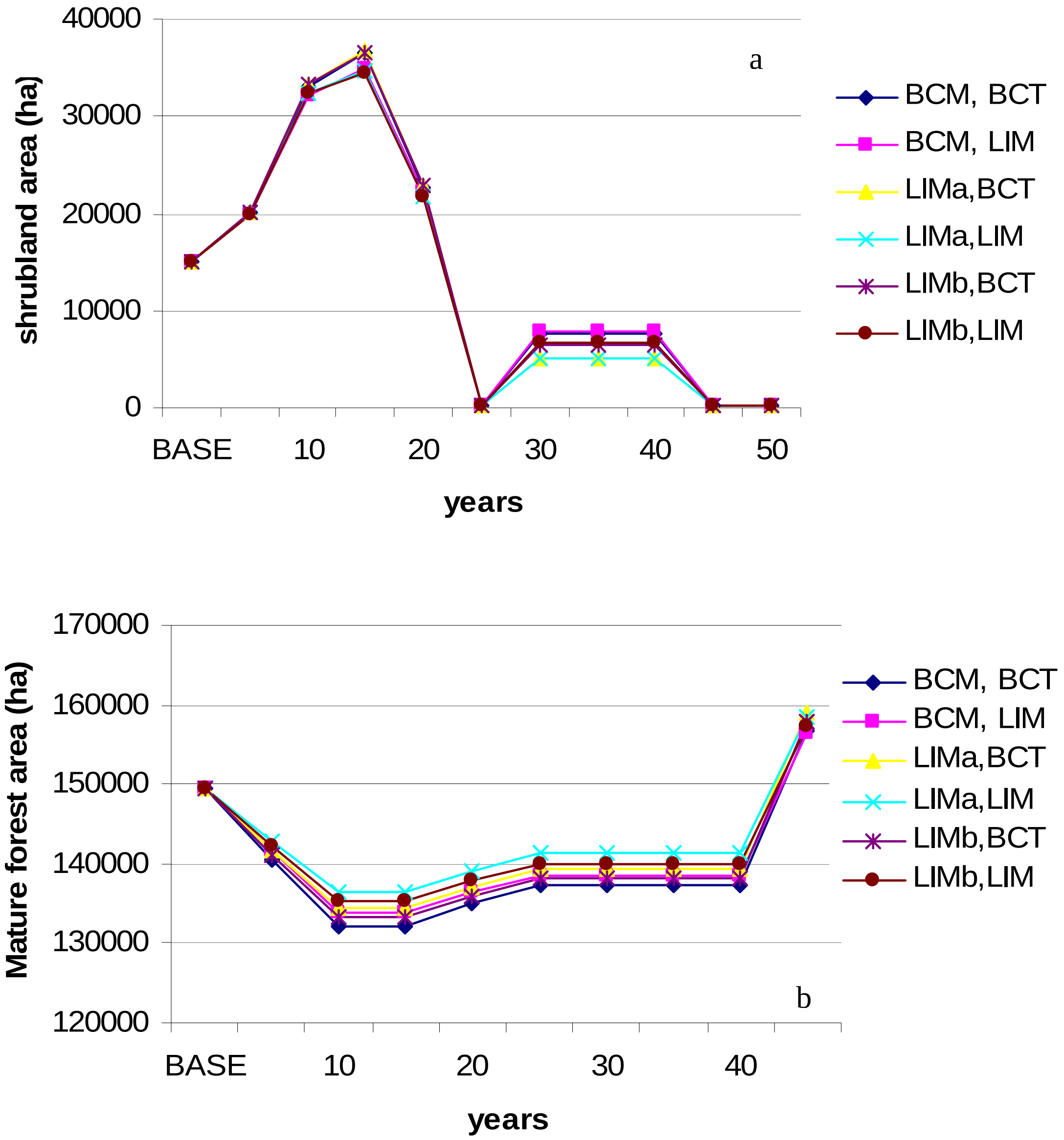
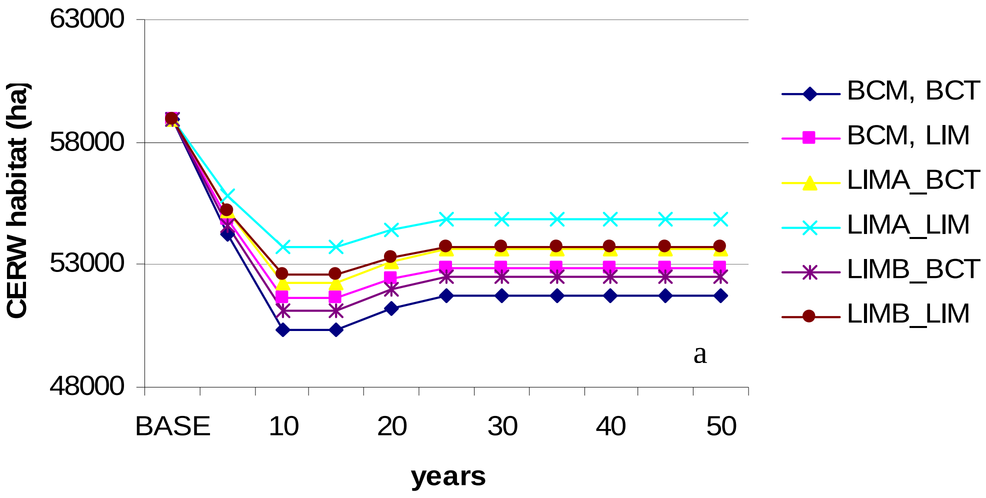


**Figure 5.7:** Projected area of shrubland (a) and mature forest cover (b) across the Cumberland Mountains landscape for 12 different scenarios of mining and timber harvesting. Disturbances are assumed to occur only during the first 10 years and then succession follows as described in Figure 5.5. See Table 5.3 for scenario abbreviations.



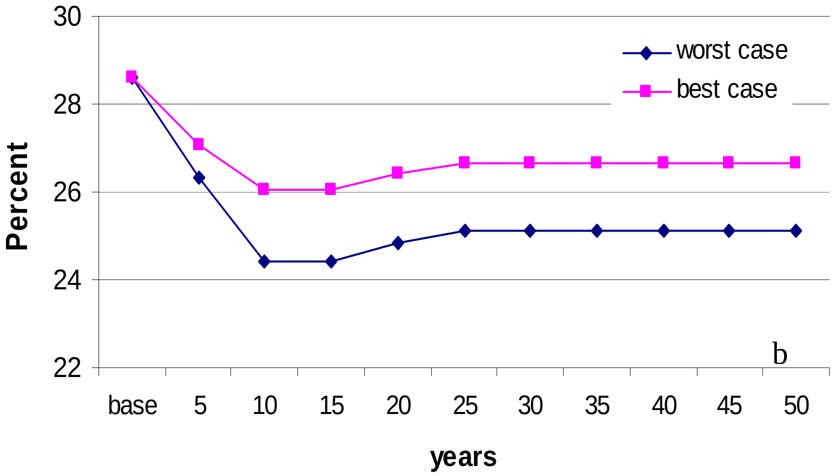


**Figure 5.8:** Projected area of high-quality CERW habitat (a) across the Cumberland Mountains landscape (~206K ha total) and the percentage of this landscape in high-quality CERW habitat (b) for the best and worst case scenarios (ranked 1 and 6 respectively in Table 5.5). Data are from the present (base) and projected 50 years into the future under different scenarios of mining and timber harvest. Disturbances are modeled only during the first 10 years. See Table 5.3 for scenario abbreviations.

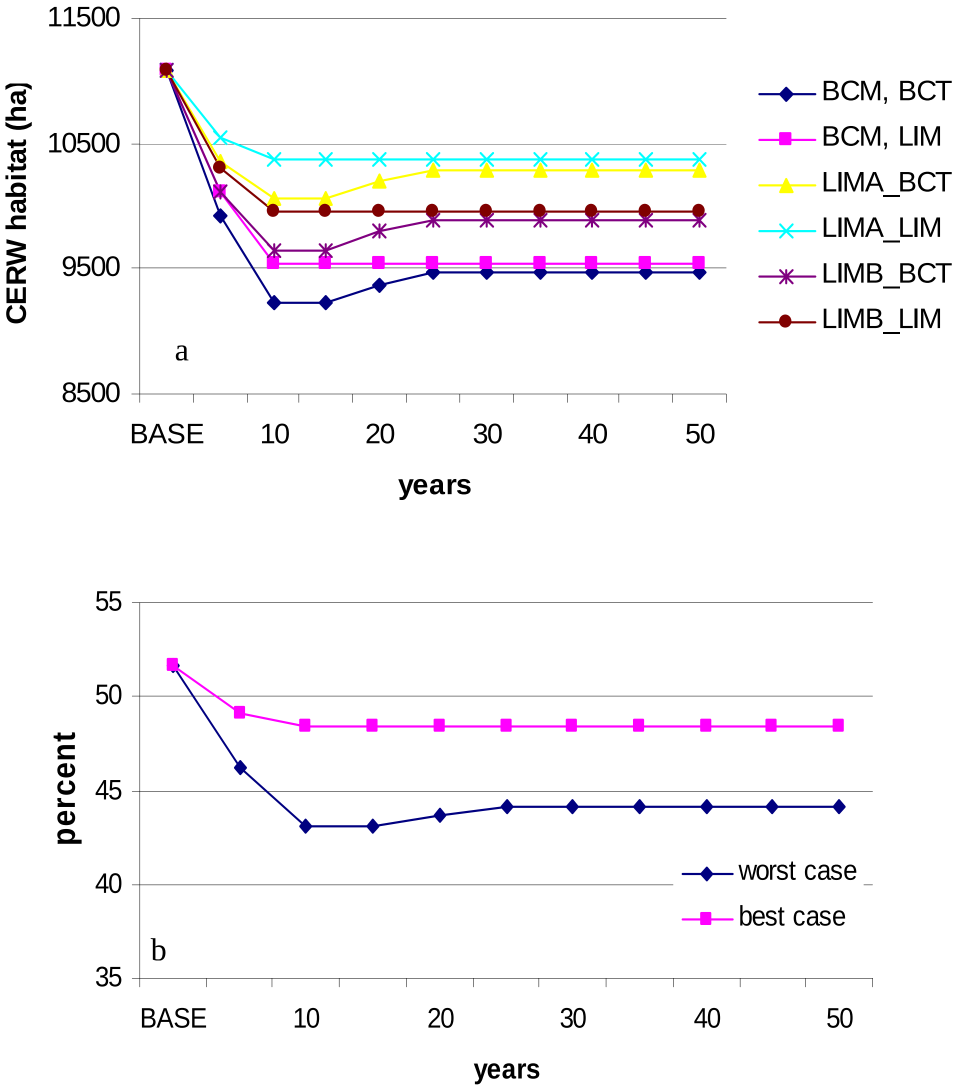
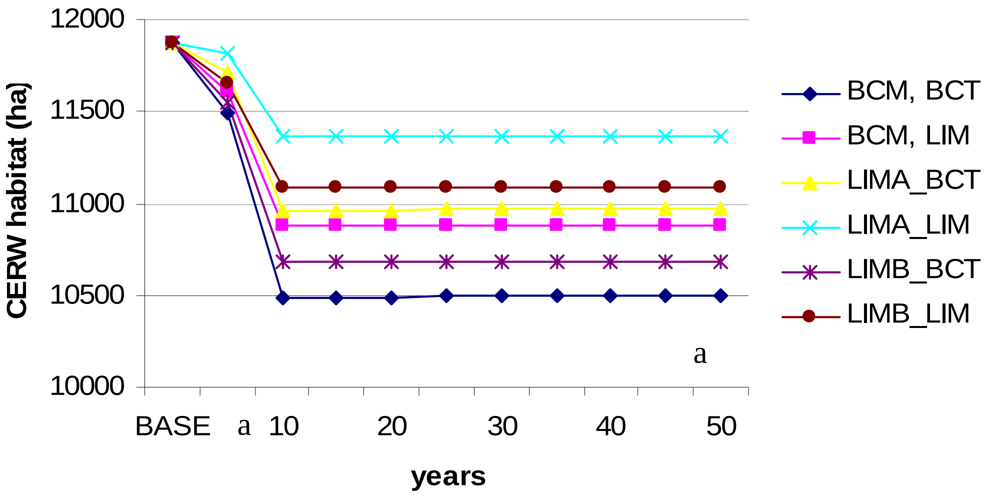


**Figure 5.9:** Projected area of high-quality CERW habitat (a) in the Royal Blue WMA (~21.5K ha total) and the percentage of this landscape in high-quality CERW habitat (b) for the best and worst case scenarios (ranked 1 and 6 respectively in Table 5.5). Data are from the present (base) and projected 50 years into the future assuming various scenarios of mining and timber harvest. Disturbances are modeled only during the first 10 years. The base-case timber harvest scenario assumes 65% shelterwood and 25% clearcuts in this WMA while the limited timber harvest scenario assumes no timber harvest in this WMA. See Table 5.3 for scenario abbreviations.



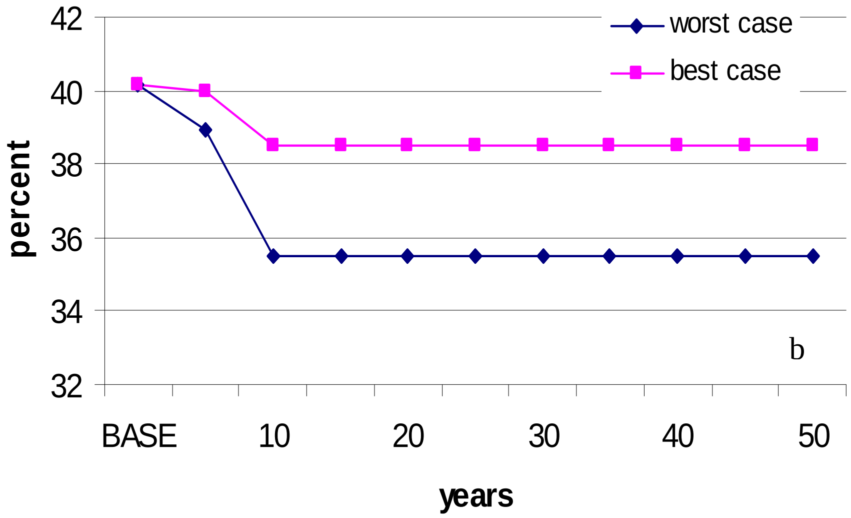


**Figure 5.10:** Projected area of high-quality CERW habitat (a) in the Sundquist WMA (~31.5K ha total) and the percentage of this landscape in high-quality CERW habitat (b) for the best and worst case scenarios (ranked 1 and 6 respectively in Table 5.5). Data are from the present (base) and projected 50 years into the future assuming various scenarios of mining and timber harvest. Disturbances are assumed to occur only during the first 10 years. All timber harvests in this WMA are silvicultural clearcuts and the limited timber harvest scenario assumes half the area cut compared to base-case timber harvest. See Table 5.3 for scenario abbreviations.

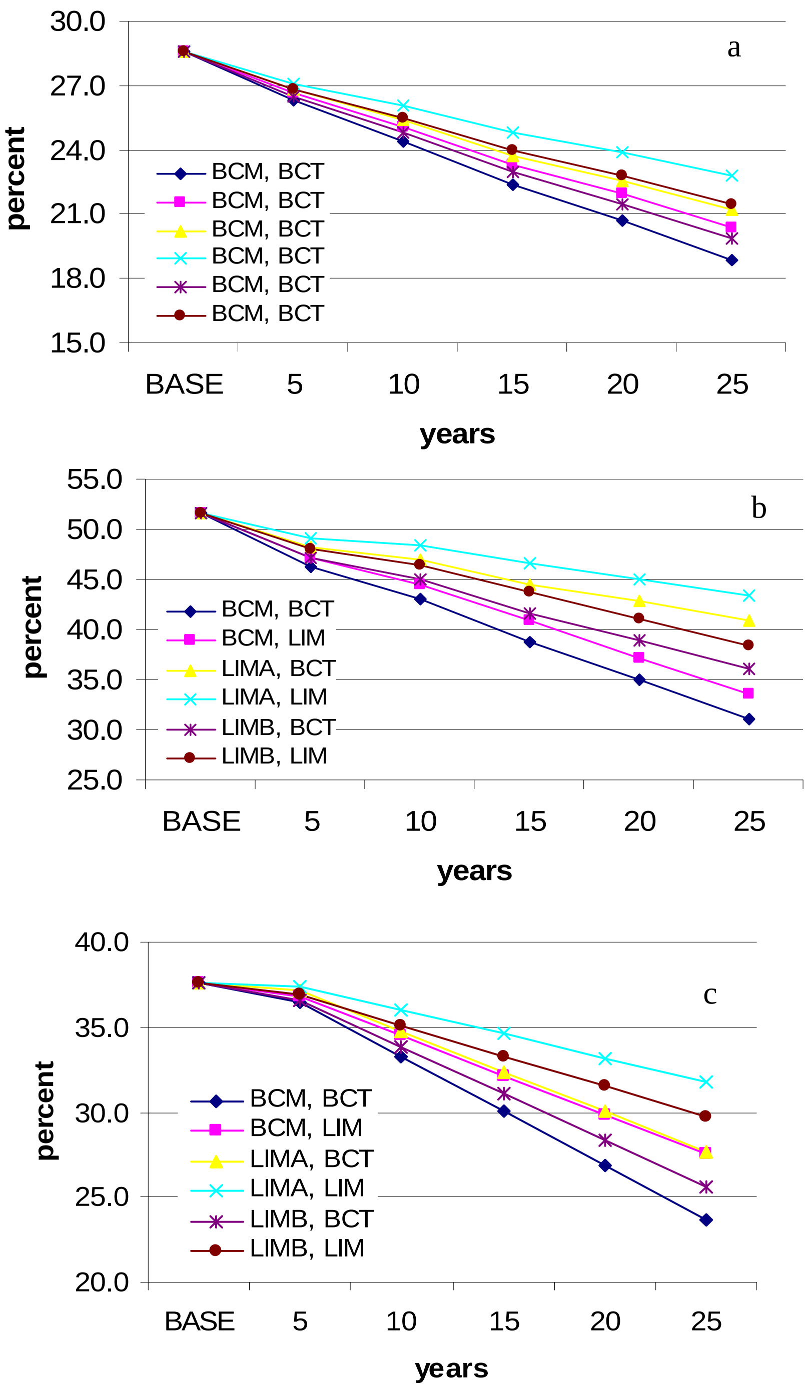


**Figure 5.11:** Percentage of the Cumberland Mountains landscape (~206K ha) (a), the Royal Blue WMA (~21.5K ha) (b), and the Sundquist WMA (~31.5K ha) (c) in high-quality CERW habitat assuming mining and timber disturbances occur beyond the first ten years, but disturbance beyond ten years is an extrapolation. See Table 5.3 for scenario abbreviations.

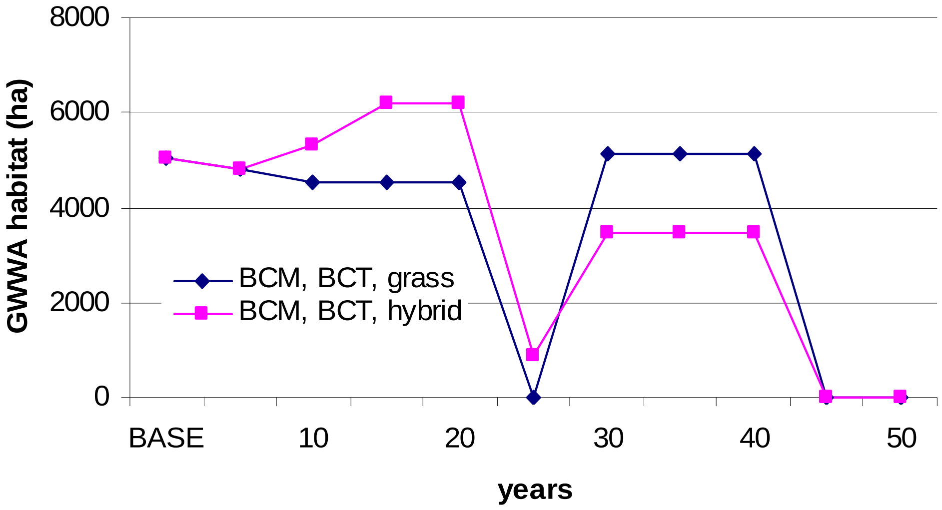


**Figure 5.12:** Effects of reclamation type on GWWA habitat availability. Area of high-quality GWWA habitat across the Cumberland Mountains landscape (~206K ha total) from the present (base) and projected 50 years into the future for the base-case scenarios with both hybrid and grassland reclamation.

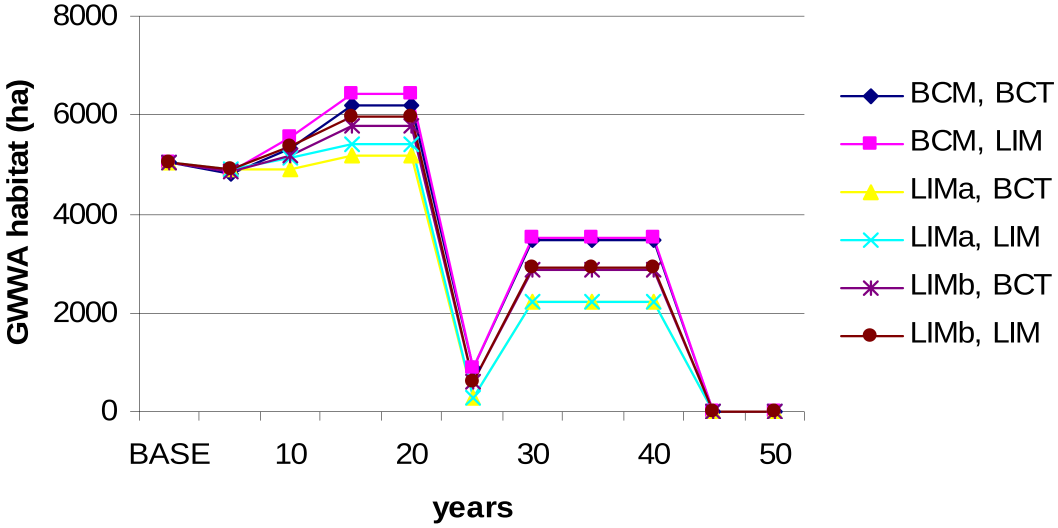


**Figure 5.13:** Projected area of high-quality GWWA habitat across the Cumberland Mountains landscape (~206K ha total) for different scenarios of mining and timber harvesting and only hybrid reclamation. Disturbances are modeled only during the first 10 years. See Table 5.3 for scenario abbreviations.

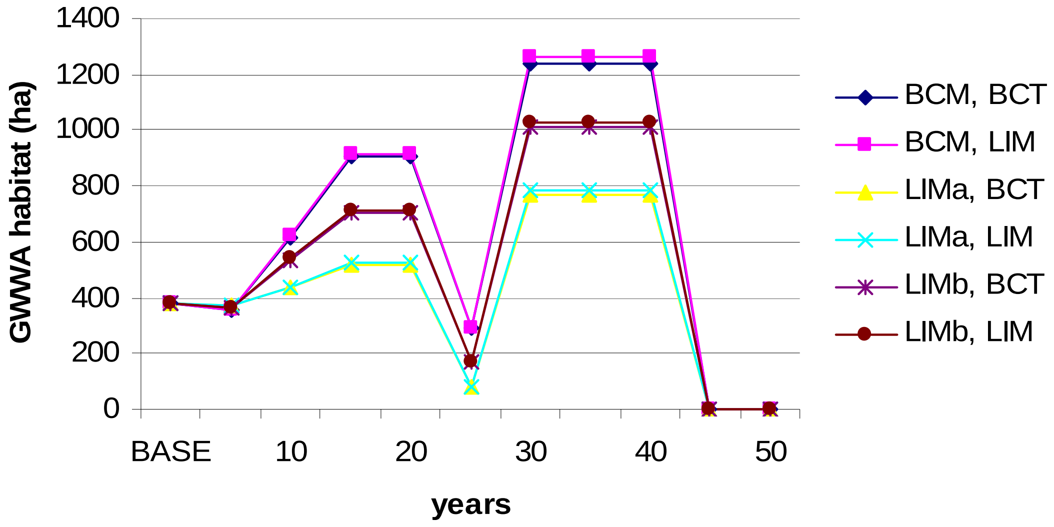


**Figure 5.14:** Projected area of high-quality GWWA habitat across the Royal Blue WMA (~21.5K ha total) from the present (base) and projected 50 years into the future for different scenarios of mining and timber harvest and only hybrid reclamation. Disturbances are modeled only during the first 10 years.

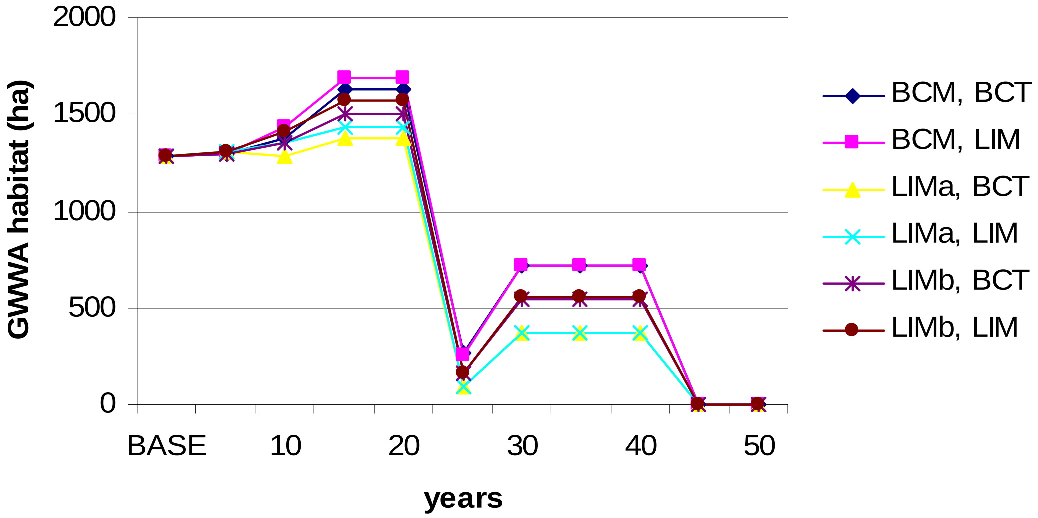


**Figure 5.15:** Projected area of high-quality GWWA habitat across the Sundquist WMA (~31.5K ha total) from the present (base) and projected 50 years into the future under different scenarios of mining and timber harvest and only hybrid reclamation. Disturbances are modeled only during the first 10 years.

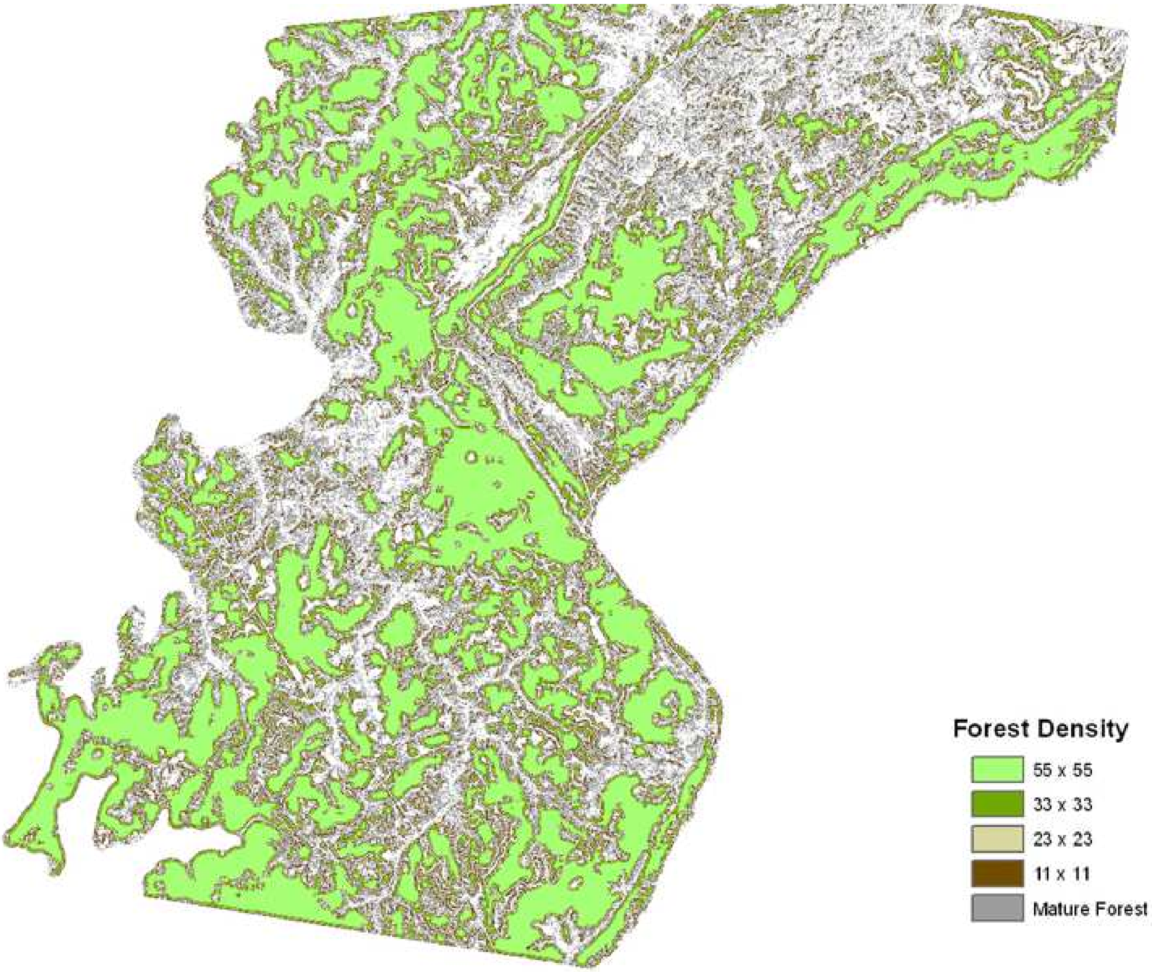


**Figure 5.16:** Current distribution of interior forest before simulating disturbance (2006). The light green areas are mature forest patches using the largest (150 m) edge effect/window size and the other colors show the additional area of interior forest added with smaller edge effect/window sizes. The grey areas are mature forest that is not considered interior and the white areas are non-mature forest. See Figure 5.18 for more detailed view.

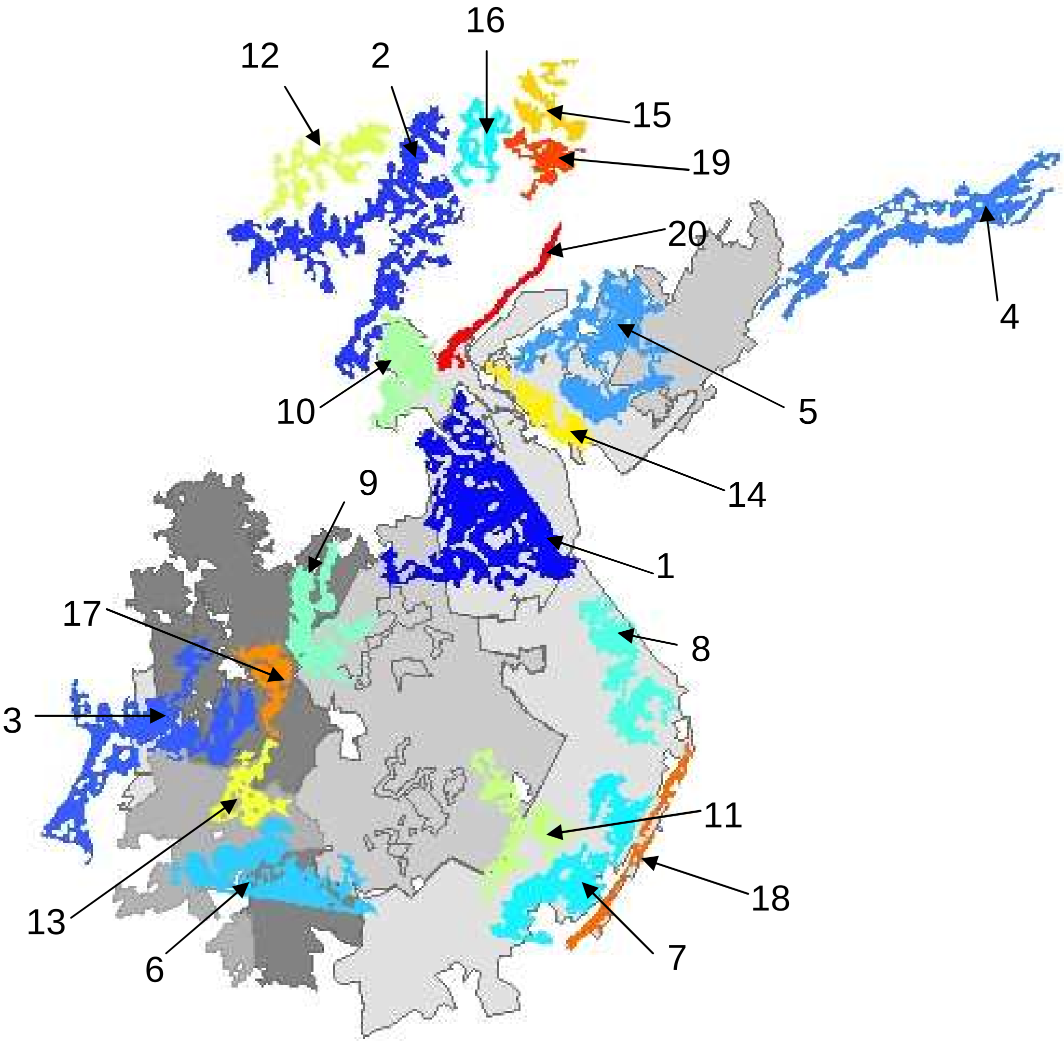


**Figure 5.17:** Location of the twenty largest interior forest patches using the 150 m edge effect window in the Cumberland Mountains based on a classified SPOT satellite image from September, 2006. Figure 5.3 defines the landowner boundaries (shaded in grey).

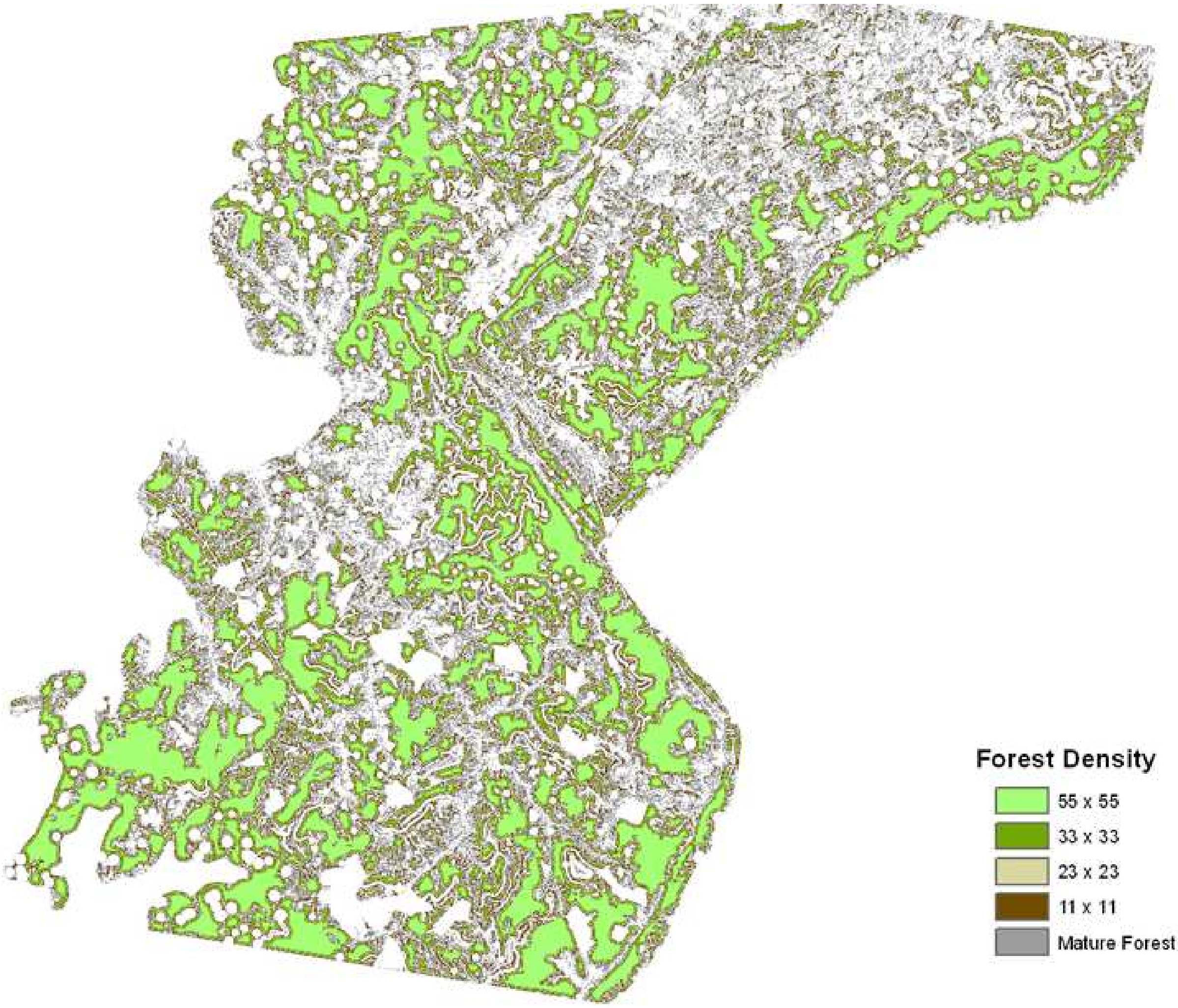


**Figure 5.18:** Projected distribution of interior forest (2016) under the base-case scenario for mining and timber harvesting. The light green areas are mature forest patches using the largest (150 m) edge effect/window size and the other colors show the additional area of interior forest added with smaller edge effect/window sizes. The grey areas are mature forest that is not considered interior and the white areas are non-mature forest. See Figure 5.18 for more detailed view.

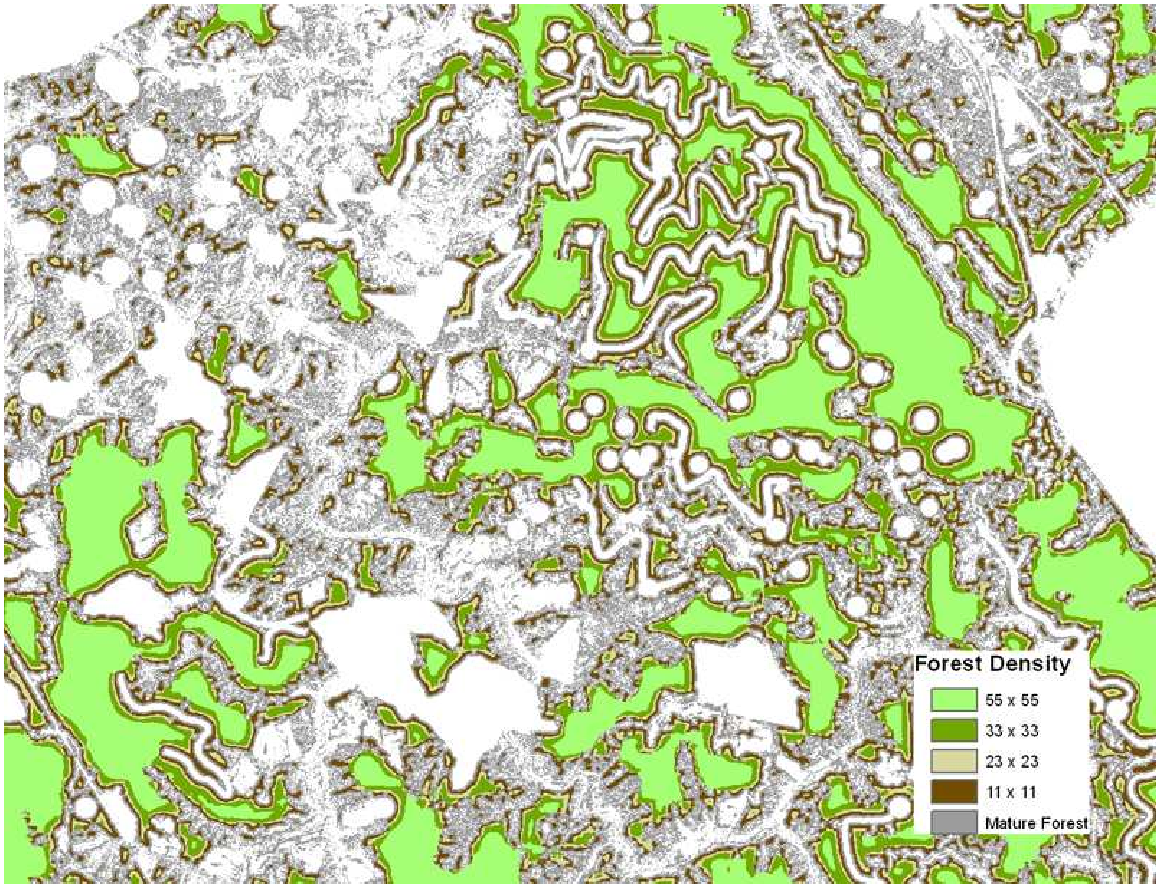


**Figure 5.19:** Projected distribution of interior forest (2016) under the base-case scenario for mining and timber harvesting zoomed in on the southern portion of Royal Blue WMA and northern portion of Sundquist Forest WMA. The linear white lines are simulated contour mines, the large white areas are simulated industrial timber harvests, and the smaller white circles are simulated deep mines or timber harvests by TWRA.

**Figure 5.20:** Interior forest for the 150-m edge effect window analysis (window size = 10.9 ha) before simulating disturbance (a) and after ten years under the base-case mining and timber harvesting scenario (b).

## Appendix B: Succession Classification

**1: Cleared / Recent Disturbance**
111: SPOT pasture / grass
121: Mining, reclamation grass, first disturbance event
122: Mining, reclamation grass, second disturbance event
131: Mining, reclamation forest, first disturbance event
132: Mining, reclamation forest, second disturbance event
141: SPOT recent clearcut; modeled clearcut, first disturbance event
142: Clearcut, second disturbance event

**2: Shrubland**
211: SPOT shrubland
221: Mining, reclamation grass, first disturbance event
222: Mining, reclamation grass, second disturbance event
231: Mining, reclamation forest, first disturbance event
232: Mining, reclamation forest, second disturbance event
241: Clearcut, first disturbance event
242: Clearcut, second disturbance event
251: Shelterwood, first disturbance event
252: Shelterwood, second disturbance event

**3: Young Forest**
311: SPOT young forest
321: Mining, reclamation grass, first disturbance event
322: Mining, reclamation grass, second disturbance event
331: Mining, reclamation forest, first disturbance event
332: Mining, reclamation forest, second disturbance event
341: Clearcut, first disturbance event
342: Clearcut, second disturbance event
351: Shelterwood, first disturbance event
352: Shelterwood, second disturbance event

**4: Mature Forest**
411: SPOT mature forest
421: Mining, reclamation grass, first disturbance event
422: Mining, reclamation grass, second disturbance event
431: Mining, reclamation forest, first disturbance event
432: Mining, reclamation forest, second disturbance event
441: Clearcut, first disturbance event
442: Clearcut, second disturbance event
451: Shelterwood, first disturbance event
452: Shelterwood, second disturbance event

**9: Non-Habitat/no succession occurs in these classes**
911: Water
921: Urban
931: Road Pasture
941: ROW Scrub
951: ROW Pasture
961: ROW Recent CC

# Part 6

# PART 6: CONCLUSION

The four primary objectives of this research were to (1) describe the basic demography and habitat use of the Cumberland Mountain golden-winged warbler population (Part 2), (2) assess the effect of habitat and demographic factors on golden-winged warbler territory size (Part 3), (3) compare the demography of the Cumberland population to a population in Ontario (Part 4), and (4) model alternative land use scenarios and the impacts on both the golden-winged and the cerulean warbler, two species of conservation concern, but with conflicting habitat requirements (Part 5). The implications of our findings are discussed below.

## Golden-winged warbler habitat management in the Cumberland Mountains

Our results suggest that golden-winged warblers require a diverse mixture of herbaceous and woody vegetation for nesting (Part 2). These necessary components are not inherently present in all early successional habitats (Bulluck and Buehler 2006), and active management is needed to ensure their presence. Mine reclamation, timber harvesting, and prescribed fire each have the potential to play a part in this active management. With the recent increase in coal mining throughout the region, alternative reclamation procedures should be clearly defined and discussed by representatives from the Office of Surface mining, mining industries, and conservation agencies to determine the best strategy, from both site-specific and landscape-level perspectives. These issues need to be discussed as soon as possible because reclamation procedures are typically decided upon in the permitting stage before mining actually begins. Planting only herbaceous cover often prevents the establishment of woody vegetation and leads to large tracts of land unsuitable for golden-wingeds and for most other early successional species. If songbird conservation is the goal, then this type of reclamation should be avoided. Alternatively, planting both herbaceous and woody vegetation (preferably native hardwoods) is important if we are to create quality early successional habitats on reclaimed mine lands that are suitable for golden-wingeds in the short term and that succeed more quickly into mature forests similar to those on the remaining landscape.

Timber harvesting can also play a role in the creation of suitable golden-winged warbler habitat in the Cumberland Mountains, although the impacts will be on a smaller temporal and spatial scale than mining. The density of golden-wingeds is typically very low in regenerating timber harvests because there is typically not sufficient herbaceous cover throughout; however, there are actions that can increase the suitability of regenerating harvests. For example, seeding the log landings and logging roads with herbaceous vegetation, preferably with native grasses and forbs, creates suitable conditions in these areas for 5-15 years following harvest (Klaus and Buehler 2001). Depending on the long-term goals for a given stand, periodic fire in harvested stands can maintain this herbaceous component and therefore its suitability for a longer period of time. Otherwise, woody regeneration generally becomes too thick within several years to support the species.

Finally, because all early successional habitats are ephemeral, periodic prescribed fire has the potential to prolong the suitability of certain target conservation areas. Early successional shrublands will always blink on and off in a landscape as natural and anthropogenic disturbances occur and succeed. However, on state-owned lands where non-game management is a goal, prescribed fire can maintain the diverse mixture of herbaceous and woody vegetation over time on specific areas while not sacrificing the integrity of mature forests in the same landscape. For example, our main study sites, in addition to several other known sites with high golden-winged density, currently support >25% of the Cumberland Mountain golden-winged population (i.e., >125 breeding pairs). If these areas are managed with periodic prescribed fire, we can be more confident that golden-wingeds will be sustained in the Cumberland region regardless of the rise and fall of successional habitats throughout the rest of the landscape from other disturbances. Such focused management in already existing successional areas will also prevent the loss of mature forests for the sake of golden-wingeds. This is especially important considering that significant loss of mature forest in the Cumberland Mountains appears to be inevitable in the near future and will have negative effects on forest-interior species (Part 5).

## Golden-winged warbler demographics

Although Tennessee and Ontario golden-winged warbler populations are located at the southern and northern extremes of this species range, respectively, we found little difference in their basic demographics (Part 4). Therefore, we cannot suggest focusing conservation efforts on increasing adult survival in one region and fecundity in another. Based on our demographic analyses, both golden-winged populations appear to be declining. We cannot be sure whether these populations are limited on the breeding grounds, the wintering grounds, during migration, or all three statges, as our knowledge of habitat and demography during the non-breeding season is extremely limited. Considering that golden-wingeds breed in successional habitats, maintaining and creating quality habitat on the breeding grounds is imperative to their long-term persistence. However, our current understanding of factors that affect nest survival is not complete (Parts 2 and 4) and conservation efforts that attempt to increase nest survival may prove ineffective. Tennessee data also suggest that nest predation is a complex and dynamic process in space and time (Part 2) such that practical management efforts that will increase nest survival rates are not apparent. Furthermore, golden-winged nest survival rates in Tennessee and Ontario are comparable with rates reported for other Neotropical migrants with stable or increasing populations. If within-season adult survival and nest survival rates are truly above average in Ontario and Tennessee, a conservation strategy on the breeding grounds that may be successful is the use of artificial con-specific attraction in currently unoccupied patches of apparently suitable habitat (i.e., projecting male song during the early breeding season in order to attract migrating individuals to stop and set up territories, Ward and Schlossberg 2004).

The maintenance of high-quality breeding habitat and con-specific attraction are certainly promising conservation efforts that could be implemented for golden-winged warblers throughout their current breeding range. However, as stated above, our ability to significantly affect golden-winged survival and reproduction on the breeding grounds may be limited, and we should therefore focus a significant portion of our conservation efforts on the wintering grounds where golden-wingeds spend >50% of their annual life cycle. Specifically, we need more data on golden-winged warbler migratory patchways and demographics, as well as wintering ground demographics, to better understand why our adult female annual survival estimates are so low.

The demographic data presented in Parts 2-4 fill a knowledge gap that previously existed for a declining species. To date, few studies have presented what factors may be related to golden-winged territory size variation or daily nest survival rates and no studies had documented annual adult survival rate estimates for this species. Not only do these data provide needed insight into breeding season demography, but they also lead to additional questions. Are the nest and adult survival rates estimated in Tennessee and Ontario representative of other portions of the breeding range (e.g. Blue Ridge Mountains and upper Midwest)? Is nest predation in regions other than the Cumberland Mountains a complex and dynamic process that does not appear to be related to vegetation structure around the nest? What are the mechanisms that cause territory size to vary with vine cover and the number of snags? What factors influence territory size in other portions of the range and other habitat types where male density may differ? There is still much to understand about this species' demography if we are to effectively manage for its persistence.

## Implications of land use modeling

The Cumberland Mountains landscape, occupied by two declining songbirds with conflicting habitat needs, presents a unique challenge to conservation biologists. None of the land use scenarios modeled in this study represented a sustainable option for both golden-winged and cerulean warbler populations in the Cumberland Mountains. The results of our interior forest analysis illustrate that fragmentation of contiguous forests in the Cumberland Mountains may have impacts far greater than the total forest loss. Not only is more interior forest lost than total forest, but lower cerulean densities in edge forest habitats may lead to much greater rates of population decline when we consider interior forest loss, than based on total forest loss. Furthermore, there may be demographic differences in edge versus interior forests such that interior forests provide reproductive sources (natality > mortality) and edges act as reproductive sinks (mortality > natality, Dias 1996). Several studies have illustrated this phenomenon, particularly with regard to nest parasitism and predation and in landscapes fragmented by agriculture (Donovan et al. 1995, Robinson et al 1995); however, similar effects have been documented in forested landscapes as well (Manolis et al. 2001).

It is possible that even golden-wingeds, considered insensitive to edge habitats, may experience negative effects of forest fragmentation once a certain threshold of forest is lost. We do not know how the contiguous nature of mature forests in the Cumberland Mountains affects golden-winged warbler habitat suitability/quality at the landscape scale; as forests are fragmented, the quality of successional patches could decrease as a result of increased nest predation and/or parasitism. The negative effects of fragmentation on ceruleans are more probable at lower levels of fragmentation considering this species sensitivity to edges (Wood et al. 2006). In general, thresholds in species persistence vary depending on the species response to fragmentation (i.e., their sensitivity to edge habitats) such that there is no general rule we can follow as to how much habitat is necessary (With and King 2001).

As mentioned in the introduction (Part 1), there is potential for disagreement regarding which species should be of higher conservation priority, the cerulean or the golden-winged warbler. This stems from whether or not the core of these species' ranges lie within the Cumberland Mountains region (i.e. the proportion of the global population occurring in the region). The Cumberland cerulean warbler population is estimated to be ~40,000 breeding pairs (Buehler et al. 2006) while the Cumberland golden-winged population is only estimated to be ~500 breeding pairs (L. Bulluck, unpublished data). Therefore, our projected loss of ~15% of 40,000 breeding pairs under the base-case scenario may be seen as not significant, especially compared to the significant increase in golden-winged warblers under this same scenario. On the other hand, the Cumberland Mountains comprise a large proportion of the cerulean global population (≥20%, Buehler et al. 2006) and only a small fraction of the golden-winged global population (<1%), suggesting that ceruleans should receive more conservation attention.

The conservation dilemma described here applies to many more species and landscapes where habitat requirements for species of concern conflict. Such a controversy presents very real and pragmatic issues worthy of discussion as our conservation dollars and lands become more limited. Rather than choosing one species as more worthy of conservation than the other, we must consider how to simultaneously conserve all species of concern. In the Cumberland Mountains, a strategy that permits simultaneous management of both species is possible. Our results suggested that new disturbance will need to be significantly limited (beyond that represented in the scenarios here) to sustain cerulean warblers. Specifically, we should prioritize areas to be free from disturbance that are currently identified as the largest interior forest patches (Figure 5.17). To ensure habitat for golden-wingeds, the successional areas currently on the landscape will need to be maintained and improved through more focused management (e.g., prescribed fire) rather than depending on future mining and timber-harvest disturbances. Prescribed fire increases herbaceous cover, reduces woody cover, and creates snags, all important components of GWWA habitat (Parts 2 and 3). In general, we can sustain both species by limiting disturbance that removes mature forests from the landscape for ceruleans, while actively managing the early successional habitats currently on the landscape to increase their quality for golden-wingeds. Land ownership may largely limit the possibility of this sustainable land stewardship to state-owned lands in the region. Regardless, if songbird conservation is a goal, then actively managing existing successional areas and greatly reducing the amount of disturbance on state-owned lands is necessary, especially considering the degree of disturbance occurring on industrial and private lands in the region.

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# Vita

Lesley Penfield Bulluck was born in Birmingham, Alabama on March 1, 1978. She and her family lived in Alabama until 1986, relocated to Louisville, Kentucky for two years, and then to Baton Rouge, Louisiana, where she graduated from St. Joseph's Academy in 1996. She received her Bachelor of Science in Biology with a minor in Chemistry from Appalachian State University in May 2000. It was at Appalachian State that she took her first field courses, including Ornithology, and decided that she wanted to pursue a career in conservation biology. She earned her Master of Science degree in Ecology from Miami University of Ohio in May 2003 where she studied factors affecting the accuracy of avian species occurrence models in the Great Basin of central Nevada. Immediately following the defense of her master's thesis, she started fieldwork for her dissertation research in the Cumberland Mountains that has culminated in the research described here. Lesley is now living in Richmond, Virginia with her husband Jason Bulluck and they expect their first child to be born in May 2007.