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I am submitting herewith a thesis written by David Aaron Keller entitled "Associations between eastern hemlock (*Tsuga canadensis*) and avian occurrence and nest success in the southern Appalachians." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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ASSOCIATIONS BETWEEN EASTERN HEMLOCK (*Tsuga canadensis*) AND AVIAN OCCURRENCE AND NEST SUCCESS IN THE SOUTHERN APPALACHIANS

A Thesis

Presented for the

Master of Science Degree

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ABSTRACT

The recent decline of eastern hemlock (*Tsuga canadensis*) is a dramatic example of the effects exotic insect pests can have on forest composition and structure. Hemlock decline is attributed to defoliation caused by hemlock woolly adelgid (HWA, *Adelges tsugae*), an exotic Hemipteran introduced to the northwest U.S. from Asia during the 1920s and the eastern U.S. during the early 1950s. Within the past several years, HWA infestations have reached the southern portions of the Appalachian mountains and threaten to eliminate both eastern and Carolina hemlock (*Tsuga carolinensis*) from the region.

Recognized as nationally important bird areas by the American Bird Conservancy, lands administered by the U.S. Forest Service and National Park Service in the southern Appalachians form one of the largest networks of contiguous forested habitat in the eastern United States and provide great quantities of high quality habitat for numerous breeding bird species. Changes in southern Appalachian forest ecosystems resulting from loss of hemlock may have impacts on the distribution and demography of several avian species in the region. This study had two primary objectives designed to investigate the potential effects of eastern hemlock decline on southern Appalachian breeding birds: 1) develop models of avian associations with eastern hemlock in southern Appalachian national forests comparable to existing models developed for Great Smoky Mountains National Park (GSMNP) (Shriner 2001) and 2) compare nest success and the mechanisms influencing productivity of three hemlock-associated species [black-throated

blue warbler (*Dendroica caerulescens*), dark-eyed junco (*Junco hyemalis*), and blue-headed vireo (*Vireo solitarius*)] in hemlock and hardwood-dominated stands.

Using the U.S. Forest Service R8BIRD database containing point-count data for Jefferson and George Washington National Forests (JGWNF), Virginia, and Cherokee National Forest (CNF), Tennessee, I developed logistic regression models predicting occurrence probabilities as a function of hemlock presence for 29 avian species. Two sets of models were developed based on single-year and multiple-year occupancy criteria for classifying a point-count location as a presence point for a given species. On JGWNF, the presence of Acadian flycatcher (*Empidonax virescens*), blue-headed vireo, black-throated blue warbler, black-throated green warbler (*Dendroica virens*), Canada warbler (*Wilsonia canadensis*), dark-eyed junco, northern parula (*Parula americana*), and veery (*Catharus fuscescens*) had significant positive associations with hemlock presence at a Bonferroni-corrected α-level of 0.0017. Eastern towhee (*Pipilo erythrophthalmus*) and indigo bunting (*Passerina cyanea*) displayed negative associations. On CNF, four species—Acadian flycatcher, black-throated blue warbler, black-throated green warbler, and northern parula—were positively associated with hemlock presence and one species—indigo bunting—was negatively associated at an α-level of 0.0017.

Three species showed a consistent positive association with eastern hemlock in JGWNF, CNF, and GSMNP: Acadian flycatcher, black-throated blue warbler, and black-throated green warbler. Although these species may experience negative impacts from hemlock decline, analysis of distributional data ignores mechanisms driving the observed species associations with hemlock, and, consequently, potential plasticity in habitat

selection and other life history traits that may mitigate the impacts of hemlock loss are unknown.

A possible proximate mechanism for the hemlock associations identified by the models for JGWNF, CNF, and GSMNP may be greater reproductive fitness afforded by hemlock sites for hemlock-associated species. My second objective was to test the prediction that nest success of three hemlock-associated species in the southern Appalachians—black-throated blue warbler (BTBW), dark-eyed junco (DEJU), and blue-headed vireo (BHVI)—was greater in breeding habitats containing hemlock than habitats without hemlock. Nest success of the three focal species was compared between hemlock and hardwood breeding sites at two spatial scales: a 15-ha stand scale and a 0.04-ha nest site scale. Data for the stand-scale comparisons were collected in two 15-ha stands in Cataloochee Valley, GSMNP, North Carolina—one in an eastern hemlock stand and one in a rich cove hardwood stand. Data for the nest-site scale comparisons were collected at the Cataloochee site and at Coweeta Long-term Ecological Research Station in Nantahala National Forest, North Carolina. In addition to nest success, I investigated potential mechanisms influencing productivity by comparing Lepidoptera larvae abundance, parental provisioning rates of nestlings, and predator abundance in hemlock and hardwood-dominated stands. The potential impacts of hemlock decline on nest sites of my primary focal species, BTBW, were examined by developing models of nest-site selection using selected vegetation composition and structure variables sensitive to hemlock loss and relevant to BTBW nest placement.

Mayfield BTBW nest success at Cataloochee in 2002-2003 (pooled) was greater in the hemlock plot than in the hardwood plot (hemlock plot = 59.4 %, hardwood plot =

30.5 %, $\chi^2 = 5.50$, $P = 0.0190$). DEJU nest success did not differ between forest types (hardwood plot = 20.5 %, hemlock plot = 17.8 % , $\chi^2 = 0.033$, $P = 0.8554$). BHVI nest success did not differ between forest types (hardwood plot = 20.8 %, hemlock plot = 29.7 %, $\chi^2 = 0.237$, $P = 0.6267$). Nest success at 0.04-ha nest sites containing hemlock did not differ from nest success at nest sites without hemlock for BTBW (Cataloochee $P = 0.4859$; Coweeta $P = 0.5879$), DEJU ($P = 0.9319$), and BHVI ($P = 0.2864$).

Although Lepidoptera larvae biomass tended to be lower on the hemlock plot compared to the hardwood plot, the difference did not appear to affect the amount of biomass delivered to BTBW nestlings. Total biomass and caterpillar biomass delivered to BTBW nestlings did not differ between plots (hardwood total biomass $\bar{x} = 13.16$, hemlock total biomass $\bar{x} = 15.29$, total biomass $P = 0.3302$; hardwood caterpillar biomass $\bar{x} = 5.90$, hemlock caterpillar biomass $\bar{x} = 9.00$, caterpillar biomass $P = 0.1050$). Surveys of diurnal predators on the hemlock and hardwood plots did not detect any differences in relative abundance for any mammalian or avian predator except American crow (Fisher's exact $P = 0.0135$), which had a greater number of detections on the hemlock plot. Using Akaike's information criterion-based best-subsets variable selection, our BTBW nest-site selection logistic regression models revealed nest sites were positively associated with high shrub stem density and negatively associated with increasing overhead midstory cover.

The greater BTBW nest success observed in hemlock stands compared to hardwood stands is consistent with the hypothesis that hemlock-dominated sites in the southern Appalachians are "optimal" breeding habitats for this species. Although nest

success in this study was not related to any measured microhabitat variables, observed differences in vegetation structure of the 15-ha plot scale may explain the nest success difference between forest types. The hemlock plot had greater means for shrub stem counts, horizontal visual obscurity (measured with a cover board), and overhead shrub cover. Therefore, based on the results of BTBW nest site selection models, the hemlock plot contained more potential nest sites and greater nest concealment, two characteristics that may have decreased predator foraging efficiency. This study suggests that impending hemlock decline from hemlock woolly adelgid may have negative reproductive consequences for black-throated blue warblers. However, these deleterious effects may be mitigated by an increase in shrub density from changing understory light conditions as canopy hemlock trees die.

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PART 1

INTRODUCTION

Among the many human-related threats to ecosystem health, the introduction of invasive exotic organisms may be most difficult to manage (Drake et al. 1989, Soulé 1990, Wilcove et al. 1998). The consequences of exotic organism invasions on ecosystems often are more pervasive and persistent than other anthropogenic influences such as habitat destruction and pollution (Coblentz 1990). For example, exotic insect pests can have devastating effects on the structural and floristic characteristics of forest stands and fundamentally alter forest ecosystem dynamics (Liebhold et al. 1995). Although disturbance and disease are important regulatory mechanisms in many ecosystems, the unique perturbations caused by exotic pathogens in forest systems may have longer lasting effects than more "natural" disturbances, such as wind throw and fire (Castello et al. 1995, Foster et al. 1998). Studying the patterns, processes, and consequences of invasive exotic introductions is critical to understanding and mitigating ecological damage during this current era of "cosmopolitization" of the earth's biota.

The recent decline of eastern hemlock (*Tsuga canadensis*) is a dramatic example of the effects that exotic insect pests can have on forest composition and structure. Hemlock decline is attributed to defoliation caused by hemlock woolly adelgid (HWA; *Adelges tsugae*), an exotic Hemipteran introduced to the northwestern U.S. from Asia during the 1920s (McClure 1987) and the eastern U.S. during the early 1950s (Orwig and Foster 1998). Although the two species of hemlock native to the western U.S.—western hemlock (*Tsuga heterophylla*) and mountain hemlock (*Tsuga mertensiana*)—are resistant to the insect, the two hemlocks of the East, eastern hemlock and the rarer Carolina hemlock (*Tsuga caroliniana*), are susceptible to HWA infestations at all stages of growth (Souto et al. 1996).

Over the past 50 years, HWA has spread throughout much of eastern hemlock's native range. Currently, HWA infestations have been reported in 15 states with severe hemlock mortality in areas of the northeastern U.S. and along the Appalachian chain south to Shenandoah National Park (USDA 2002). The insect was first reported in Great Smoky Mountains National Park (GSMNP) during Spring 2002 and has since spread throughout all areas of the park. Whereas HWA has reached all but the southernmost and westernmost areas of eastern hemlock's native range, the northward expansion of infestations into Maine and Canada may be impeded by the adelgid's intolerance to extreme low temperatures over prolonged periods (Parker et al. 1998, Parker et al. 1999, Skinner et al. 2003).

Hemlock woolly adelgids feed on hemlock ray parenchyma cells at needle attachments, causing defoliation, branch mortality, and tree death within 4-5 years of infestation (McClure 1991, Young et al. 1995, Orwig and Foster 1998). HWA has a complex polymorphic life cycle producing up to two generations per year (McClure 1989). High reproductive rates, lack of natural predators, and great dispersal ability facilitated by wind, birds, deer, and human activity have allowed HWA to spread rapidly throughout much of the native range of eastern hemlock (McClure 1990). Hemlocks are susceptible to infestation at all stages of growth, and no individual trees or stands display resistance (Orwig and Foster 1998).

The range of eastern hemlock, lying between 33º and 48º N, extends from northeastern Minnesota east to Nova Scotia and south to northwestern Alabama (McWilliams and Schmidt 2000). Eastern hemlock is commonly associated with ravines and moist soils but may occur on a variety of other sites, including slopes and dry ridges

(Rogers 1978, Kessell 1979). Although hemlock has been used as construction lumber, pulpwood, and a tannin source before the development of synthetic alternatives in the early 20th century, this species has never possessed major economic value (Benzinger 1994a). The principal value of hemlock resides in its ecological role in eastern North American forests. As a long-lived and highly shade-tolerant conifer, hemlock may grow in combination with deciduous hardwood species and eastern white pine (*Pinus strobus*) or in dense monospecific stands (Orwig and Foster 1998). Possessing a shallow root system and high moisture requirements, eastern hemlock is particularly susceptible to natural and anthropogenic disturbance, making it most common in undisturbed or historically protected sites, especially mesic coves and ravines (Foster et al. 1992, Foster and Zebryk 1993, Mladenoff and Stearns 1993, Abrams and Orwig 1996). Although fire may help hemlock seed germination by exposing soil surface, intense fires that remove the humus layer hamper hemlock regeneration (Benzinger 1994a).

Predicting the effects of hemlock decline on forest ecosystems in the southern Appalachians requires knowledge of the influence of hemlock on forest structure and dynamics, the plant and animal species associated with hemlock, and the mechanisms driving these associations. Recent research in Connecticut and other areas of the Northeast affected by HWA infestations has begun to elucidate the changes in forest ecosystem composition, structure, and function following hemlock mortality. Loss of hemlock directly impacts forests by homogenizing forest composition and structure at the landscape scale (Orwig and Foster 1998). In southern New England, hemlock forests are predicted to experience a change in cover type to birch (*Betula* spp.), oak (*Quercus* spp.), and maple (*Acer* spp.) as dead and dying hemlocks are gradually replaced by hardwoods

(Orwig and Foster 2000). HWA infestations also affect nutrient cycling rates. For example, HWA-infested stands have greater nitrogen mineralization and nitrification rates than healthy stands, presumably from changes in microclimate related to increased light penetration (Jenkins et al. 1999, Yorks et al. 2000, Yorks et al. 2003).

The impending loss of hemlock from southern Appalachian forests may impact avian communities. Eastern hemlock possesses several unique ecological characteristics that potentially influence bird communities. First, eastern hemlock provides distinctive floristic and structural components in several forest types. Its high shade tolerance allows persistence in the understory of several forest types (Benzinger 1994b, Goerlich and Nyland 2000). Additionally, hemlock tends to retain its lower branches (Benzinger 1994b), therefore adding to foliar height diversity, a measure correlated with increased avian diversity (MacArthur and MacArthur 1961, Karr and Roth 1971, Martin 1988). Homogenization of avian habitat following previous forest pest outbreaks has been shown to decrease bird diversity (Gale et al. 2001). The increased nesting cover and nest sites provided by hemlock may affect bird productivity by decreasing the effective predation pressure in hemlock stands (Holway 1991).

Eastern hemlock is associated with unique local microclimates and soil conditions. The dense foliar cover of hemlock and shading of the understory gives hemlock stand understories characteristically darker, cooler, and more humid microclimates during the growing season compared with similar hardwood-dominated stands (Benzinger 1994a). Because many avian species respond to light conditions and relative humidity and prefer mesic over xeric sites, hemlock stands may be attractive to certain species (Smith 1977). Additionally, the increased thermal cover and rain

interception afforded by hemlock forests may benefit nesting birds by helping prevent precipitation-induced cold stress that contributes to increased nestling mortality, especially early in the nesting season (Walsberg 1985). The accumulation and decomposition of needles beneath hemlocks contribute to localized acidification of soil within hemlock stands (Goerlich and Nyland 2000). Soil moisture underneath hemlocks is typically lower than under hardwood species, a property explained by high levels of competition among roots in the thin soils hemlocks typically occupy. The acidic soil conditions, low seasonal moisture, and solar insulation associated with this species help create reduced understories in stands with hemlock-dominated canopies (Orwig and Foster 1998, Benzinger 1994b). An important exception is the prevalence of rosebay rhododendron (*Rhododendron maximum*), which is tolerant of acidic soils, in the understory of many southern Appalachian hemlock stands (Benzinger 1994a).

Hemlock stands also may affect bird communities through their influence on arthropods. Insect densities and diversity on hemlock trees are lower compared with most deciduous trees (Benzinger 1994a), which could have reproductive consequences for forest birds (Holmes and Schultz 1988). However, bird presence and abundance is driven by a more complex combination of prey conditions such as arthropod biomass, life-form, and concentration (Benzinger 1994b). These factors apparently have not been well documented in hemlock forests. A unique aspect of hemlock is the deeply furrowed surface of the bark, a characteristic that differs from the smooth bark of many coexisting trees such as American beech (*Fagus grandifolia*), and can serve as a concentrated source of diverse insects (Nicolai 1986).

The contribution of hemlock to the structural and floristic diversity of several forest types has been shown to increase avian diversity. Holt (1974) characterized avian use of hemlock in the southern Appalachians and found greater bird densities and species richness in mixed hemlock-hardwood stands compared with virgin hemlock stands and mesic shrublands. Haney (1999) found greater avian diversity in Appalachian old-growth hemlock-white pine-oak stands than in adjacent younger forests, and Gates and Giffen (1991) detected increasing avian diversity along a hemlock gradient with greatest values in streamside zones containing high rhododendron, hemlock, and shrub densities. Several studies have identified avian species associated with eastern hemlock. Research in northern areas of the range of eastern hemlock has identified several avian species that consistently choose hemlock-dominated breeding habitats: black-throated green warbler (*Dendroica virens*), blue-headed vireo (*Vireo solitarius*), Acadian flycatcher (*Empidonax virescens*), and Blackburnian warbler (*Dendroica fusca*) (Benzinger 1994b, Yamasaki et al. 2000, Ross et al. 2002, Tingley et al. 2002). Several other species display weaker associations with hemlock forests.

The only study to address avian use of eastern hemlock stands in the southern Appalachians (Shriner 2001) identified several species associated with hemlock in Great Smoky Mountains National Park (GSMNP) that were not identified in studies in northern areas within the range of hemlock. In addition to frequently acknowledged hemlock associates such as black-throated green warbler and Acadian flycatcher, Shriner (2001) found that dark-eyed junco (*Junco hyemalis*), black-throated blue warbler (*Dendroica caerulecsens*), wood thrush (*Hylocichla mustelina*), and Canada warbler (*Wilsonia canadensis*) had greater probabilities of detection on sites with hemlock compared with

sites without hemlock. However, the applicability of the hemlock associations found in GSMNP to other areas of the southern Appalachians is questionable because of differences in the prevalence of the tree in the park and surrounding national forests. Additionally, the mechanisms influencing certain species' selection of hemlock as breeding habitats have not been identified.

Birds are often used as indicator species tracking ecosystem health. Birds respond to environmental change across multiple scales and are easily monitored relative to many other organisms (Temple and Wiens 1989). Additionally, avian occurrence, abundance, and reproductive success are influenced by the condition and configuration of surrounding habitats (Carignan and Villard 2002). The existence of hemlock-associated avian species suggests they may serve as useful indicators of hemlock ecosystem health and the impacts of hemlock decline. However, none of these species are limited to hemlock stands and the mechanisms influencing their hemlock associations have not been investigated. Therefore, their utility as indicators of hemlock ecosystem health has not been determined.

My study has two primary objectives designed to investigate the associations between eastern hemlock and breeding birds in the southern Appalachians: 1) develop models of the association between avian species occurrences and eastern hemlock in southern Appalachian national forests comparable to existing models developed in GSMNP and 2) compare nesting success and the mechanisms influencing productivity of three hemlock-associated species (black-throated blue warbler, dark-eyed junco, and blue-headed vireo) in hemlock and hardwood-dominated stands. The first objective supplements the work of Shriner (2001) and is intended to determine if the avian

associations identified in GSMNP, where eastern hemlock is the second most common tree species, also exist in the national forests of the southern Appalachians, where relatively greater levels of anthropogenic disturbance have reduced the prevalence of eastern hemlock. By examining the relationship between hemlock and avian productivity, the second objective addresses potential consequences of hemlock loss not explicit in species-habitat association models. Results of this study provide insight into which avian species' occurrences may change as a result of impending hemlock decline and elucidate potential mechanisms that may influence these changes.

PART 2

AVIAN SPECIES ASSOCIATED WITH EASTERN HEMLOCK IN SOUTHERN APPALACHIAN NATIONAL FORESTS

Introduction

Documenting avian species associated with eastern hemlock is an important initial step in identifying the potential effects of eastern hemlock decline on avian communities. Additionally, identifying hemlock-associated birds may be useful because birds are commonly cited as indicators of ecosystem health (Temple and Wiens 1989). Monitoring these species may provide resource managers a means of quantifying the ecological consequences of hemlock decline in eastern North America. However, the geographic inconsistencies in avian-hemlock associations that have been identified in areas of the northeastern U.S. (Benzinger 1994b, Ross et al. 2002, Tingley et al. 2003) and the southern Appalachians (Shriner 2003) warrant further investigation of the relationships between eastern hemlock and birds.

Although no avian species are limited to hemlock habitats, studies in the northern areas of eastern hemlock's range identify several species that are associated with the tree. Acadian flycatcher (*Empidonax virescens*), black-throated green warbler (*Dendroica virens*), and blue-headed vireo (*Vireo solitarius*) are strongly tied to hemlock habitats in New Jersey and Pennsylvania (Benzinger 1994b, Ross et al. 2002). Howe and Mossman (1996) found populations of red-breasted nuthatch (*Sitta canadensis*), winter wren (*Troglodytes troglodytes*), blue-headed vireo, black-throated green warbler, and Blackburnian warbler (*Dendroica fusca*) reached their greatest densities in mature hemlock forests in the western Great Lakes region. Additional species with hemlock associations in the northern areas of eastern hemlock's range include hermit thrush (*Catharus guttatus*), red-shouldered hawk (*Buteo lineatus*), northern goshawk (*Accipiter gentilis*), and barred owl (*Strix varia*) (Benzinger 1994b). In a study examining post-

hemlock decline changes in bird communities in southern New England, Tingley et al. (2002) found hemlock stands with >60% mortality had greater abundances of brown-headed cowbird (*Molothrus ater*), red-eyed vireo (*Vireo olivaceus*), eastern wood-pewee (*Contopus virens*), white-breasted nuthatch (*Sitta carolinensis*), and tufted titmouse (*Baeolophus bicolor*) than intact hemlock stands, which had greater abundances of black-throated green warbler, Acadian flycatcher, hermit thrush, and Blackburnian warbler. In addition to its documented associations with individual avian species, the presence of hemlock is also correlated with high levels of avian diversity in old-growth forests (Haney 1999), mixed hemlock-hardwood stands (Kendeigh 1946, Holt 1974, Speiser 1982), and riparian zones (Gates and Giffen 1991).

Few studies have examined avian associations with hemlock in the southern Appalachians. Models of avian-habitat relationships developed for Great Smoky Mountains National Park (GSMNP) by Shriner (2001) showed seven species out of 30 studied were positively associated with hemlock presence and nine species were negatively associated (Table 2.1; All tables located in Appendix 1). Golden-crowned kinglet (*Regulus satrapa*), veery (*Catharus fuscescens*), blue-headed vireo, and red-breasted nuthatch had less significant positive associations with hemlock presence. Of the species positively associated with hemlock in GSMNP, four species [dark-eyed junco (*Junco hyemalis*), black-throated blue warbler (*Dendroica caerulescens*), wood thrush (*Hylocichla mustelina*), and Canada warbler (*Wilsonia canadensis*)] were not mentioned in studies conducted in northern areas of hemlock's range, indicating the possibility of geographic differences in habitat associations.

The forests of GSMNP contain an abundance of eastern hemlock, a highly shade-tolerant, late-successional species adapted to mesic coves. Although only about 1% of GSMNP's 212,401 ha is dominated by eastern hemlock (Johnson et al. 2000), eastern hemlock is the second most common tree species in the national park because of its persistence in the understory, midstory, and canopy of several forest types at all but the highest elevations (Shriner 2001). Therefore, avian species associations identified in GSMNP may be unique to the region because of the tree's ubiquity there. Since the creation of GSMNP in the 1930s, the national forests of the southern Appalachians have experienced greater levels of disturbance from logging activity, resulting in forest communities with a reduced hemlock component compared with the national park (Foster et al. 1992, Foster and Zebryk 1993, Abrams and Orwig 1996). Differences in topography and precipitation amounts between GSMNP and other areas of the southern Appalachians may also contribute to the discrepancy in hemlock abundance (Benzinger 1994b). Approximately 1,286 of the 1,954,000 ha (0.066 %) in Pisgah, Nantahala, Cherokee, George Washington, and Jefferson National Forests are dominated by > 50% hemlock canopy coverage (Herman 1996). Another 3,950 ha (0.202 %) and 11,952 ha (0.612 %) are classified as white pine-hemlock and hardwood-hemlock, respectively, based on U.S. Forest Service Continuous Inventory and Stand Condition (CISC) forest type classifications. The avian species associations with hemlock detected in the hemlock-rich GSMNP may not necessarily be consistent with associations in the hemlock-poor national forests of the southern Appalachians. To date, no study has examined avian relationships with hemlock in the southern Appalachian national forests or identified species most sensitive to hemlock loss.

The objectives of this study were to (1) identify bird species associated with the presence of hemlock in southern Appalachian national forests using the methodology of Shriner (2001), (2) compare hemlock-associated species between the GSMNP and national forests to identify which species may be sensitive to impending hemlock loss, and (3) assess potential effects of hemlock decline on hemlock-associated birds in the region.

Methods

I used the USFS R8BIRD, Version 2.0 database containing avian point-count and microhabitat vegetation data for Region 8 of the USFS (R8BIRD 2001). R8BIRD was created by the USFS Southern Region as part of its Southern National Forests Migratory and Resident Landbird Conservation Strategy to monitor population trends of neotropical migrant, temperate migrant, and resident avian species and to identify species' habitat associations (Trani 1999). The most recent version of the database does not contain data for Pisgah and Nantahala National Forests in North Carolina and lacks microhabitat data for the areas of Chattahoochee National Forest, Georgia and Francis Marion-Sumter National Forest, South Carolina falling within the Southern Blue Ridge physiographic province. Therefore, I only used survey points from Jefferson and George Washington National Forests (JGWNF), Virginia and Cherokee National Forest (CNF), Tennessee, all of which are contained within the 15 million-ha southern Appalachian region (SAMAB 1996, Figure 2.1; All figures located in Appendix 2).

Point-count surveys were conducted by USFS following the protocol of Hamel et al. (1996) from 1992 to 2001, although data were not collected at all sample sites for all

years. Observers performed 10-min counts between 0600 and 1000 EDT. To reduce bias associated with differences in species detectability, only bird detections within a fixed 50-m radius around the observers were used. After eliminating sample sites with missing and incomplete data, I retained 273 survey sites on CNF and 626 survey sites on JGWNF for modeling use.

Data describing vegetation composition and structure at each survey location were collected on JGWNF in 1995 and on CNF during a single breeding season between 1992 and 2001. Data were collected on the overstory (> 9.1 m high), midstory (2.4-9.1 m high), shrub (0.3-2.4 m high), and herbaceous layers (< 0.3 m high). These data included species composition; hardwood, conifer, and hard-mast basal areas; snag abundance; canopy height; average canopy tree diameter at breast height; stand age; and CISC forest type. I assumed habitat conditions recorded during the vegetation surveys were representative of conditions throughout the period point-count surveys were conducted. However, at some sampling points in JGWNF this assumption may not be valid because of hemlock mortality from HWA infestations (Carol Hardy, USFS, pers. comm.). Most HWA-infested areas in Tennessee did not experienced significant mortality during the period represented by the bird surveys. Logging and other disturbances affected <1% of JGWNF and CNF stands during the study period.

I developed logistic regression models using a binary hemlock presence explanatory variable for 28 of the 30 bird species that Shriner (2001) examined in GSMNP to evaluate the relationship between hemlock presence and avian species occurrence. Shriner (2001) used the same technique to analyze avian-hemlock associations in GSMNP. Two of the species analyzed by Shriner (2001)—brown creeper

(*Certhia americana*) and yellow-throated warbler (*Dendroica dominica*)—had an inadequate number of detections (< 10) in both Tennessee and Virginia to allow analysis. I modeled an additional species, Blackburnian warbler, not examined in GSMNP because of its documented relationship with hemlock in the northeastern United States (Howe and Mossman 1996, Ross et al. 2002, Tingley et al. 2002). The explanatory variable of interest was the presence of hemlock, defined as a point-count location containing hemlock in any forest stratum >0.3 m high. The response variable was the presence of a given species at the point-count station in at least one survey year. In accordance with Shriner's (2001) models, I also included elevation and its squared value as explanatory variables to avoid spurious relationships caused by elevation. Shriner (2001) found hemlock presence had a quadratic relationship with elevation. Although other topographic factors such as distance to stream and landform may influence hemlock occurrence (Benzinger 1994a), these variables were not included in any of my models for two reasons: (1) I wanted my results to be directly comparable to the results of Shriner (2001) and (2) the R8BIRD database lacked data on the geographic location of all survey locations.

A second set of models was developed using a more conservation criterion for classifying species presence at points that screened the quality of the response variable by increasing the required occupancy rate (Linder and Buehler 2001). For these models, a presence for a species was classified as a point-count location with detections in ≥30% of the years surveyed. This criterion helped mitigate two problems with the first set of models based on single-year occupancy. First, it reduced noise in data resulting from the single-year detections of "floater" or unpaired males in poor or marginal quality habitat.

Second, the 30% occupancy criterion provided a means for controlling the bias associated with incorporating data from points surveyed in varying numbers of years by establishing a proportion of presence years necessary for distinguishing occupancy rather than relying on a constant number of presence years.

Logistic regression models were developed using the LOGISTIC procedure in SAS, Version 8.0 (1999). To obtain an experiment-wise α-level of 0.05, I used a Bonferroni correction and divided 0.05 by 29, the number of species modeled. Therefore, a species was considered to have a strong association with hemlock presence if the Wald *P*-value for the hemlock variable was <0.0017. A species was considered to have a weak association with hemlock if its Wald *P*-value for the hemlock variable was <0.0034. This Bonferroni-corrected α-level for each species achieves an experiment-wise α-level of 0.1. Odds ratios for the hemlock parameter are presented for models with a Wald *P*-value < 0.0034. The odds ratio for my binary hemlock presence variable can be interpreted as the odds of detecting a species at a point-count location with hemlock present (Hosmer and Lemeshow 1989).

Results

Using the single-year occupancy criterion for classifying a species presence point, logistic regression models for 29 avian species revealed 8 species strongly associated with hemlock presence in JGWNF (Table 2.2). Acadian flycatcher ($P < 0.0001$), black-throated blue warbler ($P < 0.0001$), black-throated green warbler ($P < 0.0001$), northern parula ($P < 0.0001$), and veery ($P = 0.0003$) all displayed strong positive relationships with the presence of hemlock. Eastern towhee ($P < 0.0001$), indigo bunting ($P < 0.0001$),

and pileated woodpecker ($P = 0.0002$) had strong negative relationships. No species displayed weak positive or weak negative associations with hemlock on JGWNF under the single-year occupancy criterion.

Single-year occupancy models developed for CNF revealed 3 species with strong positive relationships with hemlock presence: Acadian flycatcher ($P = 0.0005$), black-throated blue warbler ($P = 0.0009$), and northern parula ($P = 0.0002$) (Table 2.3). One species, indigo bunting, had a strong negative association ($P = 0.0001$). Black-throated green warbler ($P = 0.0022$) showed a weak positive hemlock association.

All hemlock-associated species from the single-year occupancy models for JGWNF exhibited a stronger relationship with hemlock when modeled under the 30% occupancy criterion for classifying species presence points (Table 2.4). I identified three additional species as strong positive hemlock-associates using this more conservative presence classification rule: blue-headed vireo ($P < 0.0001$), Canada warbler ($P = 0.0004$), and dark-eyed junco ($P = 0.0008$). Chimney swift, golden-crowned kinglet, red-breasted nuthatch, and winter wren were not modeled under the 30% occupancy criterion because the low number of presences for those species resulted in non-convergence of the maximum likelihood iterations for the parameter estimates.

Models developed for CNF using the 30% occupancy criterion revealed one additional species with a strong hemlock-association, black-throated green warbler ($P < 0.0001$; Table 2.5) With the exception of Acadian flycatcher, a strong positive hemlock associate under the single-year occupancy criterion ($P < 0.0001$) but not associated under the 30% occupancy criterion ($P = 0.0285$), all hemlock-associated species displayed stronger relationships under the 30% occupancy criterion than those detected in the

single-year occupancy models. Black-capped chickadee, chimney swift, golden-crowned kinglet, and red-breasted nuthatch were not modeled under this presence classification criterion because the low number of presences for those species resulted in non-convergence of the maximum likelihood iterations for the parameter estimates.

Discussion

The avian associations with hemlock presence identified by Shriner (2001) in GSMNP most closely resemble the relationships revealed by the JGWNF models. JGWNF and GSMNP shared 5 species with positive hemlock associations and 3 species with negative associations. However, Cherokee National Forest data only revealed 4 positive associates and 1 negative associate common to both GSMNP and CNF, a possible consequence of the smaller sample size for CNF compared to JGWNF (273 survey locations vs. 676 survey locations). Shriner's (2001) models for GSMNP included data from 4,157 point-count locations. Therefore, species with significant associations at $\alpha < 0.0017$ in CNF that share the same hemlock relationships with JGWNF and GSMNP could be considered the species most strongly tied to hemlock habitats in the southern Appalachians. Three positively associated species—Acadian flycatcher, black-throated blue warbler, and black-throated green warbler—and two negatively associated species—eastern towhee and indigo bunting—met this criterion.

Acadian flycatcher inhabits hardwood and coniferous forests throughout much of the eastern U.S. Despite its broad breeding distribution, it is considered a species of concern in the Southeast (Hunter et al. 1993) and Midwest (Probst and Thompson 1996). This status is primarily a result of threats to wintering grounds and its status as an

area-sensitive breeding bird (Whitehead and Taylor 2002). In the southern Appalachians, this species typically selects breeding habitat in close proximity to streams (Stupka 1963, Whitehead and Taylor 2002). The prevalence of eastern hemlock in southern Appalachian riparian areas likely explains the strong positive association between hemlock presence and Acadian flycatcher there. However, breeding adults in GSMNP choose hemlock trees as nest sites where hemlock is present (Stupka 1963), indicating that hemlock sites may represent optimal nesting habitat in the region. Therefore, the effects of hemlock decline on the regional population of this species will depend on the suitability of hardwood-dominated riparian habitat for reproduction and survival.

Black-throated blue warbler is the only species positively associated with hemlock in all three southern Appalachian study areas areas not mentioned as a hemlock associate in other studies of habitat relationships. Although Weeks (1999) found that black-throated blue warblers selectively foraged in eastern hemlock compared to other available tree species in Pisgah National Forest, North Carolina, other studies (Holmes 1994) have not examined its relationship with hemlock. As understory foragers and shrub-nesters, black-throated blue warblers select breeding habitats with high shrub densities at multiple spatial scales within the same forest type (Steele 1992). Therefore, in the southern Appalachians, they may be attracted to the high density of rosebay rhododendron (*Rhododendron maximum*) typically found in forests containing hemlock. Rhododendron is tolerant of the acidic soil conditions commonly associated with hemlock trees and also a major component of mesic coves (Benzinger 1994a). The R8BIRD vegetation database does not contain the necessary information on shrub density

at each survey location to determine the relative importance of shrub density and hemlock occurrence on black-throated blue warbler presence.

The positive association between eastern hemlock and black-throated green warbler has been detected in several previous studies (Benzinger 1994b, Ross et al. 2002, Tingley et al. 2002). Although this species may inhabit hardwood and hardwood-conifer forests, they prefer coniferous trees for nesting and foraging (Morse 1993). The decline in black-throated green warbler densities observed by Tingley et al. (2002) following hemlock mortality in southern New England may also occur in the southern Appalachians in the event of hemlock decline. Unlike Acadian flycatcher and black-throated blue warbler, studies suggest this species may respond directly to the structural contribution of hemlock (increased foliage volume) (Benzinger 1994b, Tingley et al. 2002). The increased structural diversity may mitigate competitive interaction between black-throated green warbler and other species (Morse 1993).

Species that showed weak, inconsistent, or insignificant associations with hemlock in my models still may be affected by hemlock decline. For example, hemlock may be important to golden-crowned kinglet, a species restricted to high-elevation coniferous forests in the southern Appalachians (Ingold and Galati 1997). The preferred breeding habitat of this species (spruce-fir forest) has been severely altered by balsam woolly adelgid (*Adelges piceae*), and, consequently, its population in GSMNP has declined (Rabenold et al. 1998). The documented presence of golden-crowned kinglets in forest types containing hemlock below the spruce-fir zone (Shriner 2001) indicates that stands with a hemlock component may be an important alternative breeding habitat for

the species. Loss of hemlock could further reduce the population densities of golden-crowned kinglet in the southern Appalachians.

Blackburnian warbler is a species widely acknowledged as a hemlock obligate/associate throughout much of its range (Kendeigh 1945, Morse 1994, Howe and Mossman 1996, Ross et al. 2002). Even in hardwood-dominated forests, Blackburnian warblers are almost exclusively found near scattered hemlock or spruce trees (Morse 1994). The lack of a relationship between Blackburnian warbler and hemlock presence in my analysis probably is attributable to the low number of detections in the dataset (Tables 2.2-2.5), a consequence of the patchy distribution and relative rarity of occurrence in the region. Shriner (2001) did not analyze Blackburnian warbler occurrences because it was not one of the 30 most abundant species in GSMNP based on her surveys. Previous studies have documented strong preference of Blackburnian warblers for coniferous habitats in other parts of its range. Thus, hemlock loss may negatively impact this already rare species in the southern Appalachians despite its exclusion from the hemlock-association models developed for the region (Peck and James 1989, Morse 1994, Howe and Mossman 1996, Ross et al. 2002, Tingley et al. 2002).

Although wood thrush inhabits a variety of forest types across its broad distribution (Roth et al. 1996), Shriner (2001) identified it as a hemlock associate in GSMNP. This relationship within the park may be a result of selection of eastern hemlock as nesting substrate. In a study of the factors affecting wood thrush productivity, Farnsworth and Simons (1998) found that wood thrush selection of young hemlocks as nest sites was disproportionate to their availability in GSMNP: 84% of wood thrush nests occurred in eastern hemlock. The lack of a relationship between hemlock

presence and wood thrush presence in my analysis may be a result of the comparatively lower occurrence of hemlock in southern Appalachian national forests and the plasticity in nest-site selection of this species (Roth et al. 1996). However, the selection of hemlock nest sites by wood thrush indicates that hemlock may afford reproductive benefits over large spatial and temporal scales. GSMNP contains an important source population of wood thrush for the region (Simons et al. 2000), and the elimination of their primary nesting substrate may negatively impact the species within the national park and in adjacent national forests.

Ultimately, the effects of hemlock decline on the avifauna of the southern Appalachians will depend on their ecological dependence on hemlock as foraging, nesting, and protective habitat. The analysis of distributional data presented in this study did not consider the ecological mechanisms driving the observed avian associations with hemlock, and, consequently, potential plasticity in habitat selection and other life history traits that may mitigate the impacts of hemlock loss are unknown. However, at least one species with a strong positive hemlock-association in the southern Appalachians, black-throated blue warbler, has greater reproductive success in hemlock forests than hardwood habitats (Part 3). A decrease in reproductive performance coupled with reduced densities from loss of preferred hemlock sites could result in local and regional declines in this Neotropical migrant species. However, the increase in shrub stem densities following hemlock mortality (Orwig and Foster 1998, Tingley et al. 2002) could benefit breeding black-throated blue warblers in forests with a hemlock component by increasing the availability of potential nest sites and providing additional protection from predators. Therefore, the regional impacts of hemlock decline on black-throated blue warbler and

other species will depend on hemlock's role in the mechanisms influencing breeding habitat selection, reproductive success, survival, and other demographic parameters.

Currently, the most effective tool for controlling hemlock woolly adelgid infestations at a local scale is *Pseudoscymnus tsugae*, a predator ladybird beetle native to Asia (McClure 2000). Although releases of the beetle have successfully demonstrated its ability to locally reduce adelgid populations over short time periods, the long-term utility of this biocontrol agent remains unclear (McClure 2000). The questionable future of eastern and Carolina hemlock highlights the importance of this analysis as a "baseline" study which may be referenced in the event of widespread hemlock mortality in the southern Appalachians. In George Washington and Jefferson National Forests, hemlock has been declining throughout the period the R8BIRD surveys were conducted. However, no information currently exists on the extent of mortality at individual point-count locations. Ascertaining direct effects of hemlock loss on avian distributions will require continual monitoring of hemlock health on the R8BIRD points. A post-hemlock decline analysis of avian distributional data would serve as a valuable case study on the effects an invasive exotic insect pest may have on bird communities.

PART 3

REPRODUCTIVE ECOLOGY OF HEMLOCK-ASSOCIATED BIRDS IN THE SOUTHERN APPALACHIANS

Introduction

Although avian associations with eastern hemlock (*Tsuga canadensis*) are well documented (Benzinger 1994b, Howe and Mossman 1996, Shriner 2001, Ross et al. 2002, Tingley et al. 2002, Part 2), the ecological mechanisms influencing these relationships are unknown. The potential effects of eastern hemlock decline on breeding birds in the southern Appalachians cannot be predicted without knowledge of the life history traits governing avian associations with the tree. No hemlock-associated avian species in the southern Appalachians are restricted to hemlock stands; therefore, these species may possess plasticity in their habitat selection that could mitigate potential negative impacts of hemlock decline. Such knowledge is also necessary to elucidate the potential value of hemlock-associated species as bio-indicators of hemlock ecosystem health.

A possible proximate mechanism for the hemlock associations observed in the southern Appalachians (Shriner 2001, Part 2) may be differences in reproductive fitness afforded by hemlock sites. According to ideal despotic distribution (IDD) theory, species that have better reproductive performance in sites with hemlock should exist in greater and more stable densities in that habitat over large spatial and temporal scales (Holmes et al. 1996). IDD theory states that as optimal habitats (i.e., habitats that afford high fitness) are filled by territorial males, subordinate individuals are relegated to suboptimal habitats characterized by lower fitness values (Fretwell 1972, Rodenhouse et al. 1997). These "ideal" habitats that afford high fitness should be favored through natural selection (Zimmerman 2003). Therefore, the greater than expected probabilities of detecting 7

breeding bird species in GSMNP on sites with hemlock may result from despotically distributed individuals favoring highly productive, "optimal" hemlock breeding sites.

The primary objective of this study was to test the prediction that nesting success of three hemlock-associated species in the southern Appalachians, black-throated blue warbler, dark-eyed junco, and blue-headed vireo, is greater in breeding habitats containing hemlock than habitats without hemlock. Black-throated blue warbler and dark-eyed junco were selected as focal species because of their documented association with eastern hemlock presence in GSMNP and because they exist in densities sufficient to obtain adequate nest samples. Blue-headed vireo, although not identified as an associate of eastern hemlock in GSMNP by Shriner (2001), is associated with hemlock in the northeastern U.S. (Benzinger 1994b, Ross et al. 2002) and is a species sensitive to conifer mortality in GSMNP (Rabenold et al. 1998). In addition to nesting success, I investigated potential mechanisms influencing productivity by comparing Lepidoptera larvae abundance, parental provisioning rates of nestlings, predator abundance, and microhabitat characteristics important to nest-site selection in hemlock and hardwood-dominated sites.

Methods

Study sites

Data were collected from late-April to mid-July, 2002 and 2003 at two study sites: Cataloochee Valley in Great Smoky Mountains National Park, North Carolina and Coweeta Long Term Ecological Research Station in Nantahala National Forest, North Carolina (Figure 3.1). These sites were approximately 70 km apart. At the Cataloochee

site, data were collected on two 15-ha plots: one in a 49-ha mixed old-growth/second-growth eastern hemlock-dominated stand near the Jim Branch of Cataloochee Creek (Yost et al. 1994) and one in a rich cove hardwood stand near Messner Fork. These plots were selected because they represent conditions typical of hemlock and rich cove hardwood (hereafter, cove hardwood) forest types as defined by Schafale and Weakley (1990). Both plots were dominated by northern aspects and had an average elevation of approximately 1200 m. The hemlock plot was characterized by eastern hemlock, tulip tree (*Liriodendron tulipifera*), and red maple (*Acer rubrum*) in the canopy with an undergrowth of dense rhododendron (*Rhododendron maximum*), especially near canopy gaps, and scattered thickets of American beech (*Fagus grandifolia*). The overstory of the cove hardwood plot was dominated by Carolina silverbell (*Halesia carolina*), tulip tree, and yellow birch (*Betula alleghaniensis*) with patches of eastern hemlock in the canopy. Undergrowth was characterized by scattered, dense patches of rhododendron. Table 3.1 summarizes vegetation structure of the Cataloochee plots.

At the Coweeta site, data were collected on five 15-20 ha plots, although only three plots were used in both study years. Because the Coweeta plots were designed for a separate study, these plots were not selected on the basis of forest type and, therefore, contained differing amounts of second-growth eastern hemlock. During 2002, plots in cove hardwood, acidic cove hardwood, montane oak-hickory, and high elevation red oak forest types were placed at 900 m, 900 m, 1,100 m, and 1,300 m elevation, respectively. In 2003, the cove hardwood plot at 900 m was abandoned because its topographic position in a cove created microclimate and vegetative characteristics similar to the

higher elevations plots. Therefore, a plot in a northern hardwoods stand at 1500 m was added in 2003. Forest type classifications were based on Schafale and Weakley (1990).

Nest survival

Following the protocol of Martin and Gruepel (1993), field personnel used behavioral cues and systematic searches to locate nests of the three focal species. Nest searching was concentrated within the boundaries of the plots early in the breeding season and extended to adjacent areas of similar forest type in late May and June to increase sample sizes. While nest searching, field personnel mapped territories of the study species to gain density estimates within each plot. Nests were checked every three days for activity, and nest contents were checked on the day of expected hatching and fledging dates. I estimated date of nest failure as the day after the last day the nest was observed active. Nests were considered successful if ≥1 nestling survived to expected fledging dates based on nesting period lengths reported in the literature (Holmes 1994, Ross 1998, Nolan et al. 2002). These nesting period lengths were 25.5 days for black-throated blue warblers, 28 days for dark-eyed juncos, and 32 days for blue-headed vireos.

I calculated daily nest survival rates (DSR) and cumulative nest success rates (NSR) using the Mayfield method (Mayfield 1975) and estimated associated standard errors according to Hensler (1985). Only active nests and nests with known fates were included in the analysis. I also calculated stage-specific daily survival rates for the egg stage (laying and incubation) and the nestling stage. I compared survival rates using χ^2 tests provided by Program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989). Nest success and stage-specific daily survival rates of study species were

compared between the 15-ha hemlock and cove hardwood plots at the Cataloochee site. Additionally, nests were split into two categories: (1) hemlock nests, defined as nest sites containing at least one hemlock tree >9.9-cm dbh within a 0.04-ha (11.3-m radius) circle centered on the nest, and (2) non-hemlock nests, defined as nest sites without a hemlock tree >9.9-cm dbh hemlock tree within 0.04 ha. NSR values of the species were compared between hemlock and non-hemlock nests at the Cataloochee and Coweeta sites. An α-level of 0.05 was used to determine statistical significance. For categories with sufficient sample sizes ($n \geq 10$), I made nest survival comparisons within years and study site. However, insufficient sample sizes (<10 nests/category) forced pooling of dark-eyed junco and blue-headed vireo nests between years for the stand scale comparisons and among sites and years for the nest site scale comparisons. Black-throated blue warbler nests were also pooled between years for the nest- site scale comparisons.

Lepidoptera larvae biomass index

Lepidoptera larvae constitute the majority of prey taken by breeding black-throated blue warblers and blue-headed vireos (Robinson and Holmes 1982) and a large portion of prey delivered to dark-eyed junco nestlings (Nolan et al. 2002). Therefore, caterpillar abundance was surveyed following a visual leaf inspection method (Rodenhouse 1986). To obtain an estimate of prey abundance, Lepidoptera larvae were surveyed at 44 systematic locations on each of the hemlock and cove hardwood plots at the Cataloochee study site. For each plot, sampling locations were spaced by 50 m along four 500-m transects per plot. Within a 25-m radius of each sampling location, field personnel inspected 100 leaves of five plant species—American beech, eastern hemlock, striped maple (*Acer pennsylvanicum*), rhododendron, and Carolina silverbell—between 0

and 2.5 m high for caterpillars. An eastern hemlock "leaf" was considered to be a 10 x 5-cm living twig. These five plant species were selected because they were the five most abundant shrub layer species common in both Cataloochee plots. Larvae lengths were measured to nearest mm, and dry weight biomass of each caterpillar was calculated (Rodenhouse 1986):

$$\text{weight (mg)} = 0.004 \times \text{length}^{2.64}$$

Field personnel surveyed Lepidoptera larvae three times in 2002 (May 28-31, June 10-14, and June 27-30) and five times during 2003 (May 2-9, May 19-23, June 5-8, June 19-22, July 6-8). We surveyed only the shrub layer because caterpillar abundance is not strongly stratified among forest layers (Holmes and Schultz 1988). However, because the majority of dark-eyed junco prey is obtained from leaf litter (Nolan et al. 2002), this methodology is most relevant to black-throated blue warbler and blue-headed vireo prey availability. The biomass index was calculated as average dry weight caterpillar biomass in mg per sampling point.

The Lepidoptera larvae biomass index was compared between Cataloochee hemlock and cove hardwood plots with a Friedman's test (non-parametric repeated measures ANOVA) and Wilcoxon rank sum tests (two-sample analysis of ranks) in SAS, Version 8.0 (SAS Institute 1999). Caterpillar sampling locations were ranked with respect to biomass within year using PROC RANK and the within-year ranks were then compared using the GLM procedure to obtain the equivalent of a Friedman's test. PROC NPAR1WAY was used to perform Wilcoxon rank sum tests on between-plot differences in biomass for individual sampling periods. An α-level of 0.05 was used to determine statistical significance.

Parental provisioning

The amount of food delivered to nestlings may directly affect nestling survival through starvation (Magrath 1990, Rodenhouse and Holmes 1992, Sherry and Holmes 1992) or indirectly through predation from increased begging behavior (Martin 1992a). I compared food delivery rates for black-throated blue warblers between hemlock and cove hardwood forest types, by filming nests with Sony® Hi-8 camcorders on the 7th day after hatching. Cameras were mounted on tripods 1.5-3 m from the nests, and nests were filmed for 2-4 hours between 0700 and 1200 hours. I calculated the number of deliveries per hour per nestling for each nest. Additionally, I determined the size of each food item relative to bill length (Simons and Martin 1990) according to four size categories: 1) 0-6 mm, 2) 7-13 mm, 3) 14-20 mm, or 4) >20 mm. Each item was identified as Lepidopteran or non-Lepidopteran. By multiplying the number of deliveries per hour per nestling by the average size class of food brought per trip, I calculated an overall biomass delivery index and a biomass delivery index for Lepidoptera larvae. I compared the hourly delivery rate per nestling, total biomass delivery index, and biomass delivery index for Lepidoptera larvae between the hemlock and hardwood plots using two sample, two-tailed t-tests. I tested the data for assumptions of normality and equality of variances. To eliminate differences attributable to year effects, I only used feeding rate data from 2003, the year with the largest sample size. An α-level of 0.05 was considered statistically significant for these tests.

Predator abundance

We surveyed nest predator abundance by conducting biweekly 10-min point counts for potential diurnal mammalian and avian nest predators from May to July during

the 2003 field season. We recorded the number of predators by species within a fixed, 50-m radius circle around the observer. Fifteen survey locations ≥ 100 m apart were systematically placed on both plots at the Cataloochee study site. For each survey location, the total number of detections per species were pooled among sampling periods and compared between plots with a Fisher's exact test. I used an alpha level of 0.05 to determine statistical significance.

Nest-site selection and nest success modeling

Data on vegetation composition and structure were collected within 11.3-m radius plots (0.04 ha) centered on nest sites and at 45 systematically placed locations on each plot. Nests located > 50 m from a plot boundary were paired with a vegetation sampling point placed 50 m from the nest in a random direction. Within the 11.3-m radius circle, we recorded diameter at breast height (dbh) of all trees (living stems ≥10 cm dbh) and standing snags, number of fallen logs (>50 cm diameter at butt end, >3 m long), canopy height, slope, and aspect. Percent hardwood and hemlock canopy cover were estimated using a spherical densiometer. Within a 3-m radius circle, sapling (living stems 2.5-10 cm dbh) and shrub (living woody stems <1.4 m tall) stems were counted and recorded by species. Percent overhead midstory cover (1.5- 9 m from ground) and shrub cover (<1.5 m from ground) were visually estimated. The percent area of a 1 x 2 m cover board obscured by vegetation was visually estimated at 5 m and 10 m in the four cardinal directions from plot center. Ground cover composition was recorded in 1-m radius circles at 5 m from plot center along the four cardinal directions and at plot center. The presence or absence of canopy gaps (an opening with a diameter >50% of canopy height) within 50 m of plot center was recorded.

I selected 9 explanatory variables *a priori* for inclusion in a global logistic regression model (Burnham and Anderson 1998) discriminating nest sites of my primary focal species, black-throated blue warbler, from systematically placed points: presence/absence of canopy gap within 50 m (Gap), basal area of yellow birch (baBEAL), basal area of eastern hemlock (baTSCA), basal area of hardwood species (baHARD), number of eastern hemlock sapling stems (TSCASap), number of all sapling stems (TotalSap), percent overhead midstory cover (USCOV), number of shrub stems (TotalShr), and number of fallen logs (Logs). Variables TotalSap, USCOV, and TotalShr were selected on the basis of their documented importance to black-throated blue warbler nest site selection (Holway 1991, Holmes 1994, Weeks 1999). Yellow birch may be important to nest site selection because its bark is the primary material used in nest construction (Holmes 1994). The remaining five parameters were potentially important based on personal observations of nest placement in the field. All 9 variables are potentially sensitive to effects of hemlock decline (Orwig and Foster 1998).

With the exception of baBEAL, the same variables were used in a global logistic regression models developed for both study sites predicting the probability of a black-throated blue warbler nest successfully fledging young. Yellow birch basal area was removed from the nest success models because, as a source of nest construction material, I expected yellow birch to be important to nest site selection but irrelevant to nest success.

Before proceeding with model selection, I examined the likelihood, goodness-of-fit, and predictive ability of the global logistic regression model by examining Wald χ^2 tests, Hosmer-Lemeshow tests, percent correct classification, and model sensitivity (the

percent of nest-sites correctly classified by the model) and specificity (the percent of non-nest-sites correctly classified by the model). Logistic regression analysis was performed using the LOGISTIC procedure in SAS, Version 8.0 (SAS Institute 1999). A Hosmer-Lemeshow test *P*-value > 0.05 indicated the model had acceptable fit. Percent correct classification, sensitivity, and specificity were reported at a probability cut-off level that represented a balance between false positive and false negative rates. I generated a set of candidate reduced models from the global model in SAS following the best subsets procedure of Shtatland et al. (2001) which ranks families of models with *K* parameters based on Akaike's information criterion (AIC) values. Using a SAS macro (Shtatland et al. 2001), I evaluated the 5 best models with the optimal number of parameters, as determined by the best subsets procedure. I also included the 5 best models within ± 1 parameter of the optimal model size (i.e., *K*-1 and *K* + 1). These 15 reduced models and the global model served as my list of candidate models and were ranked by Δ_i:

$$\Delta_i = AIC_i - AIC_{min}$$

where AIC_{min} is the lowest AIC value in the set of candidate models and AIC_i is the AIC value for the model being examined (Burnham and Anderson 1998). Although the model with AIC_{min} was assumed to be closest to truth relative to the other candidate models, all models with Δ value ≤ 2 should be considered when making inferences. I calculated Akaike weights (the likelihood that the given model was the best model in the set of candidate models) for each model (Burnham and Anderson 1998):

$$w_i = \exp(-\Delta_i/2)/\Sigma_{r=1}\exp(-\Delta_r/2).$$

I independently generated sets of candidate models for the Cataloochee hemlock plot, Cataloochee cove hardwood plot, Cataloochee study site (plots pooled), and Coweeta study site (plots pooled) to compare model parameters between hemlock and hardwood stands and between the two study sites.

Results

Nest survival

During 2002 and 2003, 161 black-throated blue warbler nests, 50 dark-eyed junco nests, and 33 blue-headed vireo nests were located at the Cataloochee and Coweeta study sites. At the Cataloochee site, black-throated blue warbler Mayfield nest success did not differ between years within plots (hemlock plot: $P = 0.9527$; hardwood plot: $P = 0.5345$; Table 3.2). Black-throated blue warbler nest success averaged 59.4% on the hemlock plot and was greater than the average nest success of 30.5 % on the hardwood plot for 2002-2003 pooled ($P = 0.0190$; Figure 3.2). At the 0.04-ha nest site scale, black-throated blue warbler nest success appeared to be numerically greater on hemlock sites (Cataloochee: $\bar{x} = 47.0\%$; Coweeta: $\bar{x} = 44.2\%$; Table 3.3) than non-hemlock sites (Cataloochee: $\bar{x} = 32.7\%$; Coweeta: $\bar{x} = 38.5\%$), but the differences were not significant at either study site (Cataloochee $P = 0.4859$; Coweeta $P = 0.5979$; Figure 3.3).

Black-throated blue warbler egg-stage daily survival for the hemlock plot ($\bar{x} = 0.9904$) was greater than egg-stage daily survival for the hardwood plot ($\bar{x} = 0.9603$; $P = 0.0105$; Figure 3.4). However, nestling-stage daily survival did not differ between plots (hemlock: $\bar{x} = 0.9615$; hardwood: $\bar{x} = 0.9407$; $P = 0.3856$). At the 0.04-ha nest site

scale, egg-stage daily survival appeared to be numerically greater for hemlock nests (Cataloochee: $\bar{x}$ = 0.9787; Coweeta: $\bar{x}$ = 0.9774; Table 3.4) than daily survival for non-hemlock nests (Cataloochee: $\bar{x}$ = 0.9597; Coweeta: $\bar{x}$ = 0.9557) but the difference was not significant at either site (Cataloochee: *P* = 0.2718; Coweeta: *P* = 0.0645). Nestling-stage daily survival did not differ between hemlock (Cataloochee: $\bar{x}$ = 0.9508; Coweeta: $\bar{x}$ = 0.9762) and non-hemlock nests (Cataloochee: $\bar{x}$ = 0.9520; Coweeta: $\bar{x}$ = 0.9563) at either site (Cataloochee: *P* = 1.0000; Coweeta *P* = 0.1907).

After pooling years because of low within-year sample sizes, neither dark-eyed junco nor blue-headed vireo nest success differed between the hemlock (dark-eyed junco: $\bar{x}$ = 17.8%; blue-headed vireo: $\bar{x}$ = 29.7%) and cove hardwood plots (dark-eyed junco: $\bar{x}$ = 20.5%; blue-headed vireo: $\bar{x}$ = 20.8%; dark-eyed junco: *P* = 0.8554; blue-headed vireo: *P* = 0.6267; Table 3.2; Figure 3.5). Insufficient junco and vireo nest sample sizes at the Coweeta site forced pooling data between study sites for the calculation of survival rates at 0.04-ha nest site scale. Dark-eyed junco nest success (hemlock: $\bar{x}$ = 28.8%; non-hemlock: $\bar{x}$ = 27.7%; Table 3.3) and blue-headed vireo nest success (hemlock: $\bar{x}$ = 26.1%; non-hemlock: $\bar{x}$ = 11.0%) did not differ between hemlock nest sites and non-hemlock nest sites (dark-eyed junco: *P* = 0.9432; blue-headed vireo: *P* = 0.2210; Figure 3.6).

Egg-stage and nestling-stage daily survival did not differ between the hemlock and cove hardwood plot for dark-eyed junco (egg-stage: *P* = 0.6502; nestling stage: *P* = 0.5934) or blue-headed vireo (egg-stage: *P* = 0.8533; nestling stage: *P* = 0.9125; Table 3.4). After pooling data between years and study sites, no differences were detected in

stage-specific daily survival rates for dark-eyed juncos (egg-stage: $P = 1.000$; nestling-stage: $P = 0.7704$; Table 3.5) or blue-headed vireos (egg stage: $P = 0.2673$; nestling-stage: $P = 0.7082$).

Based on daily mapping of target species territories, black-throated blue warbler density in the hemlock was 0.66 pairs/ha in 2002 and 0.56 pairs/ha in 2003 respectively. Black-throated blue warbler density on the hardwood plot was 0.60 pairs/ha in 2002 and 0.53 pairs/ha in 2003.

Lepidoptera larvae biomass index

The Friedman's test of caterpillar biomass revealed large plot and sampling period effects (plot effect $P = 0.0014$, sampling period effect $P < 0.0001$), but there was no interaction between these two factors ($P = 0.2208$). During 2002, Lepidoptera larvae biomass were numerically greater on the hemlock plot during the first two sampling periods (May 28-31, June 10-14); however, these differences were not significant (May 28-31: $P = 0.9112$, June 10-14: $P = 0.2116$; Table 3.6, Figure 3.7). The hardwood plot, however, had greater caterpillar biomass during the third 2002 sampling period (June 27-30, $P < 0.0187$). Lepidoptera larvae biomass during 2003 was numerically greater on the hardwood plot throughout the breeding season, although the between-plot differences were only significant during the May 2-9 sampling period ($P = 0.0035$) and marginally significant during the June 5-8 sampling period ($P = 0.0666$).

Parental provisioning

During 2003, 7 nests were videotaped on the hardwood plot and 8 nests were videotaped on the hemlock plot (Table 3.7). Three hundred eighty-six delivery events were recorded during 23.5 hours of filming on the hardwood plot and 296 delivery events

were recorded during 20.2 hours of filming on the hemlock plot. Using individual nests as experimental units, the average black-throated blue warbler hourly food delivery rate per nestling on the hemlock plot ($\bar{x}$ = 5.96 deliveries/hr/nestling) was greater than the food delivery rate on the hardwood plot ($\bar{x}$ = 4.70 deliveries/hr/nestling; P = 0.0242). However, the overall biomass delivery index did not differ between plots (hardwood: $\bar{x}$ = 13.16; hemlock: $\bar{x}$ = 15.29; P = 0.3302). The Lepidoptera larvae biomass delivery index also did not differ between plots (hardwood: $\bar{x}$ = 5.90; hemlock: $\bar{x}$ = 9.00; P = 0.1050). The average size class of food items brought to the nest per delivery was 2.88 for the hardwood plot and 2.53 for the hemlock plot. Lepidoptera larvae constituted 45.7% of the biomass delivered to nestlings on the hardwood plot and 57.9% of the biomass delivered to nestlings on the hemlock plot.

Predator abundance

Predator surveys were conducted six times during the 2003 breeding season. Eastern gray squirrels (*Sciurus carolinensis*), red squirrels (*Tamiasciurus hudsonicus*), eastern chipmunks (*Tamias striatus*), blue jays (*Cyanocitta cristata*), and American crows were detected during the bi-weekly predator surveys (Figure 3.7). An equal number of gray squirrel and blue jays were detected per survey location on each plot (blue jay: $\bar{x}$ = 0.135 detections/survey location; gray squirrel: $\bar{x}$ = 0.068 detections/survey location). Red squirrel (hardwood: $\bar{x}$ = 0.176 detections/survey location; hemlock: $\bar{x}$ = 0.189 detections/survey location; Fisher's exact P = 1.000) and eastern chipmunk (Fisher's exact P = 0.6198) detections/survey location did not differ between plots. Only American Crow detection frequency differed between plots

(Fisher's exact $P = 0.0135$; Table 3.8) with 0 detections/survey location on the hardwood plot and 0.09 detections/survey location on the hemlock plot.

Nest site selection modeling

The best nest-site selection model for the hemlock plot contained variables Gap, USCOV, TotalShr, and Logs, and, with the exception of Gap, had similar parameter estimates as the hardwood models (Table 3.9). In contrast to nests on the hardwood plot, hemlock nests were positively associated with the presence of a canopy gap within 50 m. These four variables were consistently used in the seven models with $\Delta_i \leq 2$. The best nest-site selection model for the cove hardwood plot contained variables Gap, baTSCA, baHARD, USCOV, TotalShr, and Logs (Table 3.9). Nest sites on the hardwood plot were positively associated with shrub stem counts and number of logs and negatively associated with midstory overhead cover, the presence of a canopy gap within 50 m, eastern hemlock basal area, and hardwood basal area. These variables, excluding Logs, were used in all five models with $\Delta_i \leq 2$Combining data between plots at the Cataloochee site resulted in a best model containing variables baBEAL, baTSCA, USCOV, TotalShr, and Logs. Nest sites were negatively associated with yellow birch basal area, eastern hemlock basal area, and midstory overhead cover and positively associated with shrub stem counts and number of logs. The global and best models for the hemlock plot, cove hardwood plot, and pooled plots had good likelihood, fit, and excellent predictive ability (Table 3.10).

The best Coweeta model contained variables Gap, baBEAL, TSCASap, and TotalShr (Table 3.11). Nest sites were positively associated with the number of hemlock saplings in the top 6 models. However, the parameter estimates for TSCASap were not

significant at $\alpha = 0.05$ in any of those models. Only variables Gap, baBEAL, and TotalShr were contained in all 9 models with $\Delta_i \leq 2$. Nest sites were positively associated with the presence of a canopy gap within 50 m, yellow birch basal area, and shrub stem counts. The best Coweeta model had good likelihood and fit (Wald $P = 0.0001$, Hosmer-Lemeshow $P = 0.3774$), excellent specificity (86.8%), but low sensitivity (32.7%).

My *a priori* black-throated blue warbler global nest success models for both Cataloochee and Coweeta performed poorly (Table 3.12). Both global models had non-significant Wald χ^2 values (Cataloochee $P = 0.5977$, Coweeta $P = 0.3746$). The optimal number of parameters for the Cataloochee and Coweeta nest success models according to the best-subsets procedure was 1. However, no models containing one variable discriminated successful nests from failed nests better than the null model (Wald $P > 0.05$).

Discussion

Black-throated blue warbler nest success in the hemlock stand was greater than nest success in the cove hardwood stand during 2002 and 2003, a result consistent with the hypothesis that hemlock-dominated sites provide "optimal" breeding habitats. However, the apparent lack of a difference in nest success between the hemlock and cove hardwood stands for dark-eyed juncos and blue-headed vireos failed to support the supposition that reproductive fitness for those two species is greater in hemlock-dominated stands. Although nest survival of all focal species appeared to be numerically

greater at 0.04-ha nest sites containing hemlock than nest sites without hemlock at both study sites, these differences were potentially spurious.

By relying on individual nests to calculate the χ^2 values used for hypothesis testing, my analysis lacked true spatial replicates at the 15-ha scale. Therefore, caution must be exercised when applying these results to other areas of the southern Appalachians because of the problems associated with treatment pseudoreplication (Hurlbert 1984). However, the low *P*-value associated with the difference in black-throated blue warbler nest success at the 15-ha scale suggested that the difference was indeed real on the observed plots. Assuming my study plots were representative of hemlock and cove hardwood plots in the GSMNP, a difference in nest survival between forest types of the observed magnitude (28.9%), would be biologically significant. The black-throated blue warbler nest success rates in the hemlock plot for 2002 (52.4%) and 2003 (64.7%) were greater than any previously reported nest success rates for this species in the southern Appalachians (Guzy 1995, Weeks 1999).

Although hemlock-dominated stands apparently afforded greater success to nesting black-throated blue warblers, predicting the effects of eastern hemlock decline on reproduction requires an understanding of relationships between hemlock forests and the mechanisms that drive nest success and nest site selection for this species. Consistent with numerous studies of avian nest success (e.g., Nice 1957, Ricklefs 1969), the vast majority (< 95%) of nest failures in the study were attributable to apparent predation events, indicating that nest failure rates were roughly equivalent to predation rates. Although avian nest success may be correlated with predator abundance (Patten and Bolger 2003), my index of diurnal predator abundance in 2003 failed to detect differences

in predator densities between the hemlock and cove hardwood plots that could explain the apparent difference in predation rates. No previous studies have specifically addressed this question in these forest types. Furthermore, linking nest success to predator densities is problematic without better information on the predator assemblage at the study sites and knowledge of the predator species most important to black-throated blue warbler nest predation rates. Whereas previous studies suggested that avian nest predators may be most important to shrub-nesting birds (Nour et al. 1993, Patten and Bolger 2003), the low number of avian predators (Corvids) detected on the plots indicated another predator may be responsible for the majority of failures in this study. The principal black-throated blue warbler nest predator on my study plots may have been red squirrel, a common predator of shrub and canopy-nesting forest birds in the eastern U.S. (Sloan et al. 1998, Wilson et al. 2003).

Although results of my surveys did not reveal differences in diurnal nest predator abundance that could explain the observed difference in black-throated blue warbler nest success, my survey design inadequately sampled the complete assemblage of potential nest predators on the plot. My surveys were not well-designed to detect snakes and nocturnal mammals, two groups of predators that may have contributed to nest predation rates. Additionally, these surveys resulted in low power because of low number of detections, so a predator abundance-based mechanism cannot be discounted without better data on predator communities in the plots.

Perhaps more important than nest predator abundance in determining nest success was predator foraging efficiency (Martin 1992b), which may be influenced by the structural complexity (e.g., plant architecture, stem densities) at both the scale of the nest

site (Martin and Roper 1988) and forest stand (Holmes et al. 1996). Based on the results of my nest success modeling, nest success in this study was not related to measured microhabitat variables describing structural complexity and nest concealment at the nest site scale. However, observed differences in vegetation structure at the 15-ha plot scale may help explain nest success differences between forest types. The Cataloochee hemlock plot had greater mean shrub stem counts, cover board obscurity measurements, and overhead shrub cover than the cove hardwood plot. Forest stands with greater densities of the preferred nesting substrate for black-throated blue warblers (shrubs) may affect predator foraging efficiency by increasing the number of potential nest sites to be searched (Martin and Roper 1988, Tarvin and Smith 1995). This mechanism would work at scales larger than the nest-site, either in conjunction or independently of other mechanisms such as the inhibition of visual, auditory, and olfactory cues by nesting cover (Martin and Roper 1988), and is consistent with observed differences in plot vegetation.

My analysis of stage-specific nest survival for black-throated blue warblers lends further support to the hypothesis that the increased availability of potential nest sites on the hemlock plot diluted the effective predation pressure at the stand scale. Nest success for this species during the egg stage was 33% greater on the hemlock plot than the cove hardwood plot. Predators may be opportunistically discovering nests during the egg stage, a period of the nestling cycle with less nest-site activity and, therefore, fewer behavior cues indicating location of a nest. Consequently, the effects of increased levels of nesting substrate density on nest survival would be strongest during the egg stage when predators rely less on adult behavioral cues and more on visual and olfactory signals.

Of the 9 parameters considered in the black-throated blue warbler nest site selection models, only two—overhead cover in the 1.5- 9 m stratum and shrub stem counts—were consistently included in all models with $\Delta_i < 2$ for the Cataloochee hemlock and cove hardwood plot data sets. Shrub stem counts also were consistently included in the best nest-site selection models using data from the Coweeta study site. The negative relationship between nest sites and dense midstory cover and the positive relationship between nest sites and shrub density at the Cataloochee study site were consistent with studies of black-throated blue warbler nest-site selection in other areas of their breeding range (Steele 1993, Holmes 1994). The number of logs also was used in all models for both Cataloochee study plots. Black-throated blue warblers may be attracted to the additional structural complexity and nest cover provided by large fallen logs. A notable divergence in models developed for the two Cataloochee plots was the difference in the direction of the association with gap presence. On the hardwood plot, nest sites were negatively associated with gaps, whereas nest sites on the hemlock plot were positively associated with gaps. One possible explanation for this discrepancy is that black-throated blue warblers were attracted to hemlock canopy gaps because these disturbed areas had greater shrub densities and, therefore, more potential nest sites, whereas shrub densities in cove hardwood stands were more evenly dispersed because of greater light penetration in the understory (Benzinger 1994a) and not as dependent on canopy openings. This premise is supported by the lower variances for shrub stem count, total shrub cover, and cover board measurements on the hardwood plot compared with the variances for these variables on the hemlock plot (Table 3.1).

Pooling data between Cataloochee plots revealed negative nest site associations with basal areas of yellow birch and eastern hemlock. Considering the documented association between eastern hemlock and black-throated blue warblers (Shriner 2001) and the importance of yellow birch bark to nest construction (Holmes 1994, personal observation), this finding is counterintuitive. However, the importance of an open understory layer (1.5-9 m) and high shrub density is consistent in the pooled Cataloochee models.

The poor performance of the nest success models developed for both study sites indicated that the microhabitat variables I selected, despite their hypothetical importance to nest concealment, have little influence on nest fates over the temporal and spatial scale of this study. Several studies have failed to find significant effects of nest concealment on nest success but detected preferences in microhabitat variables for nest-site selection (Holway 1991, Howlett and Stutchberry 1996, Weeks 1999). Many avian nests probably are found by predators by chance, and the probability that a nest will be discovered may also be related to its position in a predator's home range (Holway 1991). Therefore, over the typical time scale of nest success studies (2-4 years), diverse predator assemblages and stochastic predation events could mask small but significant fitness benefits of increased nest cover. Unobservable at small scales, modest reproductive fitness effects attributable to cover could influence natural selection over evolutionary time (Holway 1991).

This study, when considered in the context of the potential decline of eastern hemlock in GSMNP and surrounding national forests, suggests the impact of hemlock loss on black-throated blue warbler reproduction may be most directly related to potential

changes to the shrub layer. Determining the relative importance of eastern hemlock and high shrub densities in forest stands is difficult given my unreplicated study design at that scale and the understory conditions on the two Cataloochee plots. However, two lines of evidence indicated that the shrub layer may be more critical than the presence of hemlock to nest-site selection and nest success of black-throated blue warblers. First, eastern hemlock had no relationship with the presence of a nest-site in both forest types examined, whereas shrub stem count was the most important variable in all nest-site selection models. Second, consistent with previous work on black-throated blue warblers, greater shrub density throughout the hemlock plot may have diluted the effective predation pressure on nests in that plot (Holmes et al. 1996). This second point was supported by observed differences in egg-stage survival between the hemlock and hardwood plots.

The immediate effects of hemlock loss on the shrub layer and, consequently, on black-throated blue warbler nest-site selection and nest success will likely vary among forest types. For example, cove hardwood stands in the southern Appalachians typically have small patches of eastern hemlock interspersed in a matrix of hardwoods. As adelgid-infested hemlock trees die, the resulting canopy gaps could create suitable light conditions for shrub layer growth (Orwig and Foster 1998, Orwig and Foster 2000). The increased shrub density may benefit nesting black-throated blue warblers through an increase in potential nest sites and the associated reduced risk of predation. However, in a hemlock-dominated stand affected by HWA infestations, the removal of a majority of the canopy may create expansive early successional conditions unsuitable for black-

throated blue warblers. Such a scenario is dependent on pattern of hemlock decline within a stand and the time scale over which mortality occurs.

Although Lepidoptera larvae biomass appeared lower on the hemlock plot for all sampling periods in 2003, this difference did not correspond with observed black-throated blue warbler parental provisioning rates on the plots. Caterpillar biomass was lower on the hemlock plot yet the biomass of caterpillars delivered to nestlings did not differ between plots. Therefore, Lepidoptera larvae availability did not appear to limit black-throated blue warbler feeding rates in the hemlock plot. However, black-throated blue warbler parents in the hemlock plot made more hourly provisioning trips to the nest per nestling and delivered less biomass per trip than parents in the hardwood plot. Although there was no difference in overall biomass of food delivered between hemlock and hardwood nests, high quality (large) food items may have been more difficult to obtain in the hemlock plot. These conditions did not seem to affect nest success. However, low availability of high-quality food may exert negative effects on post-fledgling survival as nutritional requirements increase (Weathers 1996). The immediate effects of hemlock loss on avian prey availability are poorly understood, but Harris and Reed (2002) found greater abundance of black-throated blue warbler prey near forest clearcut edges, indicating the creation of canopy gaps by dying hemlock trees may increase food availability for the species, at least for a period of time.

Although this study focused primarily on the potential impacts of hemlock decline on black-throated blue warbler reproduction, the effects of such a drastic alteration in the composition and structure of southern Appalachian forests will almost certainly have impacts for numerous species. Whether the consequences of hemlock mortality are

negative or positive for a particular species, this unique human-induced event in the history of eastern North American forests provides an opportunity to gain a better understanding of the wide-ranging effects that exotic forest pathogens can have on ecological systems, and presents an impetus for preventing harmful introductions in the future. From that perspective, this study provided useful baseline data that may be referenced in future studies conducted during and after hemlock decline. Such studies in hemlock forests should emphasize the mechanisms driving observed changes in species distributions and demography.

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APPENDICES

APPENDIX 1

TABLES

Table 2.1. Avian species associated with eastern hemlock presence in Great Smoky Mountains National Park (Shriner 2001). Hemlock associations for each species were examined using logistic regression analysis. Wald *P*-values are for the hemlock presence variable.

Common Name	Scientific Name	Wald *P*-value
Positive Association		
Acadian flycatcher	*Empidonax virescens*	<0.0001
Black-throated blue warbler	*Dendroica caerulescens*	<0.0001
Black-throated green warbler	*Dendroica virens*	<0.0001
Blue-headed vireo	*Vireo solitarius*	0.0233
Canada warbler	*Wilsonia canadensis*	<0.0001
Dark-eyed junco	*Junco hyemalis*	<0.0001
Golden-crowned kinglet	*Regulus satrapa*	0.0084
Red-breasted nuthatch	*Sitta canadensis*	0.0416
Veery	*Catharus fuscenscens*	0.0037
Winter wren	*Troglodytes troglodytes*	<0.0001
Wood thrush	*Hylocichla mustelina*	0.0015
Negative Association		
American crow	*Corvus brachyrhynchos*	0.0002
Black-and-white warbler	*Mniotilta varia*	<0.0001
Blue jay	*Cyanocitta cristata*	0.0318
Chestnut-sided warbler	*Dendroica pensylvanica*	0.0484
Eastern towhee	*Pipilo erthrophthalmus*	<0.0001
Indigo bunting	*Passerina cyanea*	<0.0001
Ovenbird	*Seiurus aurocapillus*	0.0011
Pileated woodpecker	*Dryocopus pileatus*	0.0007
Red-eyed vireo	*Vireo olivaceos*	0.0052
Tufted titmouse	*Baeolophus bicolor*	<0.0001
Yellow-throated warbler	*Dendroica dominica*	0.0009
Scarlet tanager	*Piranga olivacea*	<0.0001
No Association		
Hooded warbler	*Wilsonia citrina*	
Northern parula	*Parula americana*	
Worm-eating warbler	*Helmitheros vermivorus*	
Black-capped chickadee	*Parus atricapillus*	
Carolina chickadee	*Parus carolinensis*	
Brown creeper	*Certhia americana*	
Chimney swift	*Chaetura pelagica*	

Table 2.2. Results of logistic regression modeling of avian species detections in Jefferson and George Washington National Forests, 1995-2001, using the single-year occupancy criterion. Wald *P*-values are given for the hemlock presence variable adjusted for elevation and elevation^2. Presence is the number of point locations out of 626 with a species detection in at least 1 survey year. Odds ratios and the direction of species' association with the hemlock parameter are listed for species with a *P*-value < 0.05. Species names in **bold** showed a significant association with hemlock at the Bonferroni α of 0.05/29 = 0.0017.

Species	# Presences	Wald *P*-value	Association	Odds Ratio
Acadian flycatcher	**221**	**<0.0001**	+	**10.12**
American crow	467	0.7125	NS	
Black-and-white warbler	275	0.9736	NS	
Black-capped chickadee	205	0.8982	NS	
Blue-headed vireo	218	0.0358	NS	
Blackburnian warbler	31	0.0426	NS	
Blue jay	351	0.7491	NS	
Black-throated blue warbler	**77**	**<0.0001**	+	**4.93**
Black-throated green warbler	**115**	**<0.0001**	+	**6.41**
Carolina chickadee	132	0.0538	NS	
Canada warbler	53	0.0044	NS	
Chimney swift	25	0.6006	NS	
Chestnut-sided warbler	162	0.4307	NS	
Dark-eyed wunco	149	0.7532	NS	
Eastern towhee	**441**	**<0.0001**	−	**0.29**
Tufted titmouse	463	0.4993	NS	
Golden-crowned kinglet	11	0.0150	NS	
Hooded warbler	317	0.7271	NS	
Indigo bunting	**406**	**<0.0001**	−	**0.26**
Northern parula	**114**	**<0.0001**	+	**6.81**
Ovenbird	555	0.3529	NS	
Pileated woodpecker	**444**	**0.0002**	−	**0.45**
Red-breasted nuthatch	23	0.0980	NS	
Red-eyed vireo	601	0.6949	NS	
Scarlet tanager	554	0.0370	NS	0.53
Veery	**98**	**0.0003**	+	
Worm-eating warbler	368	0.2665	NS	3.75
Winter wren	17	0.4083	NS	
Wood thrush	420	0.4380	NS	

Table 2.3. Results of logistic regression modeling of avian species detections in Cherokee National Forest, 1992-2001, using the single-year occupancy criterion. Wald *P*-values are given for the hemlock presence variable adjusted for elevation and elevation^2. Presence is the number of survey locations out of 273 with a species detection in at least 1 survey year. Odds ratios and the direction of species' association with the hemlock parameter are listed for species with a *P*-value < 0.05. Species names in **bold** showed a significant association with hemlock at the Bonferroni α of 0.05/29 = 0.0017.

Species	# Presences	Wald *P*-value	Association	Odds Ratio
Acadian flycatcher	**41**	**0.0005**	+	**3.690**
American crow	91	0.2347	NS	
Black-and-white warbler	136	0.9363	NS	
Black-capped chickadee	14	0.8058	NS	
Blue-headed vireo	121	0.3377	NS	
Blackburnian warbler	19	0.3554	NS	
Blue jay	88	0.3695	NS	
Black-throated blue warbler	**84**	**0.0009**	+	**3.033**
Black-throated green warbler	161	0.0022	+	2.482
Carolina chickadee	151	0.8723	NS	
Canada warbler	38	0.4141	NS	
Chimney swift	10	0.3727	NS	
Chestnut-sided warbler	62	0.0205	NS	
Dark-eyed junco	74	0.0740	NS	
Eastern towhee	131	0.0098	NS	
Tufted titmouse	133	0.4366	NS	
Golden-crowned kinglet	4	0.1980	NS	
Hooded warbler	190	0.0578	NS	
Indigo bunting	**174**	**0.0001**	**−**	**0.335**
Northern parula	**40**	**0.0002**	+	**4.040**
Ovenbird	200	0.4951	NS	
Pileated woodpecker	116	0.4954	NS	
Red-breasted nuthatch	9	No model		
Red-eyed vireo	241	0.2620	NS	
Scarlet tanager	170	0.1741	NS	
Veery	69	0.7245	NS	
Worm-eating warbler	102	0.9739	NS	
Winter wren	32	0.7617	NS	
Wood thrush	113	0.2889	NS	

Table 2.4. Results of logistic regression modeling of avian species detections in Jefferson and George Washington National Forests, 1995-2001, using the 30% occupancy criterion. Wald *P*-values are given for the hemlock presence variable adjusted for elevation and elevation^2. Presence is the number of locations out of 626 with a species detection in at least 30% of years surveyed. Odds ratios and the direction of species' association with the hemlock parameter are listed for species with a *P*-value < 0.05. Species names in **bold** showed a significant association with hemlock at the Bonferroni α of 0.05/29 = 0.0017.

Species	# Presences	Wald *P*-value	Association	Odds Ratio
Acadian flycatcher	**143**	**<0.0001**	+	**10.058**
American crow	330	0.1778	NS	
Black-and-white warbler	108	0.6735	NS	
Black-capped chickadee	64	0.1899	NS	
Blue-headed vireo	**88**	**<0.0001**	+	**2.951**
Blackburnian warbler	11	0.0099	NS	
Blue jay	147	0.0809	NS	
Black-throated blue warbler	**35**	**<0.0001**	+	**6.922**
Black-throated green warbler	**55**	**<0.0001**	+	**12.817**
Carolina chickadee	38	0.1310	NS	
Canada warbler	**15**	**0.0004**	+	**8.221**
Chimney swift	2	No model		
Chestnut-sided warbler	83	0.1793	NS	
Dark-eyed junco	**83**	**0.0008**	+	**3.808**
Eastern towhee	**340**	**<0.0001**	−	**0.271**
Tufted titmouse	308	0.3931	NS	
Golden-crowned kinglet	6	No model		
Hooded warbler	191	0.0844	NS	
Indigo bunting	**298**	**<0.0001**	−	**0.253**
Northern parula	**63**	**<0.0001**	+	**14.778**
Ovenbird	473	0.7956	NS	
Pileated woodpecker	260	0.1670	NS	
Red-breasted nuthatch	11	No model		
Red-eyed vireo	547	0.0392	NS	
Scarlet tanager	448	0.0070	NS	
Veery	**65**	**0.0001**	+	**4.743**
Worm-eating warbler	210	0.1716	NS	
Winter wren	4	No model		
Wood thrush	255	0.5050	NS	

Table 2.5. Results of logistic regression modeling of avian species detections in Cherokee National Forest, 1992-2001, using the 30% occupancy criterion. Wald *P*-values are given for the hemlock presence variable adjusted for elevation and elevation^2. Presence is the number of survey locations out of 273 with a species detection in at least 30% of years surveyed. Odds ratios and the direction of species' association with the hemlock parameter are listed for species with a P-value < 0.05. Species names in **bold** showed a significant association with hemlock at the Bonferroni α of 0.05/29 = 0.0017.

Species	Presences	Wald *P*-value	Association	Odds Ratio
Acadian flycatcher	20	0.0285	NS	
American crow	51	0.2238	NS	
Black-and-white warbler	96	0.4086	NS	
Black-capped chickadee	1	No Model		
Blue-headed vireo	71	0.2877	NS	
Blackburnian warbler	14	0.0507	NS	
Blue jay	52	0.7520	NS	
Black-throated blue warbler	**70**	**0.0008**	+	**3.785**
Black-throated green warbler	**127**	**<0.0001**	+	**3.268**
Carolina chickadee	108	0.1708	NS	
Canada warbler	29	0.9641	NS	
Chimney swift	1	No Model		
Chestnut-sided warbler	49	0.0181	NS	
Dark-eyed junco	58	0.1221	NS	
Eastern towhee	95	0.0079	NS	
Tufted titmouse	91	0.1381	NS	
Golden-crowned kinglet	3	No Model		
Hooded warbler	160	0.0078	NS	
Indigo bunting	**146**	**<0.0001**	**–**	**0.300**
Northern parula	**27**	**<0.0001**	+	**6.062**
Ovenbird	172	0.9183	NS	
Pileated woodpecker	65	0.4070	NS	
Red-breasted nuthatch	3	No Model		
Red-eyed vireo	230	0.9784	NS	
Scarlet tanager	123	0.1940	NS	
Veery	56	0.8532	NS	
Worm-eating warbler	68	0.4126	NS	
Winter wren	22	0.8024	NS	
Wood thrush	75	0.1140	NS	

Table 2.6. Avian associations with eastern hemlock based on results of logistic regression modeling for Great Smoky Mountains National Park (Shriner 2001), Jefferson and George Washington National Forests, VA (JGWNF) and Cherokee National Forest, TN (CNF). National forest results are presented for models using both the single-year occupancy and 30 % occupancy criteria for presence classification. Single + and – symbols indicate significance at Bonferroni corrected $\alpha = 0.0034$. Double + and – symbols indicate significance at the Bonferroni-corrected $\alpha = 0.0017$.

Species	GSMNP (Shriner 2001)	JGWNF Single Year	JGWNF 30%	CNF Single Year	CNF 30%
Positive Associations					
Acadian flycatcher	++	++	++	++	
Blue-headed vireo			++		
Blackburnian warbler	No model		+		
Black-throated blue warbler	++	++	++	++	++
Black-throated green warbler	++	++	++	+	++
Canada warbler	++		++		
Dark-eyed junco	++		++		
Northern parula		++	++	++	++
Veery		++	++		
Winter wren	++		No model		
Wood thrush	++				
Negative Associations					
American crow	– –				
Black-and-white warbler	– –				
Eastern towhee	– –	– –	– –		
Indigo bunting	– –	– –	– –	– –	– –
Ovenbird	–				
Pileated woodpecker	– –	– –			
Scarlet tanager	– –				
Tufted titmouse	– –				

Table 2.7. Avian species positively associated (X) with eastern hemlock in 7 study areas in the eastern United States.

Species	Wisconsin and Upper Michigan[a]	Delaware Water Gap NRA, PA[b]	New Jersey[c]	Connecticut[d]	JGW NF, VA	GSMNP, NC and TN[e]	Cherokee NF, TN
Acadian flycatcher		X	X	X	X	X	X
Barred owl			X				
Blackburnian warbler	X	X		X	X		
Black-throated blue warbler					X	X	X
Black-throated green warbler	X	X	X	X	X	X	X
Blue-headed vireo	X	X	X		X		
Brown creeper							
Canada warbler					X	X	
Dark-eyed junco					X	X	
Hermit thrush	X		X	X			
Northern goshawk			X				
Northern parula	X				X		X
Red-breasted nuthatch	X						
Red-shouldered hawk			X				
Veery					X		
Winter wren	X		X			X	
Wood thrush						X	
Yellow-rumped warbler	X						

[a] Howe and Mossman 1996
[b] Delaware Water Gap National Recreation Area, PA, Ross et al. 2002
[c] Benzinger 1994b
[d] Tingley et al. 2002
[e] Great Smoky Mountains National Park, Shriner 2001

Table 3.1. Means and standard errors for vegetation structure variables measured on 45 systematically placed 0.04-ha sampling locations per 15-ha plot collected at Cataloochee study site, North Carolina, 2002-2003.

	Hardwood Plot		Hemlock Plot	
Variable	**Mean**	**Standard Error**	**Mean**	**Standard Error**
Height to top of canopy (m)	30.03	0.69	30.72	1.11
Basal area (m^2/ha)	39.00	2.75	43.50	3.00
Basal area of standing snags (m^2/ha)	2.75	0.75	3.00	1.00
% Canopy coverage	83.18	1.87	78.60	2.17
Sapling stems/ha	1368.82	198.07	1520.91	162.70
Sapling height (m)	4.01	0.26	4.10	0.37
Midstory overhead coverage	60.89	3.98	56.02	4.33
Rhododendron maximum stems/ha	2221.24	746.24	5775.92	944.38
Shrub stems/ha	5606.15	760.46	7236.70	954.99
% Cover board obscured (5m)	22.49	2.51	34.03	3.17
% Cover board obscured (10m)	38.43	3.11	51.91	3.54
% Herbaceous ground coverage	29.35	3.46	15.92	2.76
Number of logs/ha	18.00	3.50	30.25	4.00

Table 3.2. Nest data from Cataloochee study site, North Carolina, 2002-2003, calculated at the stand scale (15 ha).

Year	Category	*n*	Nest days	# Failed	# Successful	DSR[a] ± SE	NSR[b] ± SE	Fledglings/Suc. nest
Black-throated blue warbler								
2002	Hardwood plot	15	195	9	6	.9538 ± .0150	.2997 ± .1204	2.83
2002	Hemlock plot	12	200	5	7	.9750 ± ..0110	.5243 ± .1514	3.29
2003	Hardwood plot	20	310	14	6	.9548 ± .0118	.3078 ± .0969	3.83
2003	Hemlock plot	14	295	5	9	.9831 ± .0075	.6467 ± .1261	2.89
Yrs. Pooled	Hardwood plot	35	505	23	12	.9545 ± .0093	.3046 ± .0755	3.33
Yrs. Pooled	Hemlock plot	26	495	10	16	.9798 ± .0063	.5943 ± .0978	3.06
Dark-eyed junco								
Yrs. pooled	Hardwood plot	22	218	10	12	.9450 ± .0154	.2049± .0938	3.30
Yrs. pooled	Hemlock plot	12	117	5	7	.9402 ± .0219	.1777 ± .1161	3.40
Blue-headed vireo								
Yrs. pooled	Hardwood plot	11	146	4	7	.9521 ± .0177	.2076 ± .1234	3.25
Yrs. pooled	Hemlock plot	11	188	4	7	.9628 ± .0138	.2969 ± .1363	3.75

[a] Mayfield daily survival rate.
[b] Mayfield nest success.

Table 3.3. Nest data from Cataloochee and Coweeta study sites, North Carolina, 2002-2003, calculated at the nest-site scale (0.04 ha). Data were pooled between years.

Site	Category	n	Nest days	# Failed	# Successful	DSR[a] ± SE	NSR[b] ± SE	Fledglings/ Successful nest
Black-throated blue warbler								
Cataloochee	Non-hemlock nest sites	14	210	5	9	.9708 ± .0060	.3273± .1219	3.26
Cataloochee	Hemlock nest sites	46	788	23	23	.9571 ± .0140	.4698 ± .0740	2.80
Coweeta	Non-hemlock nest sites	40	572	21	19	.9633 ± .0079	.3853 ± .0802	3.47
Coweeta	Hemlock nest sites	61	890	28	33	.9685 ± .0059	.4424 ± .0682	3.09
Dark-eyed junco								
Sites pooled	Non-hemlock nest sites	16	156	7	9	.9551 ± .0215	.2765 ± .1344	3.78
Sites pooled	Hemlock nest sites	34	368	16	18	.9565 ± .0106	.2880 ± .0896	3.17
Blue-headed vireo								
Sites pooled	Non-hemlock nest sites	11	135	9	2	.9333 ± .0215	.1099 ± .0809	3.50
Sites pooled	Hemlock nest sites	23	341	14	9	.9589 ± .0107	.2614 ± .0937	3.56

[a] Mayfield daily survival rate.
[b] Mayfield nest success

Table 3.4. Stage-specific daily survival rates from Cataloochee study site, North Carolina, 2002-2003, calculated at the stand scale (15 ha).

Category	Egg days	Egg failures	Egg DSR[a] ± SE	Nestling days	Nestling failures	Nestling DSR[b] ± SE
Black-throated blue warbler						
Hardwood plot	335	14	.9603 ± .0104	152	9	.9407 ± .0191
Hemlock plot	313	3	.9904 ± .0055	182	7	.9615 ± .0143
Dark-eyed junco						
Hardwood plot	107	6	.9439 ± .0222	111	6	.9459 ± .0125
Hemlock plot	50	2	.9600 ± .0277	67	5	.9254 ± .0231
Blue-headed vireo						
Hardwood plot	68	2	.9706± .0205	78	5	.9359 ± .0277
Hemlock plot	121	3	.9752 ± .0141	67	4	.9403 ± .0289

[a] Mayfield daily survival rate during the egg stage (laying and incubation).
[b] Mayfield daily survival rate during the nestling stage.

Table 3.5. Stage-specific daily survival rates from Cataloochee and Coweeta study sites, North Carolina, 2002-2003, calculated at the nest-site scale (0.04 ha).

Site	Category	Eggs days	Egg failures	Egg DSR ± SE	Nestling days	Nestling failures	Nestling DSR ± SE
Black-throated blue warbler							
Cataloochee	Non-hemlock nests	149	6	.9597 ± .0161	61	3	.9508 ± .0277
Cataloochee	Hemlock nests	517	11	.9787 ± .0063	271	13	.9520 ± .0130
Coweeta	Non-hemlock nests	362	16	.9557 ± .0108	211	5	.9762 ± .0105
Coweeta	Hemlock nests	547	13	.9774 ± .0046	345	15	.9563 ± .0110
Dark-eyed junco							
Sites pooled	Non-hemlock nests	86	4	.9535 ± .0227	70	3	.9568 ± .0244
Sites pooled	Hemlock nests	174	8	.9540 ± .0159	194	10	.9483 ± .0159
Blue-headed vireo							
Sites pooled	Non-hemlock nests	90	6	.9333 ± .0263	45	3	.9333 ± .0372
Sites pooled	Hemlock nests	204	7	.9657 ± .0127	137	7	.9489 ± .0188

[a] Mayfield daily survival rate during the egg stage (laying and incubation).
[b] Mayfield daily survival rate during the nestling stage.

Table 3.6. Lepidoptera larvae biomass index values and *P*-values for Wilcoxon rank sums tests comparing biomass means between plots within each sampling period at Cataloochee study site, North Carolina, 2002-2003.

Sampling period	*n*[a]	Hardwood plot biomass (mg/point)	*n*[a]	Hemlock plot biomass (mg/point)	*P*
2002					
May 28-31	15	1.41	16	2.10	0.9112
June 10-14	19	1.95	13	2.12	0.2116
June 27-30	30	1.36	14	1.08	0.0187
2003					
May 2-9	44	5.40	33	3.65	0.0035
May 19-23	40	3.08	25	2.34	0.2938
June 5-8	21	2.72	10	0.50	0.0666
June 19-22	46	2.30	30	2.29	0.8939
July 6-8	28	3.65	28	1.47	0.6104

[a] Number of Lepidoptera larvae found during sampling period

Table 3.7. Parental provisioning rate data from Cataloochee study site, North Carolina, 2003. *P*-values are for two-sided, two-sample t-tests comparing plot means for number of deliveries per hour per nestling, biomass index values per hour per nestling, and Lepidoptera biomass index values per hour per nestling.

	Hardwood Plot	**Standard Error**	**Hemlock Plot**	**Standard Error**	***P-value***
Nests Filmed	7		8		—
Deliveries/Hr/Nestling	4.70	0.35	5.96	0.34	0.0242
Biomass/Hr/Nestling	13.16	1.08	15.29	1.73	0.3302
% Lepidoptera larvae	45.70		57.90		—
Lepidoptera biomass/Hr/Nestling	5.90	1.05	9.00	1.38	0.1050

Table 3.8. Proportion of survey points with the presence of a predator and associated Fisher's exact test *P*-value (two sided) at Cataloochee study site, North Carolina, 2003.

Species	Hardwood plot	Hemlock plot	Fisher's exact *P*
Gray squirrel	0.0135	0.0135	1.0000
Red squirrel	0.1757	0.1892	1.0000
Eastern chipmunk	0.0405	0.0135	0.6198
Blue jay	0.0676	0.0676	1.0000
American crow	0.0000	0.0946	0.0135

Table 3.9. Cataloochee, North Carolina, 2002-2003 logistic regression models of black-throated blue warbler nest-site selection with $\Delta_i \leq 2$ determined by best subsets selection. Parameter estimates are presented for variables included in the models. Boldfaced parameter estimates indicate $P < 0.05$, * indicates $P < 0.01$, ** indicates $P < 0.001$, and *** indicated $P < 0.0001$.

Model Rank	Δi	w_i	Gap	baBEAL	baTSCA	baHARD	TSCASap	TotalSap	USCOV	TotalShr	Logs
Hardwood Plot											
1	0.000	0.388	-0.937		**-5.981****	**-2.107***			**-0.041***	**0.082*****	0.635
2	1.814	0.157	-0.939	-0.911	**-5.819***	**-2.025***			**-0.042***	**0.081*****	0.612
3	1.960	0.146	-0.620		**-5.384****	**-2.149***			**-0.040***	**0.075*****	
4	1.969	0.145	-0.929		**-5.973****	**-2.103***			**-0.041***	**0.082*****	0.635
5	1.986	0.144	-0.924		**-5.976****	**-2.099***		-0.013	**-0.041***	**0.082*****	0.634
Global	5.790	0.021	-0.924	-0.881	**-5.815****	**-2.021***	-0.085	-0.005	**-0.041***	**0.081*****	0.613
Hemlock Plot											
1	0.000	0.181	**0.832**						**-0.038**	**0.076*****	**0.676**
2	0.124	0.170	**0.980**				0.091	0.206	**-0.049***	**0.088*****	0.616
3	0.219	0.163	**0.850**				0.480		**-0.041**	**0.085*****	0.574
4	0.751	0.125	**0.955**			1.167	0.534		**-0.043**	**0.090*****	0.709
5	0.864	0.118	**0.903**			0.979			**-0.039**	**0.079*****	**0.815**

Table 3.9 Continued.

Model Rank	Δi	w_i	Gap	baBEAL	baTSCA	baHARD	TSCASap	TotalSap	USCOV	TotalShr	Logs
Hemlock Plot (continued)											
6	1.613	0.081	0.794	-2.590					**-0.038**	**0.076*****	0.653
7	1.804	0.074	0.802	-2.841			0.484		**-0.043**	**0.086*****	0.556
8	1.990	0.067	**0.825**		0.046				**-0.038**	**0.076*****	0.678
Global	4.247	0.022	**1.061**	-2.640	-0.041	1.221	0.182	0.199	**-0.052***	**0.094*****	0.729
Plots Pooled											
1	0.000	0.350		-3.302	**-0.865***				**-0.021***	**0.055*****	**0.476**
2	1.381	0.175		-3.406	**-0.894***			0.054	**-0.023***	**0.056*****	**0.466**
3	1.521	0.163		-3.386	**-0.874***		0.167		**-0.022***	**0.057*****	**0.465**
4	1.598	0.157			**-0.779**				**-0.019**	**0.054*****	0.511
5	1.771	0.144		-3.280	**-0.919***	-0.215			**-0.021***	**0.055*****	**0.442**
Global	7.043	0.010	0.019	-3.145	**-0.939***	-0.178	0.111	0.038	**-0.024***	**0.056*****	**0.429**

Table 3.10. Wald χ^2 test *P*-values, Hosmer-Lemeshow tests, and classification information for global and AIC-optimal black-throated blue warbler nest-site selection models at Cataloochee and Coweeta study sites, North Carolina, 2002-2003.

Model	Wald *P*	Hosmer-Lemeshow *P*[a]	% Correct classification	Sensitivity[b]	Specificity[c]
Cataloochee site					
Hemlock plot global	0.0393	0.0557	84.8	85.7	84.3
Hemlock plot AIC-optimal	0.0009	0.6821	87.3	85.7	88.2
Hardwood plot global	0.0113	0.7457	81.1	78.0	83.3
Hardwood plot AIC-optimal	0.0018	0.9413	83.2	82.9	83.3
Plots pooled global	<0.0001	0.8235	78.6	79.1	78.3
Plots pooled AIC-optimal	<0.0001	0.6110	79.2	79.1	79.2
Coweeta site					
Plots pooled global	0.0015	0.9928	65.0	37.4	83.6
Plots pooled AIC-optimal	0.0001	0.3774	65.0	32.7	86.8

[a] A Hosmer-Lemeshow *P*-value >0.05 indicates the model had acceptable fit.
[b] Percentage of nest sites correctly classified
[c] Percentage of non-nest sites correctly classified

Table 3.11. Coweeta, North Carolina, 2002-2003 logistic regression models of black-throated blue warbler nest-site selection with $\Delta_i \leq 2$ determined by best subsets selection. Parameter estimates are presented for variables included in the models. Boldfaced parameter estimates indicate $P < 0.05$, * indicates $P < 0.01$, ** indicates $P < 0.001$, *** indicates $P < 0.0001$.

Model Rank	Δi	w_i	Gap	baBEAL	baTSCA	baHARD	TSCASap	TotalSap	USCOV	TotalShr	Logs
1	0.000	0.145	**0.908**	3.094			0.246			**0.012****	
2	0.422	0.117	**0.862**	**2.999**		-0.379	0.225			**0.011****	
3	0.429	0.117	**0.881**	**3.014**			0.221		0.006	**0.012****	
4	0.549	0.110	**0.936**	**3.109**	0.643		0.215			**0.012*****	
5	0.653	0.104	**0.907**	**2.994**			0.224	0.022		**0.011****	
6	0.967	0.089	0.808	2.690		-0.443			0.007	**0.012****	
7	1.106	0.083	**0.914**	2.899	0.804					**0.011****	
8	1.198	0.080	**0.849**	**2.780**					0.007	**0.011****	
9	1.303	0.075	**0.826**	2.761		-0.439				**0.011****	
10	1.482	0.069	**0.877**	2.753				0.027		**0.010****	
Global	5.396	0.010	**0.864**	2.848	0.489	-0.297	0.173	0.013	0.005	**0.012****	0.098

Table 3.12. Wald χ^2 test *P*-values, Hosmer-Lemeshow tests, and classification information for global black-throated blue warbler nest success models at Cataloochee and Coweeta study sites, North Carolina, 2002-2003

Model	Wald *P*	Hosmer-Lemeshow *P*[a]	% Correct classification	Sensitivity[b]	Specificity[c]
Cataloochee global	0.5977	0.2953	51.8	44.0	58.1
Coweeta global	0.3746	0.9970	58.9	60.0	57.8

[a] A Hosmer-Lemeshow *P*-value >0.05 indicates the model had acceptable fit.
[b] Percentage of nest sites correctly classified
[c] Percentage of non-nest sites correctly classified

APPENDIX 2

Figures

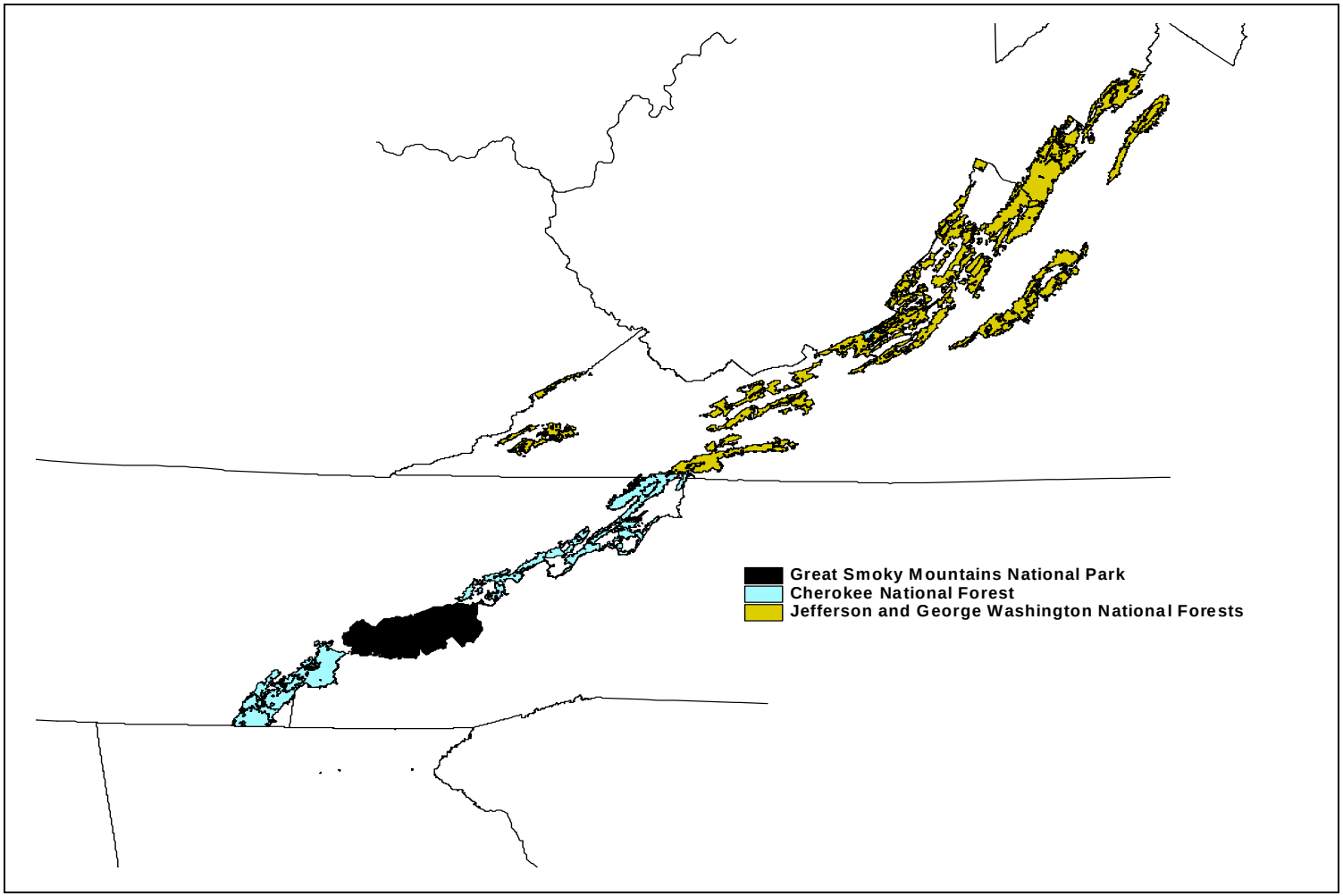


Figure 2.1. Map of southern Appalachian national forests and Great Smoky Mountains National Park.

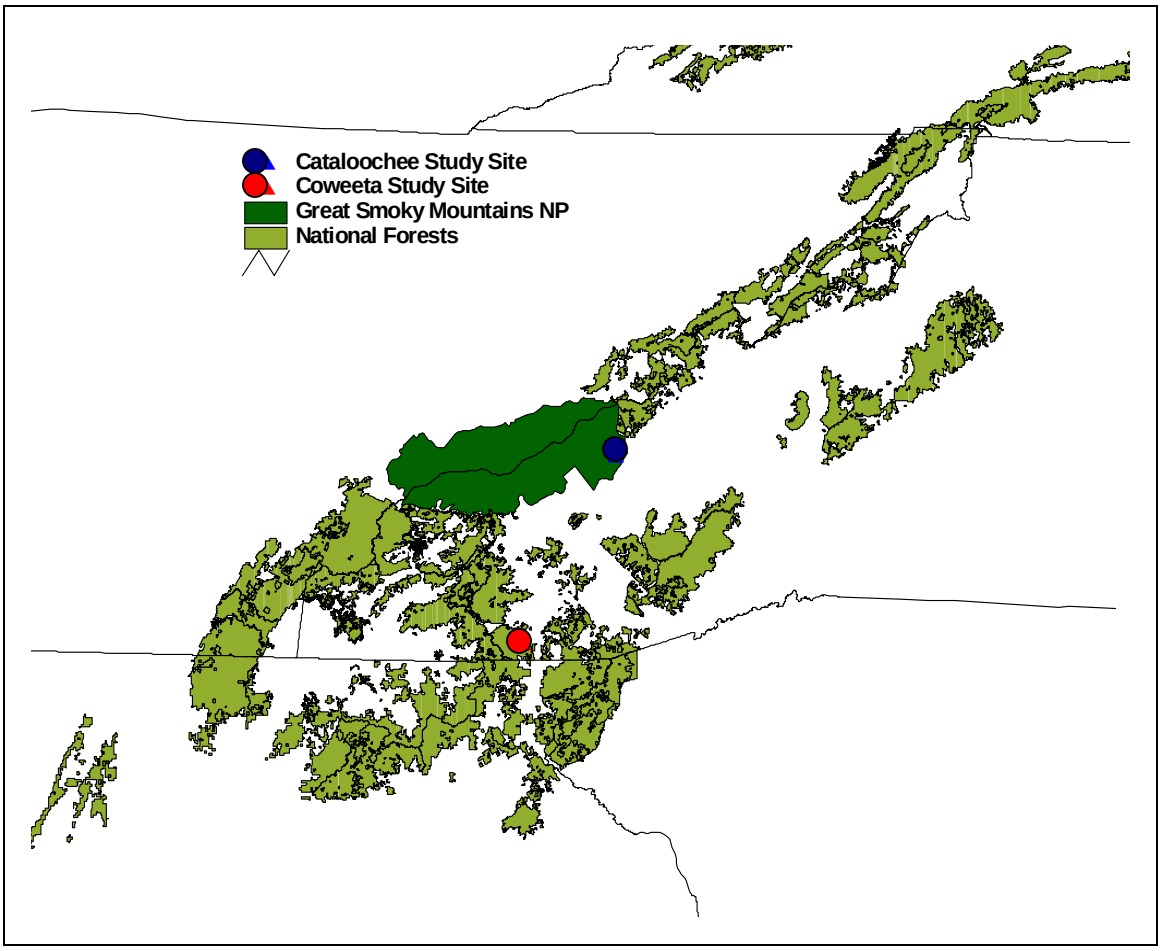


Figure 3.1. Map showing Cataloochee and Coweeta study site locations, North Carolina.

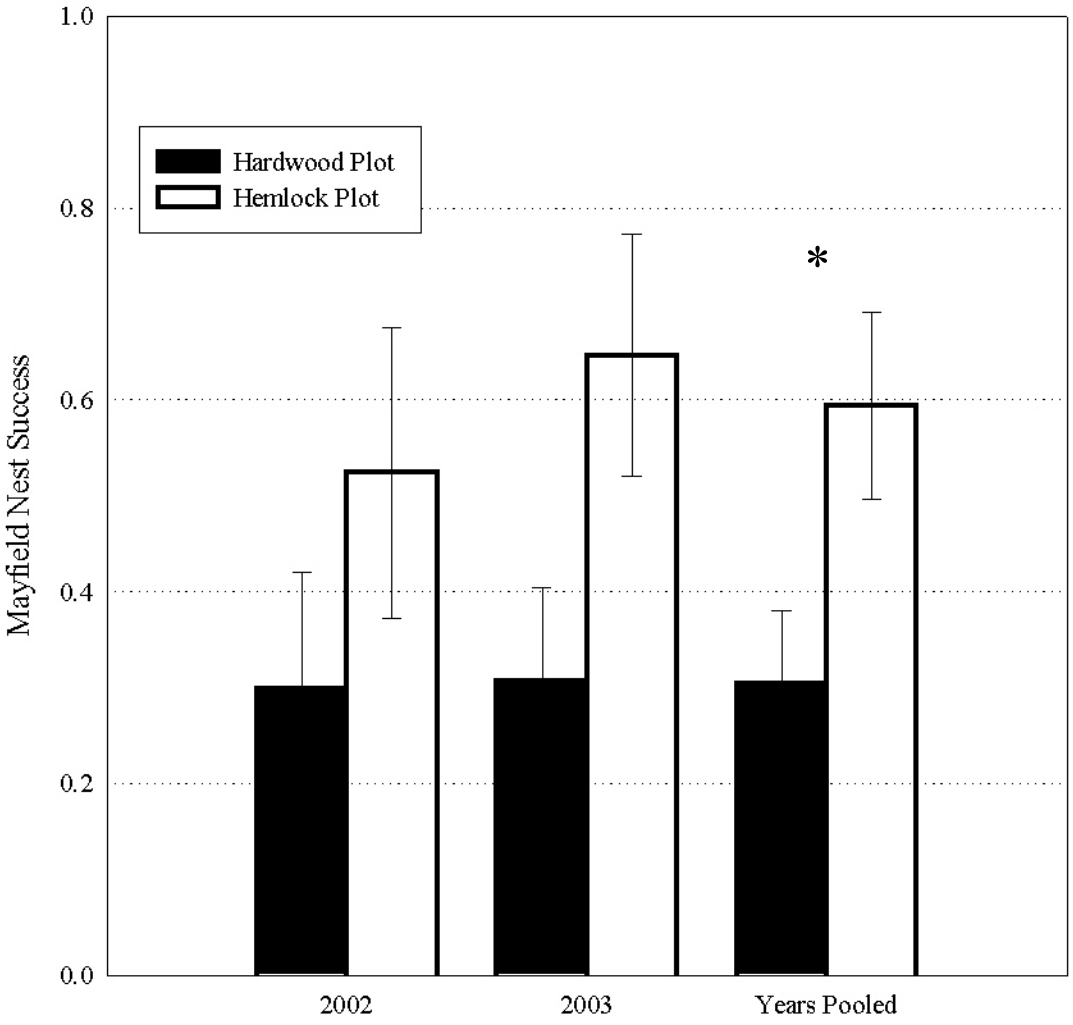


Figure 3.2. Black-throated blue warbler Mayfield nest success comparisons (assuming 25.5-day nest cycle) at the stand scale (15 ha) at Cataloochee study site, North Carolina, 2002-2003. Asterisk indicates significant difference (P = 0.0190). Bars represent ± one standard error.

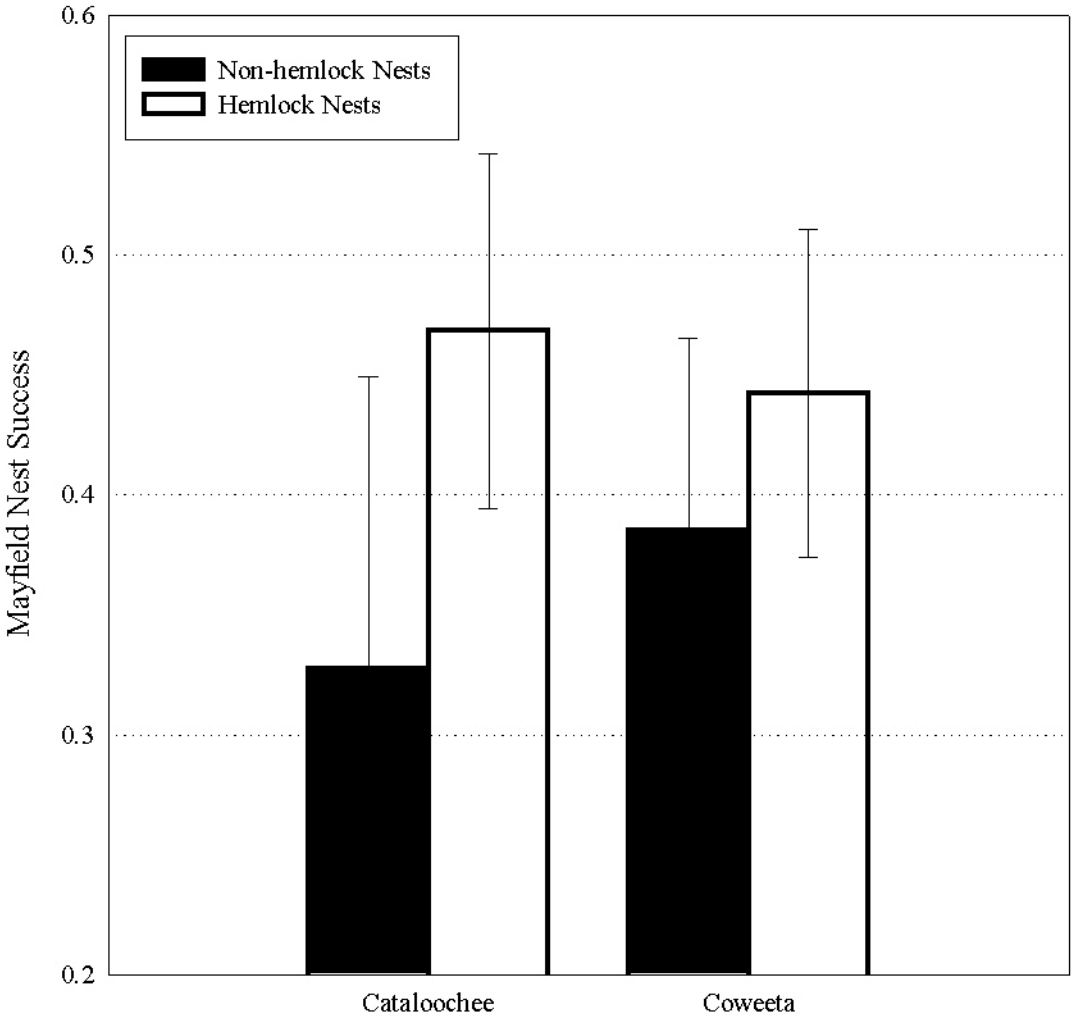


Figure 3.3. Black-throated blue warbler Mayfield nest success comparisons (assuming 25.5-day nest cycle) at the nest-site scale (0.04 ha) at Catalooche and Coweeta study sites, North Carolina, 2002-2003. Bars represent ± 1 standard error.

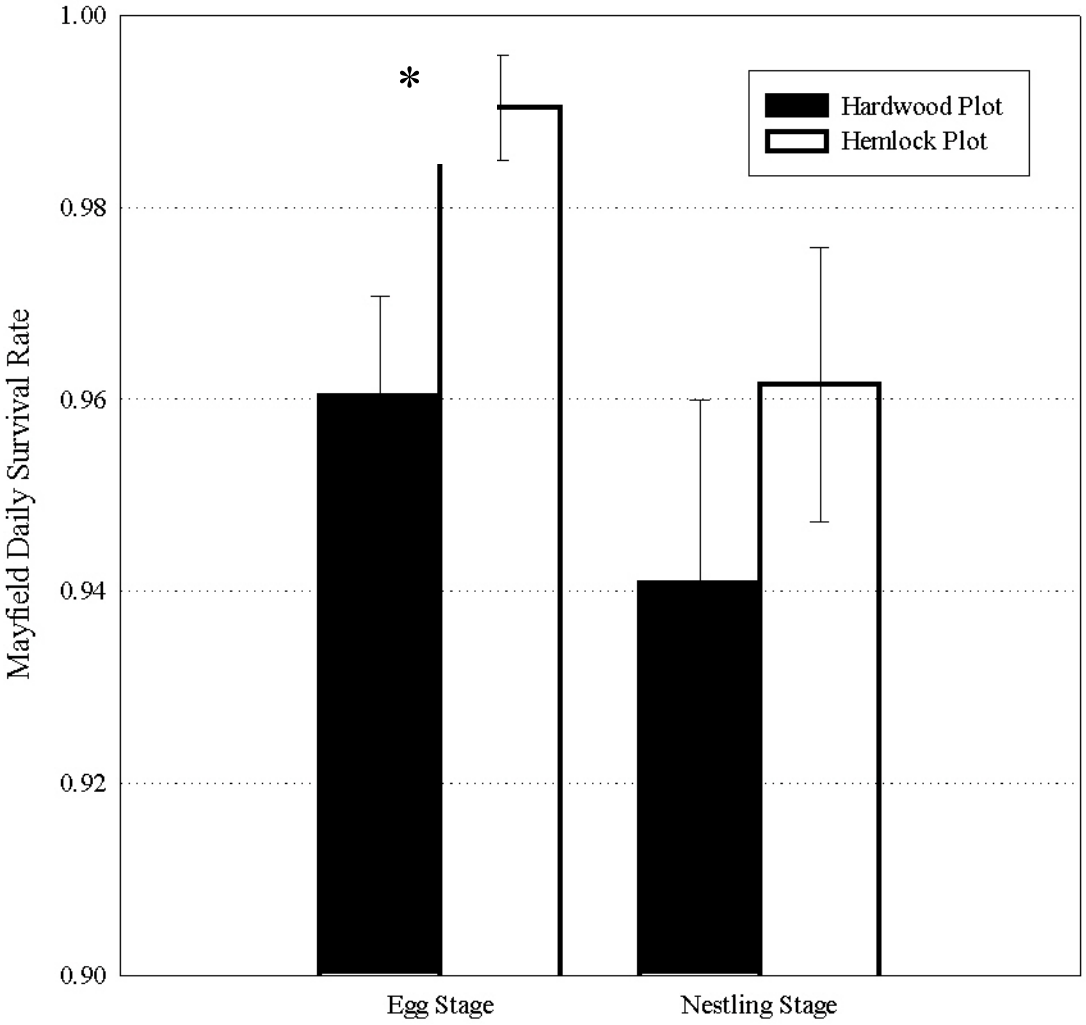


Figure 3.4. Black-throated blue warbler stage-specific Mayfield daily survival rate comparisons at the stand scale (15 ha) for Cataloochee study site, North Carolina, 2002-2003, with nest data pooled between years. Asterisk indicates a significant difference ($P = 0.0105$). Bars represent ± 1 standard error.

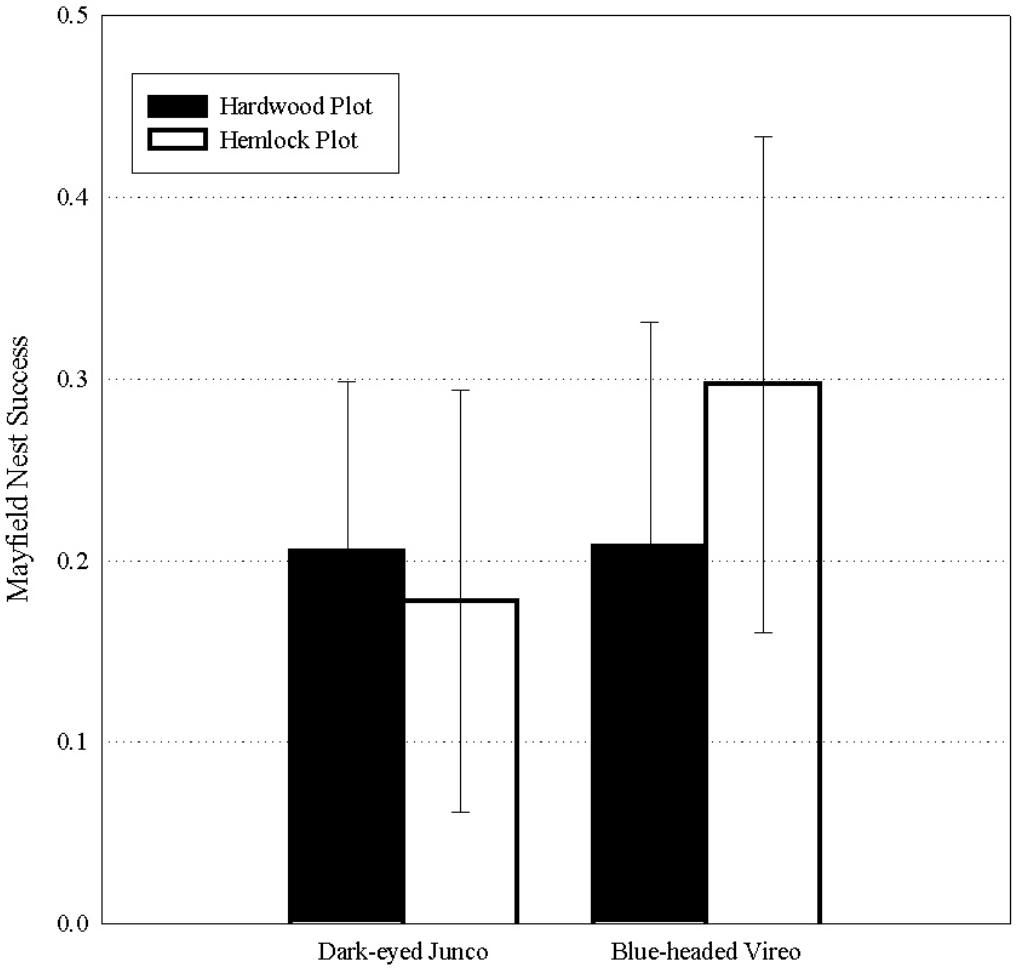


Figure 3.5. Dark-eyed junco and blue-headed vireo Mayfield nest success comparisons (assuming 28-day junco nest cycle and 32-day vireo nest cycle) at the stand scale (15 ha) for Cataloochee study site, North Carolina, 2002-2003, with nest data pooled between years. Bars represent ± 1 standard error.

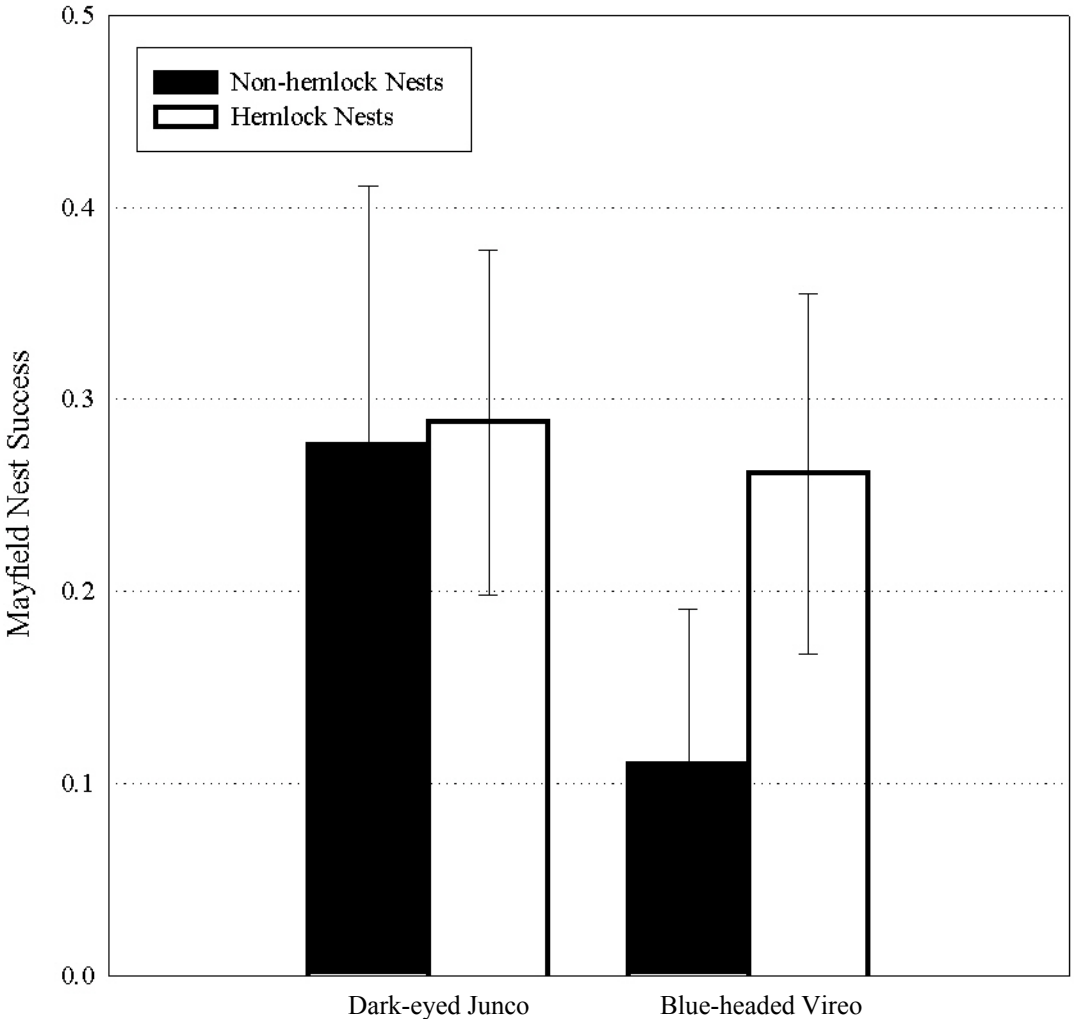


Figure 3.6. Dark-eyed junco and blue-headed vireo Mayfield nest success comparisons (assuming 28-day junco nest cycle and 32-day vireo nest cycle) at the nest site scale (0.04 ha) for Cataloochee and Coweeta study sites, North Carolina, 2002-2003. Bars represent ± 1 standard error.

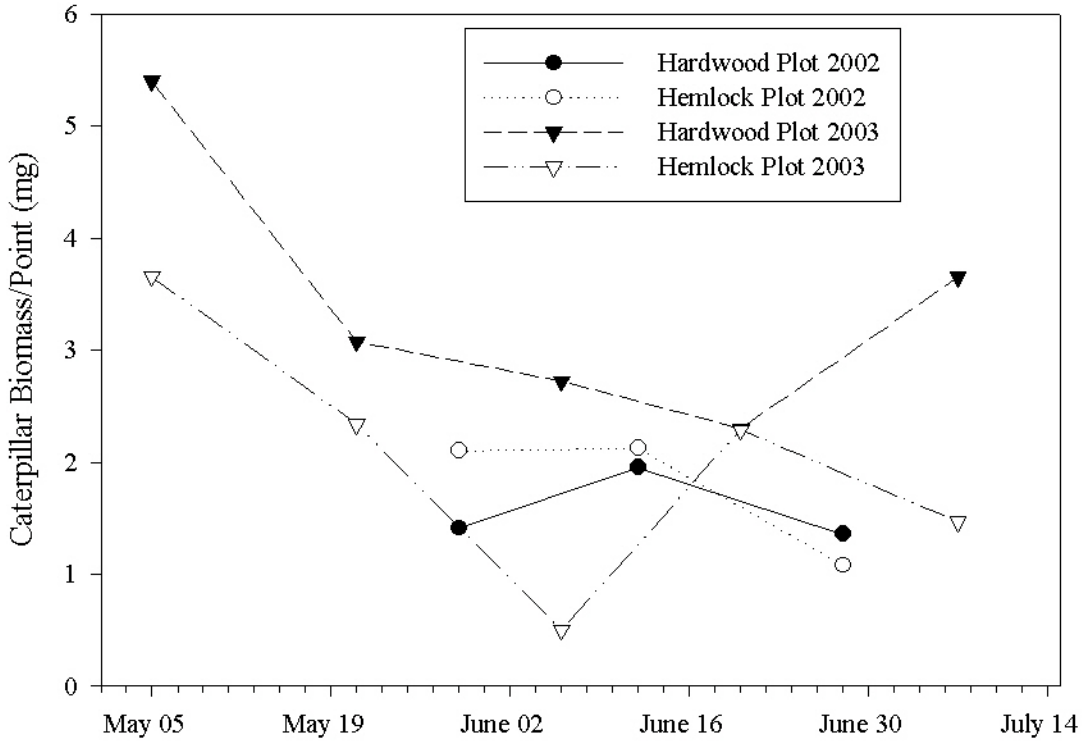


Figure 3.7. Dry weight Lepidopteran larvae biomass per sampling point from Cataloochee study site, North Carolina, 2002-2003.

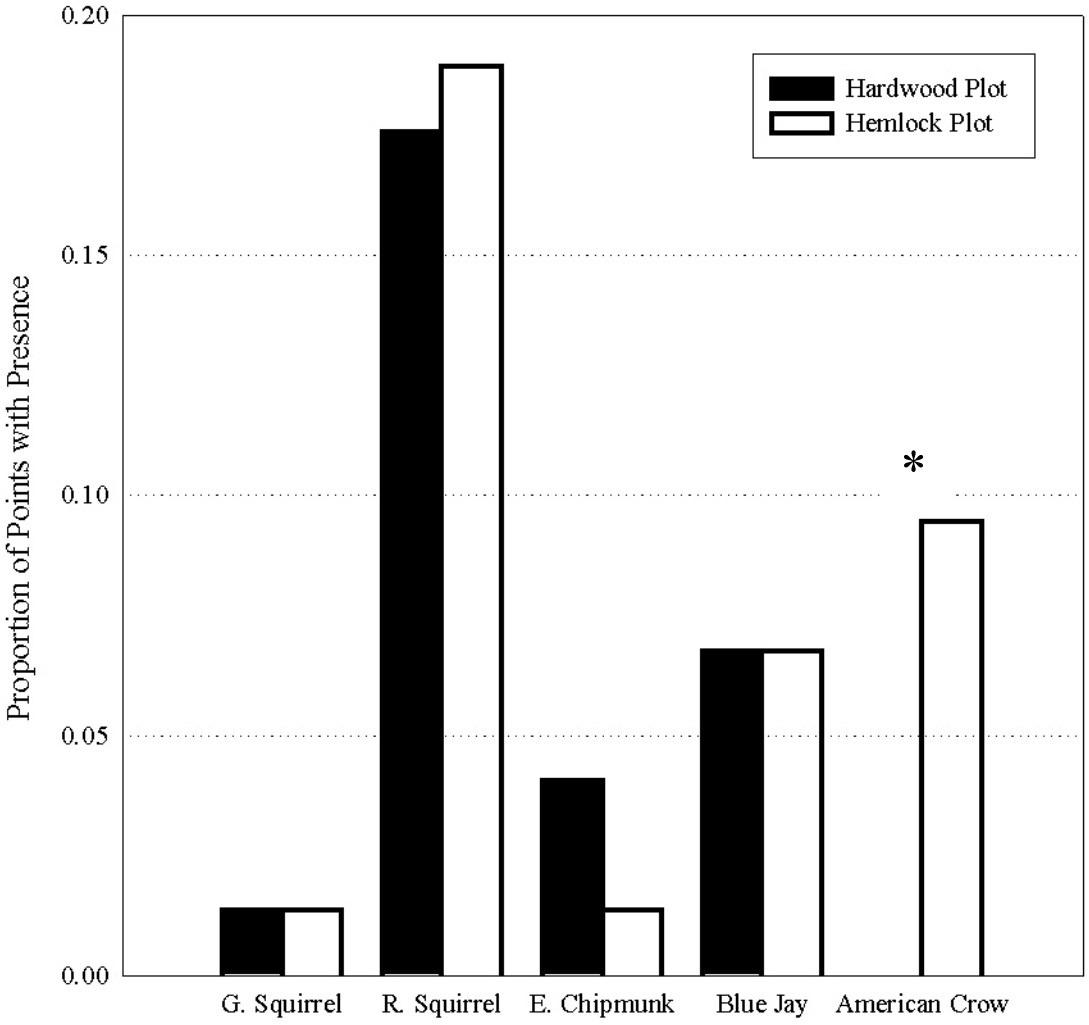


Figure 3.8. Proportions of survey points with predator detections at Cataloochee study site, North Carolina, 2003. Asterisk indicates significant difference ($P = 0.0135$).

VITA

David Aaron Keller was born in 1979 in Raleigh, North Carolina. He was raised in the small mountain community of Bat Cave, North Carolina, where he first developed an appreciation for the outdoors. Aaron received a B.S. degree in Wildlife and Fisheries Science with a minor in Environmental Science from North Carolina State University in 2000. Prior to entering the University of Tennessee—Knoxville in 2002, Aaron assisted with research on avian and predator response to agricultural field borders in North Carolina and Virginia, northern bobwhite breeding ecology at Tall Timbers Research Station in Florida, avian response to ponderosa pine restoration in northern Arizona, and tiger rattlesnake ecology in southern Arizona. His research interests include population biology, avian ecology and management, and herpetology.