COMPARISONS OF ARTHROPOD AND AVIAN COMMUNITIES IN INSECTICIDE-TREATED AND UNTREATED HEMLOCK STANDS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

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Inspire the children around you: my father, Bill Trimble, put binoculars in my hands at twelve, and my mother, Becky Trimble, showed me that happiness is a choice and is all in your perspective.

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PREFACE

This thesis is organized in manuscript format. Chapter 1 is an introduction focused on the project's regional relevance in the Southern Appalachian Mountains and Great Smoky Mountains National Park. Chapter 2 is a review of scientific literature related to the topics in Chapter 3. Chapter 3 is a manuscript to be submitted to the journal *Forest Ecology and Management*. Effort was made to minimize redundancy in Chapters 1 through 3. Literature Cited lists references from all chapters. Appendix A contains the geographic locations of hemlock study sites in Great Smoky Mountains National Park.

ABSTRACT

COMPARISONS OF ARTHROPOD AND AVIAN COMMUNITIES IN INSECTICIDE-TREATED AND UNTREATED HEMLOCK STANDS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

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Great Smoky Mountains National Park is using systemic imidacloprid in Hemlock Conservation Areas to treat eastern hemlocks (*Tsuga canadensis*) infested with hemlock woolly adelgid (*Adelges tsugae*, HWA). The purpose of this study was to investigate the effects of systemic imidacloprid treatments on the insectivorous bird community and on the hemlock canopy arthropod community in the context of food availability for insectivores. Territory mapping of three hemlock-associated Neotropical migratory foliage-gleaning bird species was conducted in six pairs of treated and untreated hemlock study sites. Relationships between bird territory density and hemlock foliar density were also examined. Canopy arthropods were sampled in these paired sites by clipping mid-canopy hemlock branches. Arthropods were identified to order except Hemiptera to suborder. Arthropods were further categorized into focal bird prey guilds and non-target herbivorous insect guilds.

Focal bird densities did not differ between treated and untreated sites but were positively related to branch foliage mass, implying a preference in these birds for well-foliated hemlocks. There was no difference in HWA infestation between treated and untreated sites, indicating that treated hemlock trees were not sampled at peak efficacy of imidacloprid treatments. Over 900 non-HWA arthropods from 16 orders were collected. There were no differences in richness, abundance, composition, or density between treated and untreated sites for total arthropods or for the two focal bird prey guilds arthropods ≥ 3 mm and larvae ≥ 3 mm, revealing little impact on the overall arthropod crop from imidacloprid treatments. However, non-target herbivorous Hemiptera and larval Lepidoptera were significantly reduced in treated hemlocks. Although larval Lepidoptera are primary prey for focal birds, lack of differences in bird densities suggests the birds are finding other food resources in these mixed hemlock-deciduous stands. Results of this study indicate that controlling HWA-induced defoliation through use of imidacloprid may in the short term benefit hemlock-associated birds. However, while imidacloprid treatments did not appear to affect most non-target arthropods, guilds of non-target herbivorous insects should be monitored for long-term declines.

CHAPTER 1: INTRODUCTION

Eastern hemlocks (*Tsuga canadensis* [L.] Carr.), described as the redwoods of the east (Great Smoky Mountains National Park 2008), range from Canada through the Southern Appalachian Mountains. Economically, hemlocks were once a valuable sawtimber tree in the Northeast (Ward et al. 2004). Today they are valued more for the important ecological niche they provide, their prominent use in the landscaping industry, and as a sightseeing attraction in state and national parks (Quimby 1996) including Great Smoky Mountains National Park (GSMNP). Their shade tolerance promotes dense foliage to grow throughout the hemlock canopy, thus providing a cool, shaded habitat that supports unique assemblages of flora and fauna (Quimby 1996, Ward et al. 2004). GSMNP, a World Heritage Site and International Biosphere Reserve (Sharkey 2001), contains some of the largest and oldest eastern hemlock stands in the world (Buck et al. 2005). Unfortunately, these beautiful trees and their associated ecosystems are at risk from hemlock woolly adelgid (*Adelges tsugae* Annand, HWA). This minute non-native insect anchors at the base of hemlock needles to feed on plant fluids which causes the hemlock to shed its needles and eventually die (McClure et al. 2001).

Non-native insects and pathogens are major sources of stress in the forests of eastern North America. Well known examples of exotic pathogens that have caused extensive damage include chestnut blight (*Cryphonectria parasitica* [Murr.] Barr) in American chestnut (*Castanea dentata* [Marsh.] Borkh.) and Dutch elm disease (*Ophiostoma* spp.) in elm species (*Ulmus* spp). A familiar non-native insect pest is the gypsy moth (*Lymantria dispar* L.), whose larvae have extensively defoliated hardwoods in decadal outbreak cycles throughout the eastern US (Lovett et al. 2006). While gypsy moth infestations may cause only short-term negative impacts because many trees within a stand survive attack and the moth is not host-specific (Lovett et al. 2006), HWA infestations cause severe, long-term damage because of its host-specificity on *Tsuga* species and the lack of resistance in eastern hemlocks (Lovett et al. 2006).

HWA infestation is spreading at a pace of approximately 12 km per year with faster expansion in the southern part of the range (Evans and Gregoire 2007). HWA was first recorded in GSMNP in 2002 (Soehn et al. 2005). In GSMNP, large areas of hemlocks have been killed, especially in the Cataloochee Valley region (Kincaid and Parker 2008, T. Remaley, pers. comm., pers. obs.). As hemlocks have declined, other changes in the ecosystem have been observed. Deterioration of hemlock vigor has been shown to cause shifts in forest flora (Orwig and Foster 1998, Eschtruth et al. 2006) and cause decreases in the numbers of birds that preferentially use hemlocks (Tingley et al. 2002), including several Neotropical migratory birds such as the black-throated green warbler (*Dendroica virens* [Gmelin]) which are targeted for conservation (Robbins et al. 1993). To conserve the hemlock ecosystem in GSMNP, hemlocks in specially designated Hemlock Conservation Areas are being treated for HWA using systemic imidacloprid, a chemical which is applied near the roots and is distributed throughout the hemlock via sap flow (Webb et al. 2003). This systemic insecticide application can control HWA infestation up to 100% in individual trees. Despite its effectiveness, the overall environmental impact of using insecticides such as imidacloprid in natural forested areas must be evaluated (Cowles et al. 2006, Devine and Furlong 2007).

The purpose of this study was to investigate the effects of systemic imidacloprid on the hemlock-associated insectivorous bird community and on the hemlock canopy arthropod community in the context of food availability for insectivores in GSMNP. Canopy arthropods were sampled to compare diversity between treated and untreated hemlock stands, and bird densities were surveyed in the same stands as an indirect assessment of resource availability in hemlock habitat. Relationships between hemlock health and densities of hemlock-associated birds were also investigated. Arthropod specimens collected in this study were preserved for the GSMNP Museum Collection as baseline data for future studies (National Park Service Park Profiles 2009).

CHAPTER 2: LITERATURE REVIEW

Hemlock Ecosystem

Eastern hemlocks (*Tsuga canadensis* [L.] Carr.) range from Nova Scotia west to Minnesota and south along the Appalachian Mountains to Georgia (Ward et al. 2004). They are one of the most common conifers in northeastern forests where they can occur in nearly pure stands with little understory (Lovett et al. 2006). Throughout their range they are typically associated with mesic, sheltered sites (Schafale and Weakley 1990). In the Southern Appalachians, the greatest densities of eastern hemlocks are found in coves or north-facing slopes in mixed hemlock-deciduous forests (Wilcove 1988, Johnson et al. 2000, Ward et al. 2004), often with a dense shrub layer of Ericaceae species such as rhododendron (*Rhododendron* spp.) (Kendeigh and Fawver 1981, Wilcove 1988). Eastern hemlock is widely distributed in forests throughout eastern North America, while the Carolina hemlock (*T. caroliniana* Engelm.) is a rare relict species patchily distributed in the Southern Appalachians (Rentch et al. 2000). These two species typically occupy different habitat niches where their ranges overlap.

Eastern hemlock (hereafter hemlock) is a late-successional species that may take centuries to dominate the forest canopy (Quimby 1996). It is the most long-lived, most shade tolerant tree species in eastern North America (Ward et al. 2004). This tolerance for low light permits the evergreen foliage to fill in throughout the canopy and down to the forest floor (Ward et al. 2004). This vertical canopy density is distinct from most conifer species that self-prune (Benzinger 1994). The dense hemlock foliage modifies the surrounding environment in protected coves and along waterways by moderating air temperatures and aiding retention of soil moisture (Benzinger 1994, Quimby 1996). The shallow root systems make hemlock subject to windthrow which creates canopy gaps and a pit-and-mound pattern of microhabitats on the forest floor (Quimby 1996). Often ericads will occupy gaps in the canopy such as the edges of streams (Kendeigh and Fawver 1981), while low light regimes and acidic soil chemistry may limit the herbaceous layer (Quimby 1996, Lovett et al. 2006).

The ecosystem characteristics created by hemlocks attracts unique biotic communities. Brook trout (*Salvelinus fontinalis* [Mitchill]) favor streams along hemlock stands because of the cooler microclimate created by hemlocks (Quimby 1996), and hemlocks support unique bird assemblages throughout their geographic range (Kendeigh 1946, Benzinger 1994, Quimby 1996, Yamasaki et al. 2000, Shriner 2001, Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008). The moth species hemlock angle (*Semiothisa fissinotata* [Wlk.]) is a hemlock species obligate (Soehn et al. 2005), and Buck et al. (2005), and Dilling et al. (2007) have documented diverse arthropod assemblages associated with hemlocks in GSMNP.

Hemlock Woolly Adelgid

Life History

HWA is believed to have been introduced to North America from Asia, though the details of its introduction are unknown (McClure et al. 2001). It was first observed in western species of hemlock in the 1920s, and was first detected in the eastern US in Virginia in the 1950s. It was first detected in GSMNP in 2002 (Soehn et al. 2005). In 2008 HWA occurred from Maine to Georgia along the Appalachian Mountains (Hemlock Woolly Adelgid 2009), and its range is expanding more rapidly in the warmer southern extents (Evans and Gregoire 2008). In eastern North America it attacks both eastern and Carolina hemlock (McClure et al. 2001). Western species of hemlock seem to tolerate infestation, while eastern *Tsuga* species appear to have little to no resistance.

HWA is a tiny insect (less than 1.5 mm in length) that taps nutrient reserves in plants (Ward et al. 2004). This pest feeds on starch reserves in the xylem ray parenchyma cells of hemlock needles rather than feeding directly on phloem like many related Hemiptera (McClure et al. 2001). The life cycle of HWA is complex, with typically two generations produced per year in North America (McClure et al. 2001, Ward 2004). All reproducing HWA in North America are parthenogenetic non-winged females that lay up to 300 eggs in woolly white ovisacs (McClure et al. 2001). Mobile nymphs emerge from the eggs and are easily dispersed by wind and animals. These nymphs crawl to the base of a needle where they insert a feeding apparatus called a stylet bundle into the ray cells. As they molt through several stages they remain attached to the same needle throughout their lives and build a woolly ovisac that will eventually hold the eggs they produce. Eggs laid in late winter hatch in the spring as either non-winged or winged adults. The non-winged adults settle at the base of a needle and eventually lay eggs that will hatch in the summer, which develop into only non-winged adults that overwinter and lay eggs the following spring. The winged adults fly off in search of a spruce species (*Picea* sp.) to complete their life cycle. However, no North American spruce species is a compatible host for winged HWA survival and reproduction, therefore these winged individuals do not contribute to future HWA infestations. As health in hemlocks deteriorates, proportionately more non-reproducing winged HWA are born, which can ironically cause declines in overall infestation in severely damaged trees in North America (McClure 1991).

Effects on the Hemlock Ecosystem

HWA can infest and kill all age classes of hemlocks. The feeding action of HWA causes hemlock needles to desiccate, discolor, and drop, and it also kills most buds preventing future growth (McClure et al. 2001). Defoliation and subsequent death of tree limbs typically progresses from lower to upper canopy and can begin within a few months of infestation. Tree death can occur in as little as four years.

Lovett et al. (2006) recognized HWA infestation as having a particularly potent combination of host specificity and lack of host resistance, and thus both short- and long-term impacts to hemlock ecosystems are occurring. Ecosystem and community level effects of HWA forest infestation have been documented primarily in Northeast forests. In New England, hemlock decline has been shown to change forest floor parameters and alter nutrient cycling in hemlock-dominated ecosystems (Jenkins et al. 1999, Stadler et al. 2006, Orwig et al. 2008). In Delaware and Pennsylvania, Eschtruth et al. (2006) reported that as hemlocks declined in vigor light levels increased, resulting in a significant increase in understory growth that included invasive plant species. In Connecticut, Orwig and Foster (1998) observed rapid understory growth but few hemlock seedlings following hemlock decline. Similarly, Small et al. (2005) documented a shift in the understory to more shrub species and more hardwood saplings. As hemlocks die, early successional hardwoods such as birch (*Betula* spp.) and red maple (*Acer rubrum* L.) typically replace them (Orwig and Foster 1998).

Hemlock-associated avian populations have also been shown to decline in response to HWA attack. In the northeastern US, Tingley et al. (2002) found breeding birds such as black-throated green warblers (*Dendroica virens* [Gmelin]) and Acadian flycatchers (*Empidonax virescens* [Vieillot]) that strongly associate with intact hemlock forests decline significantly with hemlock mortality from HWA. Becker et al. (2008) also observed a positive relationship between the numbers of breeding territories of these two bird species and hemlock health in Pennsylvania. Blue-headed vireos (*Vireo solitarius* [Wilson]) have also been negatively impacted by hemlock decline (Tingley et al. 2002). These three Neotropical migrants are prioritized for conservation primarily because of breeding and wintering habitat loss (Hunter et al. 1993, Robbins et al. 1993). Loss of hemlock habitat in the Southern Appalachians caused by HWA is critical for Neotropical migrants such as blue-headed vireos and black-throated blue warblers (*Dendroica caerulescens* [Gmelin]), that were already experiencing declines in their southern range related to habitat fragmentation (Holt 2000). Because of habitat specificity of these birds in the Southern Appalachians, they are bioindicators of hemlock habitat integrity and can, therefore, be used in forest conservation and management (O'Connell et al. 2000). Assessment tools for hemlock management are imperative in light of the rapid spread of HWA in the Southern Appalachians (Evans and Gregoire 2007).

In addition to HWA, other non-native insect pests have been associated with declines in Neotropical migratory bird species. Often these impacts are related to habitat preferences in birds. In GSMNP, Rabenold et al. (1998) found densities of ten of the eleven most common territorial bird species in spruce-fir forests had declined by nearly half from 1974 to 1986. These declines were attributed to the effects of balsam woolly adelgid (*Adelges piceae* [Ratzeburg]) on Fraser fir (*Abies fraseri* [Pursh] Poir.). Birds showing the most severe declines were Neotropical migratory insectivorous canopy foragers such as the black-throated green warbler and the blue-headed vireo.

Invertebrates within tree canopies can be an important food source for vertebrate communities such as insectivorous birds, and non-native forest insect pests can cause both positive and negative changes in prey availability. When food resources are altered, foraging and breeding ecology of birds associated with the habitat can be affected. In the case of gypsy moth, Gale et al. (2001) found while defoliation caused a short-term decline in birds with a preference for closed forest canopy, this guild returned to pre-infestation density after five years. Some bird species can benefit from gypsy moth larval outbreaks. For example, cuckoos (*Coccyzus* spp.), which are Neotropical migratory canopy insectivores that preferentially prey on hairy caterpillars like the gypsy moth (Hamel 1992), increase in numbers during larval outbreak years (Barber et al. 2008).

Although effects on hemlock-associated birds by HWA are relatively well-documented, it is unknown if the presence of HWA affects arthropod assemblages in the hemlock canopy. Kenis et al. (2009) observed that while studies of ecological responses of forest communities to invasion are numerous, few examine displacement and competition between native and non-native insects at the same trophic level and with similar resource requirements. One such study found native picture-winged flies (Tephritidae) were significantly reduced in the presence of high densities of a non-native weevil (*Rhinocyllus* sp.) released for biocontrol of non-native thistles (*Carduus* spp.) (Louda et al. 1997). In another study, the invasive Argentine ant (*Linepithema humile* [Mayr]) was shown to disrupt the community assemblage of native ants in northern California (Sanders et al. 2007). Sample et al. (1996) found gypsy moth-infested plots with low levels of defoliation and high numbers of the larvae supported fewer numbers of some native lepidopteran taxa, implying that competition was a greater factor in depressing native caterpillars than the secondary effect of defoliation. Finally, in a study of habitat preferences in canopy arthropods, Halaj et al. (2000) observed that experimentally manipulated defoliation of a western *Tsuga* species caused significant declines in Araneae, Psocoptera, and Collembola numbers. These results may be applicable to the secondary effects of conifer pests such as HWA that cause changes in the structural microhabitat of the canopy through defoliation.

Chemical Control of Hemlock Woolly Adelgid

The severe decline of hemlock communities in response to HWA infestations in eastern North America has prompted development of measures to control HWA in both landscaped and forested environments. Control measures include the release of predatory beetles for biocontrol, and the use of chemical controls in the form of foliar sprays and systemic applications (Ward et al. 2004). One such systemic insecticide application used for long term control of HWA is soil drenching with imidacloprid. Imidacloprid (1-[(6-Chloro-3-pyridinyl)methyl]-N-nitro-2-imidazolidinimine) is a broad spectrum chloronicotinyl insecticide that affects the nervous system in arthropods (Silcox 2002, Imida E-Pro 2008). Its primary actions are against plant fluid-feeding insect pests such as herbivorous Hemiptera and thrips (Thysanoptera), but it is also effective against other insect orders such as Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Orthoptera (Mullins 1993). It is commonly used for both crop and ornamental pest management.

In soil drenching applications, the soil around the base of the hemlock is drenched with the insecticide, allowing uptake of imidacloprid by the roots and subsequent systemic distribution throughout the tree (Tattar et al. 1998, Webb et al. 2003). Imidacloprid efficacy from soil drenching treatments can last for more than two years (Webb et al. 2003, Cowles et al. 2006). This application has been shown to eliminate infestation in hemlocks in forests (Cowles et al. 2006) and urban environments and to significantly reduce infestation in unhealthy trees (Webb et al. 2003). Elimination of HWA has also been demonstrated in forests.

Effects of Insecticides on Non-target Arthropods

Despite the effectiveness of imidacloprid at controlling HWA, effects on non-target organisms are a major concern when using any pesticide (Cowles et al. 2006, Devine and Furlong 2007). It is unknown if the use of systemic imidacloprid negatively impacts the canopy arthropod community in hemlocks. However, effects of imidacloprid on non-target fauna have been documented in other systems. Both plant and ground dwelling arthropod assemblages have shown short-term reduced abundance and diversity in a crop system (Sánchez-Bayo et al. 2007). Marquini et al. (2002) found spray imidacloprid application did not reduce richness but did reduce abundance in overall crop arthropods. There were no declines in two common taxa, namely spiders (Araneae) and leafhoppers (Cicadellidae), but some thrips species significantly declined. Marquini et al. (2002) suggested these impacts on non-target taxa may cause stress on the trophic webs of arthropod communities in crop systems.

Beneficial arthropods are a particular concern when chemical controls are used. Mizell and Sconyers (1992), and Smith and Krischik (1999) reported that beneficial predatory arthropod densities declined with systemic imidacloprid use, while other studies have shown little negative impact from spray treatments in crops (Kilpatrick et al. 2005) or turfgrass (Kunkel et al. 1999). Although direct mortality has not been documented, levels of imidacloprid found in pollen of crop species have been measured at sub-lethal and lethal levels for non-target honey bees (*Apis mellifera* Linnaeus) (Halm et al. 2006), which are critical pollinators in many agroecosystems. Non-target aquatic arthropods also may be impacted by systemic imidacloprid, especially when applied along watercourses. Kreutzweiser et al. (2007) found laboratory simulations of leaf fall and leaching from systemic tree applications caused sub-lethal and lethal effects in aquatic leaf-chewing decomposers. Sub-lethal and lethal effects have also been demonstrated in the laboratory on black fly larvae (*Simulium vittatum* (Zetterstedt) cytospecies IS-7) (Overmyer et al. 2005).

Similar to imidacloprid, other insecticides have had unintended effects on non-target arthropods. Several insecticides such as the chemical diflubenzuron (N-[[(4-chlorophenyl)amino]carbonyl]-2,6-difluoro-benzamide) and the bacterium *Bacillus thuringiensis* var. *kurstaki* are sprayed to control outbreaks of non-native gypsy moth larvae, and this forest pest-insecticide system has been well studied in field settings. Multiple studies have shown that arthropod canopy assemblages in deciduous trees were reduced following applications of various insecticides to control larval lepidopteran gypsy moths (Sample et al. 1993a, Sample et al. 1996, Butler et al. 1997a, Butler et al. 1997b). In these studies, native larval lepidopterans were particularly negatively impacted. In an experimental control application, Marshall et al. (2002) found significant reductions in non-gypsy moth caterpillar taxa in treated versus untreated stands. Rieske and Buss (2001) detected significant declines in thrips and centipedes (Chilopoda), as well as negative trends in other taxa in the litter and ground dwelling community of stands treated to control gypsy moth.

In another forest pest-insecticide system, treatments for spruce budworm (*Choristoneura occidentalis* Freeman) have been shown to have little impact on overall lepidopteran metrics in the shrub layer, though uncommon taxa were significantly reduced (Miller 1990). Simon et al. (2007) reported mixed results apple (*Malus* spp.) orchards chemically treated for a moth pest versus organic orchards, with a trend toward higher arthropod abundance in the organic sites but significantly higher diversity in treated sites. Yearly sprays to control the pine wilt nematode (*Bursaphelenchus xylophilus* [Steiner and Buhrer] Nickle) caused short-term declines in forest arthropod metrics but did not cause significant long term declines (Kwon et al. 2008).

Effects of Insecticides on Forest Birds

Use of insecticides to control non-native pests can affect trophic levels other than non-target arthropods. For example, a variety of effects have been documented in birds breeding in insecticide-treated forest systems. Gypsy moth control has had variable effect on insectivorous canopy-dwelling birds in terms of foraging and productivity (e.g., number or condition of fledglings). Bell and Whitmore (1997) documented no significant effects from gypsy moth control on the overall songbird assemblage (primarily insectivores) in Virginia forests, and they noted that pest defoliation in untreated forests may actually contribute to greater habitat complexity, which in turn may be beneficial for some bird species. Sample et al. (1993b) found a significant reduction in non-gypsy moth lepidopteran biomass in gut contents of insectivorous birds from treated versus untreated stands. Gut arthropod biomass in two bird species was significantly reduced in treated stands, while four bird species showed no biomass declines but a significant overall dietary shift in treated stands; migrants were impacted more than resident birds. The shift to other prey was interpreted as compensation for loss of non-target caterpillars killed by the insecticide.

Productivity in insectivorous birds may also be negatively impacted from insecticide use. Holmes (1998) found insectivorous female Tennessee warblers (*Vermivora peregrina* [A. Wilson]) spent less time feeding nestlings and more time foraging in treated stands, and noted productivity trends were lower in treated stands for clutch size, brood size, and hatch rate. Nagy and Smith (1997) observed that nesting success of another insectivore, the hooded warbler (*Wilsonia citrina* [Boddaert]), was higher in untreated stands for one year of a multi-year study. Rodenhouse and Holmes (1992) tracked natural reductions in food availability resulting in primarily a decline in caterpillars for insectivorous Neotropical migratory black-throated blue warblers over three years, and they compared the natural effect to an insecticide-induced reduction in caterpillars. They found the naturally caused decline caused stronger negative trends in productivity for this bird species than the insecticide-caused declines. Red-eyed vireos (*Vireo olivaceus* [Linnaeus]), also insectivorous Neotropical migrants, may also suffer little impact from gypsy moth treatments, though later nest initiation may be a cautionary sign (Marshall et al. 2002).

In a study combining effects of gypsy moth defoliation and effects of insecticide use, Marshall and Cooper (2004) found territory size in red-eyed vireos did not relate to caterpillar density (preferred food) after caterpillars were reduced via insecticide application. However, the authors did find an inverse relationship between foliar density and territory size – territories with more defoliation from gypsy moth were larger to compensate for fewer food resources (Marshall and Cooper 2004).

Resource Selection in Forest Birds

Resource Availability and Limiting Factors

Habitat selection in vertebrate animals is a complex equation of life history traits, population and community dynamics, and regional geographic and climatic influences (MacArthur 1972). Species can be habitat generalists or habitat specialists, and habitat preferences are interconnected with other resources such as food on which a species depends, as well as pressures such as predation and inter- and intraspecific competition. Food density may regulate population densities in some territorial animals, and territoriality is a reflection of aggression toward competitors in an effort to secure these resources (food value theory of territoriality, Wilson 2000).

Resources are not infinite in the environment, and availability of specific resources may limit the numbers of any one species or guild within a given habitat (limiting factors, MacArthur 1958, Wilson 2000). One potential limiting factor affecting densities of breeding insectivorous birds is food availability (Marshall and Cooper 2004). Studies have shown strong density dependence away from the breeding grounds for insectivorous birds. During migration Graber and Graber (1983) documented warbler density dependence on lepidopteran availability, and Johnson and Sherry (2001) correlated wintering warbler numbers (including black-throated green warblers) with arthropod density and found no relationship between bird density and habitat structural variables.

Territorial behavior in breeding birds, such as vocal advertising and agonistic interactions between conspecifics, is often associated with protection of food supplies (Wilson 2000, Ralph et al. 2003). Conclusions regarding correlation of breeding insectivore territory densities and food resource availability in the habitat are mixed. The brown creeper (*Certhia americana* Bonaparte) is a bark-gleaning insectivorous short-distance (non-Neoptropical) migrant whose abundance is possibly related to arthropod abundance during the breeding season (Mariani and Manuwal 1990). Similarly, Haney (1999) and Barber et al. (2008) reported increases in the numbers of territories of canopy-feeding Neotropical migrants during outbreak years of caterpillar infestations, including two parulid warbler species in Haney's (1999) study. Morse (1976) found territory sizes of four warbler species including the black-throated green warbler in island and mainland spruce-fir forests of Maine were inversely related to arthropod density for one month of one season in a multi-year study, but this relationship was not upheld for other canopy insectivores in the study. He concluded that variations in habitat structure, and to a lesser extent interspecific competition, played larger roles than food availability in territory densities for this foraging guild.

There is a growing body of literature showing that some migratory breeding birds indirectly measure general resource availability when arriving to establish territories through assessing habitat structural cues (structural cues hypothesis, Smith and Shugart 1987). In the seminal study of structural cues, territory size in Neotropical parulid insectivorous ovenbirds (*Seiurus aurocapilla* [Linnaeus]) was found to more strongly relate to prey availability predicted by habitat variables rather than actual prey availability measured in the habitat, implying that ovenbirds used habitat cues to determine territory size (Smith and Shugart 1987). Similarly, Marshall and Cooper (2004) found no relationship at the beginning of the season between territory size of red-eyed vireos (another Neotropical insectivore) and arthropod density, yet there was an inverse relationship between territory size and foliar density (i.e., territories in less foliated areas were larger). During mid-season when adults were feeding young, these established territory sizes showed an inverse relationship with food density (in this case, Lepidoptera). These findings supported the structural cues hypothesis at the time of territory establishment and food value theory at the time when food resources were in the greatest demand.

Resource Selection in Three Southern Appalachian Hemlock-associated Birds

Bird species can be grouped into habitat and behavioral guilds based on shared habitat and dietary choices (Vale et al. 1982). A specialized habitat and foraging guild common to the Southern Appalachian forests is hemlock-associated insectivorous foliage-gleaning birds. Hemlocks support unique assemblages of birds, with some variation between the northern and southern parts of the range (compare Ross et al. 2004 and Kendeigh and Fawver 1981). The black-throated green warbler, black-throated blue warbler, the blue-headed vireo are three Neotropical migratory insectivores common in the Southern Appalachian Mountains (Hamel 1992, Simons et al. 2006) and are well documented in hemlock and cove forests of GSMNP (Kendeigh and Fawver 1981, Wilcove 1988).

Habitat Selection

– Black-throated Green Warbler

Black-throated green warblers show a high affinity for conifers (Bent 1953, MacArthur 1958, Hamel 1992, Robichaud and Villard 1999), and specifically hemlocks (Hamel 1992, Benzinger 1994, Yamasaki et al. 2000, Tingley et al. 2002, Ross et al. 2004) in the Southern Appalachians (Kendeigh and Fawver 1981, Wilcove 1988, Shriner 2001). They typically reside above 640 m elevation in the southern portion of their breeding range (Hamel 1992, Kendeigh and Fawver 1981), but are documented in the mountains of Tennessee down to 240 m (Nicholson 1997). They prefer interiors of extensive closed-canopy mature forests in the southern part of their range (Hamel 1992) and preferentially nest in the canopies of conifers (Bent 1953, Hamel 1992).

In mixed conifer-deciduous forests, black-throated green warblers generally forage disproportionately in conifers on their breeding grounds (Holmes and Robinson 1981, Parrish 1995a, Robichaud and Villard 1999). Parrish (1995b) documented populations in New Hampshire that favored deciduous forests for foraging, and this preference was linked to distinct regional morphological characteristics in the birds. This warbler favors foraging in the middle of the branch to the outer tips (Rabenold 1978) in the mid- to upper canopy (MacArthur 1958, Hamel 1992), but will also use the lower branches of trees (MacArthur 1958). Average foraging heights range from 1 to 12 m in Maine (Morse 1968), 14 m in New Hampshire (Holmes et al. 1979), and 3 to 6 m in spruce-fir forests of GSMNP (Rabenold 1978). These strong conifer and hemlock associations, particularly in the Southern Appalachian region, make the black-throated green warbler a good bioindicator for measuring potential loss of hemlock habitat in the region.

– Black-throated Blue Warbler

Black-throated blue warblers are associated with habitat attributes of cove forests (Wilcove 1988, Hamel 1992) which is where hemlocks typically are found in the Southern Appalachians (Johnson et al. 2000, Ward et al. 2004). They have also been documented as mixed-hemlock associates (Kendeigh 1946, Kendeigh and Fawver 1981), in GSMNP (Shriner 2001). Some deciduous forests also are suitable for this bird species in the southern part of its range (Hamel 1992). Black-throated blue warblers strongly favor forests with a dense shrub understory (Bent 1953, Hamel 1992) for nesting (Steele 1993), with a preference for broadleaved evergreens such as rhododendrons (Bent 1953, Hamel 1992) that are commonly associated with hemlock and cove forests in the Southern Appalachians (Kendeigh and Fawver 1981, Wilcove 1988). These warblers typically are found above 640 m in the Southern Appalachians (Kendeigh and Fawver 1981), though one study conducted in the region between 380 and 1460 m elevation found this warbler absent only at the lowest elevations, with a steady increase in numbers up to 1000 m before densities leveled off (Lichstein et al. 2002). The black-throated blue warbler prefers interiors of closed-canopy mature forests in the southern part of its range (Hamel 1992).

The foraging microhabitat of the black-throated blue warbler is shrub and low- to mid-canopy (Holmes et al. 1979, Hamel 1992), with an average foraging height of 6 m in shrub to tree strata in New Hampshire (Holmes et al. 1979, Steele 1993), and an average of 8 m in the Southern Appalachians (Weeks 2001). They show little foraging substrate preference for any particular plant species (Weeks 2001) and have been documented foraging on hemlocks in GSMNP (pers. obs.). They favor leaves over branches for foraging (Robinson and Holmes 1982).

– Blue-headed Vireo

Blue-headed vireos are similar to black-throated green warblers in their strong preference for conifer (Hamel 1992) and cove forest types (Bent 1950, Kendeigh and Fawver 1981, Hamel 1992, Ross et al. 2004) including hemlocks (Yamasaki et al. 2000, Tingley et al. 2002, Ross et al. 2004) in the Southern Appalachians (Kendeigh and Fawver 1981, Wilcove 1988). Some deciduous forests are also suitable for this species in the southern part of its range (Hamel 1992). They breed above elevations of 410 m in GSMNP (Kendeigh and Fawver 1981) and prefer extensive mature forests in the southern part of their range (Hamel 1992). They build nests in shrub to low canopy layers (Hamel 1992, Benzinger 1994) including building directly in hemlocks (Benzinger 1994) in GSMNP (pers. obs.).

Blue-headed vireos show a foraging preference for conifers (Holmes and Robinson 1981) and have been documented foraging in hemlocks in GSMNP (pers. obs.). Although they will forage along the entire branch, they prefer the interior near the trunk to the middle of the branch in the mid-canopy at heights between 1 and 6 m in spruce-fir forests of GSMNP (Rabenold 1978). They glean more prey off of bark than leaves (Holmes and Robinson 1981, Robinson and Holmes 1982).

Food Selection

Black-throated green warblers, black-throated blue warblers, and blue-headed vireos are all in the same feeding guild of "insectivores" (prey include some Arachnida, e.g., Araneae) which primarily glean sessile (e.g., larval) arthropods such as larvae from the surfaces of plants (Hamel 1992). All use similar major search and capture tactics, either directly gleaning prey when encountered, or flying up to nearby surfaces and gleaning prey during a brief hover (Robinson and Holmes 1982), and these stereotypic behaviors are observable and quantifiable in the field (Graber and Graber 1983, Hutto 1990, Johnson 2000).

Prey energy value should exceed the energy expended to capture and handle the prey, which relates in part to the morphology and feeding ecology of the predator (Stephens and Krebs 1986). The black-throated green warbler typically does not take prey less than 2 mm long (Morse and Poole 2005), and another warbler in the same family (Parulidae), the Wilson's warbler (*Wilsonia pusilla* [A. Wilson]), has been found to under-exploit prey 1 to 3 mm long (Raley and Anderson 1990). A proposed minimum prey length eaten by passerine birds (Passeriformes) is 2.5 mm (Jansson and von Brömssen 1981, as cited in Pettersson et al. 1995). HWA is 0.4 to 1.4 mm in length (Kohler 2007), and avian predation on HWA remains undocumented in the literature.

Black-throated green warblers, black-throated blue warblers, and blue-headed vireos prefer larval Lepidoptera (Kendeigh 1946, Bent 1950, Bent 1958, MacArthur 1958, Robinson and Holmes 1982, Jones et al. 2003) and also feed nestlings in part with caterpillars (Bent 1950, Bent 1958). Other arthropod prey include but are not limited to Hemiptera, Coleoptera, Diptera, and various arachnids (Bent 1950, Bent 1958, Robinson and Holmes 1982).

Limiting Factors

Niche segregation may serve to allocate limited resources in species with similar resource requirements (niche theory, Morin 1999; e.g., MacArthur 1958). While both habitat and diet overlap in these three species, foraging and nesting microhabitat selection may serve to segregate these three species' niches and moderate interspecific competition.

Predation may also play a role in limiting numbers within a population (Wilson 2000); however, there has been limited documentation of predation on adults of black-throated green warblers (Morse and Poole 2005), black-throated blue warblers (Holmes et al. 2005), and blue-headed vireos (James 1998). Hawks (Accipitridae) will prey on these warblers (Holmes et al. 2005, Morse and Poole 2005), yet the vireo has been recorded nesting near hawks rather than avoiding them (James 1998). Nest predation in the warblers is known to be mostly from small mammals and some birds (Holmes et al. 2005, Morse and Poole 2005), but little information is available on nest predation in the vireo (James 1998). All three species build nests with an open cup-like structure. A study of open cup nest predation in GSMNP revealed a 2% predation rate which was significantly lower than other tested locations (Wilcove 1985), indicating that nest predation may not be a strong factor controlling numbers of these species in the Park.

Quantifying Food Resources for Insectivorous Forest Birds

Food availability relies on two major factors: what the bird perceives and consumes as prey, and where a given species forages at the microhabitat level (Hutto 1990, Wolda 1990). Quantifying food resources for specific bird guilds continues to challenge researchers (Smith and Rotenberry 1990). The difficulty lies in sampling the actual food available to the bird rather than the standing crop of arthropods (Hutto 1990, Wolda 1990). In the case of hemlock-associated foliage-gleaning insectivores, ideally one would sample arthropods in the canopy within the microhabitats exploited by the guild, and adjust the results of sampled arthropod standing crop to better represent what the guild of birds preferentially consumes.

Common sources of error in arthropod sampling arise from temporal and spatial variation in arthropod abundance because of seasonality and patchiness within microhabitats (e.g., tree canopy strata and structure) (Majer et al. 1990). Sampling on consecutive days and within the same window of time can aid in controlling temporal variation. While studies are often designed to investigate the seasonal (Schowalter and Ganio 1998, Marshall and Cooper 2004) and daily fluctuations in arthropods (Costa and Crossley 1991), snapshot surveys where collections take place in a small window of time (e.g., Rango 2005, Kwon et al. 2005) offer a way to temporally control for seasonal pulses in arthropods. Canopy arthropod communities typically are stratified vertically because of the distribution of microhabitats, predators, and food resources within the layers of the trees (Lowman and Rinker 2004), so sampling in the same part of the canopy may control for spatial variation at the microhabitat level. In arthropod studies with two forest treatments (e.g., insecticide treatment and control), pairing sites in proximal areas with similar geographic characteristics can also aid in controlling spatial variation (Sample et al. 1993a, Pettersson et al. 1995).

Arthropod collection methods can sample relative (over time; e.g., pitfall traps) or absolute (instantaneous; e.g., collecting all or part of plant) arthropod abundance (Cooper and Whitmore 1990). Methods for arthropod sampling in tree canopies have been evaluated for their usefulness in different habitats and in their effectiveness for sampling food availability for different bird species and guilds (Cooper and Whitmore 1990, Dahlsten et al. 1990, Hutto 1990, Johnson 2000). A recommended method for measuring primarily sessile, foliage-dwelling arthropods, the major food resource for foliage-gleaning birds, is collecting vegetation and prey crop via branch clipping (Blanton

1990, Johnson 2000). This method is considered effective (Schowalter et al. 1981, Cooper and Whitmore 1990, Majer et al. 1990, Johnson 2000), feasible, and affordable (Cooper and Whitmore 1990). Often standardized lengths of branches such as 1 m are clipped (e.g., Costa and Crossley 1991, Johnson 2000). Clipping 1 m branch tips in the hemlock canopy at heights between 5 and 10 m would sample the lower vertical foraging microhabitat of black-throated green warblers, the higher foraging microhabitat of black-throated blue warblers, and the outer horizontal branch microhabitat of blue-headed vireos.

Arthropods collected using the branch clipping method represent a sample of the foliage-dwelling arthropod community but not necessarily a measure of food availability or preferences for a specific predator. Other characteristics of arthropods such as life stage and size can be valuable information in studies of avian food availability. Biomass of total arthropod crop can be measured directly (Schowalter et al. 1981, Mariani and Manual 1990, Pettersson et al. 1995) or through length-to-mass conversions of individual specimens if available for local fauna (Moran and Southwood 1982, Johnson 2000). However, when preservation of specimens is warranted or when local conversion tables are not available, arthropods can also be grouped into relative size classifications by measuring length (Rabenold 1978, Raley and Anderson 1990). Taking taxonomy, life stage, and size into account, arthropods can be pooled into guilds based on similarities (e.g., larvae ≥ 3 mm) (Schowalter et al. 1981, Moran and Southwood 1982) as more accurate measures of avian food resources (Cooper et al. 1990, Wolda 1990).

Identification of arthropods to the species level may not be necessary for studies of avian food availability when higher taxonomic levels or functional groups may answer questions adequately (Wolda 1990). For example, if an insectivorous bird forages on caterpillars preferentially, larval Lepidoptera do not necessarily need to be identified to species to assess caterpillar availability. Analysis of lower taxonomic levels with frequent zero values may also impede detection of trends (Cooper et al. 1990). Taxonomic levels commonly used in arthropod literature for analysis of insectivore food availability include order (Cooper et al. 1990, Rodenhouse and Holmes 1992, Sample et al. 1993a) and family (Butler et al. 1997a, Raley and Anderson 1990, Sample et al. 1993a).

Arthropod taxa or guilds can be quantified as abundance, relative abundance, or density. Density can be calculated in several ways including abundance per branch (Franklin et al. 2003), abundance per mass of foliage (Majer et al. 1990, Costa and Crossley 1991, Sample et al. 1996; Butler et al. 1997a, Marshall and Cooper 2004), and abundance per total branch mass (woody and foliage) (Pettersson et al. 1995, Schowalter 1995). While no effort to measure food availability for insectivorous foliage-gleaning birds can be exact because we cannot perceive the foraging environment precisely the way a predator does, categorizing arthropod crop according to avian guild life history of foraging microhabitat and dietary preferences can offer approximate assessments of available food resources.

CHAPTER 3: MANUSCRIPT

Introduction

Eastern hemlock (*Tsuga canadensis* [L.] Carr., hereafter hemlocks) is a late-successional, shade-tolerant conifer (Quimby 1996) ranging from Nova Scotia south along the Appalachian Mountains to Georgia (Ward et al. 2004). They are found in dense, pure stands and mixed-deciduous forests (Orwig and Foster 1998, Rankin and Tramer 2002, Lovett et al. 2006), and in the Southern Appalachian Mountains they are common in coves and on north-facing slopes with a dense shrub layer (Kendeigh and Fawver 1981, Wilcove 1988, Schafale and Weakley 1990, Ward et al. 2004, Lovett et al. 2006). Throughout their range hemlock forests attract unique arthropod (Buck et al. 2005, Dilling et al. 2007) and avian assemblages (Kendeigh 1946, Benzinger 1994, Shriner 2001, Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008) including Neotropical migratory birds prioritized for conservation (Hunter et al. 1993, Robbins et al. 1993).

The hemlock ecosystem is threatened by the hemlock woolly adelgid (Hemiptera: *Adelges tsugae* Annand, hereafter HWA), a non-native herbivorous insect from Asia that feeds on cellular nutrient reserves in hemlock needles (McClure et al. 2001). This feeding action causes defoliation, inhibits new growth, and can kill trees in as little as four years. Infestation is commonly observed as white woolly ovisacs formed by mature non-winged HWA attached at the base of hemlock needles. A winged form of mature HWA is also produced but requires a spruce (*Picea* spp.) host not found in North America for survival and reproduction. These winged HWA are produced in greater proportion as hemlock health declines (McClure 1991). Hemlock deterioration from HWA causes increased light levels at the forest floor, alters soil chemistry (Orwig et al.

2008), and increases understory vegetation (Eschtruth et al. 2006). In the northeastern US, numbers of hemlock-associated birds in the avian assemblages of hemlock forests have declined as habitat quality declines from HWA infestation (Tingley et al. 2002).

In Great Smoky Mountains National Park (GSMNP), efforts are underway to conserve the hemlock ecosystem by establishing Hemlock Conservation Areas (HCAs) in mixed forest stands with high hemlock density. Hemlocks in these HCAs are treated with the insecticide imidacloprid (1-[(6-Chloro-3-pyridinyl)methyl]-N-nitro-2-imidazolidinimine) (Imida E-Pro 2008) via soil drenching (Soehn et al. 2005, T. Remaley, pers. comm.), which allows trees to take up the chemical through their roots for systemic distribution (Webb et al. 2003). This broad-spectrum insecticide targets plant fluid feeders such as herbivorous Hemiptera and thrips (Thysanoptera), and it also controls some Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Orthoptera (Mullins 1993). Imidacloprid soil drenching has been shown to eradicate HWA in hemlocks (Cowles et al. 2006) and permit complete recovery of hemlock foliage (Webb et al. 2003). However, effects of this insecticide on non-target taxa of the hemlock canopy arthropod community are unknown. Marquini et al. (2002) found imidacloprid spray applications did not reduce species richness but did reduce abundance in total arthropods associated with a canopy of a legume (Fabaceae) crop. Smith and Krischik (1999) found imidacloprid negatively impacted a beneficial predatory beetle (Coleoptera) in agro-horticultural crops, while other studies have shown little negative impact from treatments on beneficial arthropod predators of pests in crop (Kilpatrick et al. 2005) and turfgrass systems (Kunkel et al. 1999).

Impacts from imidacloprid in hemlock canopy arthropods might be more pronounced in herbivorous insect guilds such as larval Lepidoptera because these non-target taxa also feed directly on treated tree tissues or fluids. Caterpillars are a major food source for many avian foliage-gleaning forest insectivores in North America (Robinson and Holmes 1982, Holmes 1990), and this foraging guild of birds could be indirectly affected by declines in Lepidoptera in treated hemlock stands. Graber and Graber (1983) concluded that biomass of non-lepidopteran prey in Illinois deciduous forests would be insufficient forage for migrating foliage-gleaning insectivores. Jones et al. (2003) observed a direct relationship between Lepidoptera abundance and numbers of breeding foliage-gleaning birds including black-throated green warblers (*Dendroica virens* [Gmelin]), black-throated blue warblers (*Dendroica caerulescens* [Gmelin]), and red-eyed vireos (*Vireo olivaceus* [Linnaeus]). Densities of other breeding foliage-gleaning insectivores have also been shown to directly relate to lepidopteran availability (Haney 1999, Barber et al. 2008).

The purpose of this study was to investigate the effects of systemic imidacloprid on the hemlock-associated insectivorous bird community and the hemlock canopy arthropod community in the context of food availability for insectivores. I asked if 1) hemlock-associated insectivorous foliage-gleaning bird density differs between imidacloprid-treated and untreated hemlock stands, and 2) hemlock canopy arthropod diversity and food availability for avian insectivores differ between imidacloprid-treated and untreated hemlock stands.

Methods

Study Sites

The study took place within GSMNP in Cocke County, TN, and Haywood County, NC, in the easternmost region of the Park (Figure 1). All study sites were in discrete patches of mixed hemlock forest. Six sites were selected in HCAs where all hemlocks in the mid- to upper forest canopy had received imidacloprid soil drench treatments within

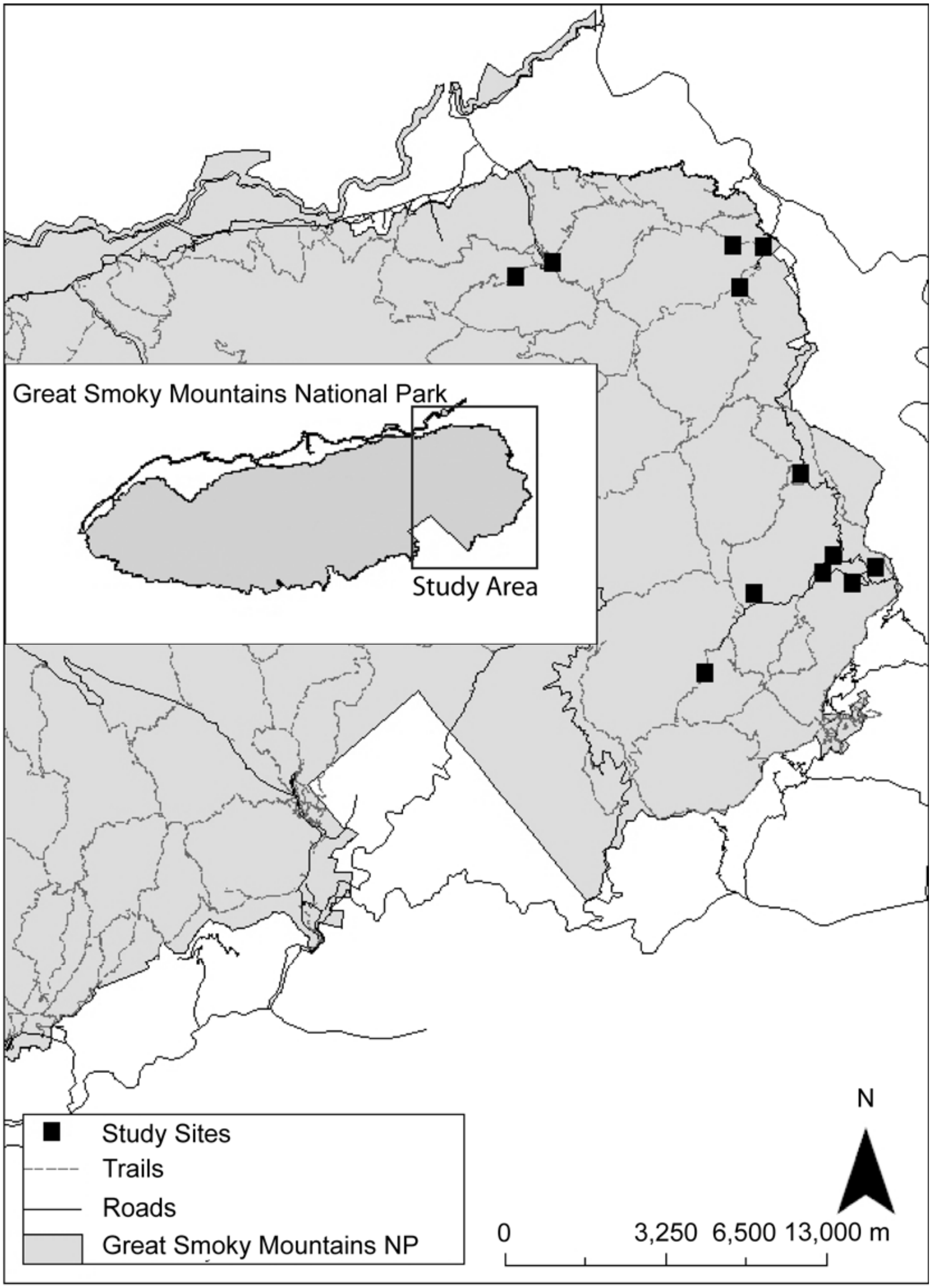

Figure 1. Map of hemlock study sites in Great Smoky Mountains National Park.

the previous two years. These six sites in HCAs were paired with six untreated sites with similar hemlock density and vigor to the adjacent HCAs. Site pairs were matched to minimize geographic variation in site characteristics, and all were within 1-3 km of one another with the exception of one pair which was 7 km apart. Elevation, slope, aspect, forest cover, hemlock diameter at breast height (DBH), and hemlock foliage density measures were used to verify that sites within a pair represented similar habitat.

Focal Birds

The Neotropical migratory black-throated green warbler, black-throated blue warbler, and blue-headed vireo (*Vireo solitarius* [Wilson]) were selected for this study. These species are common in the mid-elevations of GSMNP (Kendeigh and Fawver 1981, Shriner 2001, Simons et al. 2006) where the study sites were located, and they have similar habitat and foraging preferences. All three have an affinity for hemlock forests during the breeding season (Kendeigh and Fawver 1981, Shriner 2001, Tingley et al. 2002, Ross et al. 2004). Black-throated green warblers and blue-headed vireos forage disproportionately in conifers (Holmes and Robinson 1981, Parrish 1995a, Robichaud and Villard 1999) while black-throated blue warblers are less selective (Steele 1993, Weeks 2001). The foraging niches of all three species include mid-canopy branches below 10 m (MacArthur 1958, Rabenold 1978, Holmes et al. 1979, Steele 1993, Weeks 2001). All three feed on primarily sessile (e.g., larval), foliage-dwelling arthropods (Hamel 1992) and typically take prey > 2.5 mm (Jansson and von Brömssen 1981, as cited in Pettersson et al. 1995) with a preference for larval Lepidoptera (Kendeigh 1946, Bent 1950, Bent 1958, MacArthur 1958, Robinson and Holmes 1982, Jones et al. 2003) using primarily perch-gleaning and hover-gleaning capture maneuvers (Robinson and Holmes 1982).

Focal bird species territories were mapped using the spot mapping method. This technique, which uses behavioral observation to determine how many territories are occupied in a given area (Kendeigh and Fawver 1981), is recommended for determining densities of birds in patchy habitats (Ralph et al. 1993) such as the hemlock cove forests in this study. Fieldwork was conducted between 5 May and 11 June 2007 when temperate North American breeding birds typically have established territories and are actively defending them through singing and other territorial behaviors (Ralph et al. 1993). For two to three consecutive days, each site was traversed between sunrise and 1100 when territorial males typically sing the most, and in fair weather and calm winds. All territorial behaviors (e.g., singing, counter-singing of two or more males, pairs foraging together, and agonistic interactions) of the three focal species were recorded on a global positioning system unit map. Daily maps were compared to determine a final number of focal bird territories in a given study site.

Arthropods

During bird spot mapping censuses, five hemlocks within each site were marked for arthropod sampling in which at least one individual focal bird was observed foraging directly in the hemlock. DBH was measured for these hemlocks. Percent hemlock cover, including mid-story hemlocks not accounted for in GIS cover classes, was estimated in a 50 m radius around the foraging hemlocks. These five foraging hemlocks per site were also sampled for arthropods. To increase arthropod sampling size, the closest hemlock with similar DBH and canopy height to each foraging hemlock was also sampled, with distance between these trees typically less than 20 m ($\bar{x}$ = 16.2 ± 12.2 m).

Each pair of sites was revisited between 14 June and 22 July 2007 for arthropod collection when focal bird pairs were feeding young, a stage during the insectivorous bird breeding season that commonly coincides with pulses in arthropod resources (Rabenold 1978). Canopy arthropods were snapshot-sampled (Rango 2005) using the branch clipping method as described by Schowalter et al. (1981), Costa and Crossley (1991), and in detail by Blanton (1990) and Johnson (2000). This method is recommended for collecting food availability data for insectivorous foliage-gleaning birds because the samples are biased toward sessile, foliage-dwelling prey (Cooper and Whitmore 1990, Johnson 2000). One meter long samples were clipped and bagged from the ends of hemlock branches in the mid-canopy between 5 and 10 m ($\bar{x}$ = 7.4 ± 1.0 m) using telescoping poles. One branch was clipped from 10 hemlocks at each of the 12 sites for a total of 120 samples or 60 samples per treatment; this number has been shown to be sufficient for detecting arthropod differences in other compared habitats (Johnson 2000). Chloroform-soaked cotton balls were added to branch collection bags to immobilize arthropods and samples were stored at 5°C and processed within five days (Costa and Crossley 1991).

The length ($\bar{x}$ = 1.1 ± 0.2 m) and area (L x W; $\bar{x}$ = 1.3 ± 0.4 m^2) of each branch were measured and percent of dead woody material (non-foliated twigs) on branches was estimated visually. HWA ovisacs were counted on branches. Branches were then vigorously shaken to dislodge arthropods from vegetation (Morse 1976, Janes 1994, Johnson 2000) over a white surface. Arthropod specimens, including winged HWA, were collected and stored in vials of non-denatured ethanol (70%). Branch materials were air-dried for 10 months in paper bags and foliage and branches separated from each other and weighed.

Unidentified (*n* = 4) and partial arthropod specimens (*n* = 61) were excluded from arthropod diversity analyses. All other arthropods were classified to order, a taxonomic level used in other avian insectivore food availability studies (Cooper et al. 1990, Rodenhouse and Holmes 1992, Sample et al. 1993a), and the order Hemiptera to suborder, based on Borror et al. (1989) and Chu and Cutkomp (1992). Nomenclature was updated using the Integrated Taxonomic Information System (ITIS 2009). Specimen length was measured to the nearest millimeter and life stage recorded as larval or adult. Specimens not able to be categorized by life stage (n = 11) were excluded from larval analyses. Arthropods were sub-categorized into two focal bird prey guilds as a finer assessment of food availability (Wolda 1990): arthropods ≥ 3 mm and larvae ≥ 3 mm. Because of imidacloprid's action against the herbivore HWA, arthropods were sub-categorized into two herbivorous insect guilds: herbivorous Hemiptera and larval Lepidoptera. Larval Lepidoptera also served as the third focal bird prey guild.

Both adult forms of HWA, HWA ovisacs and winged HWA, were excluded from arthropod diversity and food availability analyses because HWA is 0.4 to 1.4 mm in length (Kohler 2007), which is smaller than typical insectivorous bird prey (Jansson and von Brömssen 1981, as cited in Pettersson et al. 1995), and there are no documentations in the literature of birds preying on HWA. HWA ovisacs and winged HWA were analyzed separately from one another because of their different life strategies in hemlocks. The non-winged HWA in ovisacs feed (and ingest imidacloprid) and reproduce on hemlocks, while winged HWA do not remain on hemlocks and are unable to reproduce in North America (McClure et al. 2001).

Data Analysis

Study Site and Branch Characteristics

Mean site elevation, slope, and area-weighted percents of northern and southern aspects were based on USGS National Elevation Dataset layers (National Map Seamless Server 2008) and calculated using ArcGIS software (Version 9.2, ESRI 2006).

Area-weighted percents of collapsed GIS forest cover classifications in pooled treatments were calculated in ArcGIS using vegetation map layers provided by GSMNP (Madden et al. 2004). The four classifications were hemlock-cove forest, mixed hardwood forest, mixed pine forest, and other. Site means were calculated for percent hemlock cover and DBH of hemlocks sampled for arthropods. Site means were also calculated for the following branch metrics from clipped vegetation: foliage mass, foliage ratio (ratio of foliage mass to total branch mass), and percent dead woody material.

To verify that paired sites represented similar habitat, paired *t*-tests (two tailed, $\alpha = 0.05$) were used to test for differences between insecticide-treated and untreated sites for the following site and branch characteristics: elevation, slope, proportion of northern aspect, hemlock cover, hemlock DBH, foliage mass, foliage ratio, and percent dead woody material. GIS cover classes were not statistically tested.

Focal Bird Density

Bird density at each site was measured as focal bird territories per 5 ha. To examine the first hypothesis regarding the effects of imidacloprid on hemlock-associated insectivorous bird density, paired *t*-tests (two tailed, $\alpha = 0.05$) were used to test for differences in focal bird density between insecticide-treated and untreated sites.

Arthropod Diversity, Food Availability, and Adelgid Infestation

Abundance (numbers per branch), relative abundance (ratio of order or guild abundance to total arthropod abundance), density (abundance per 100 g branch foliage) and richness (number of orders pooled per site) were used where applicable to express arthropod diversity, food availability, and HWA infestation. The 10 sampled branches per site were averaged for all metrics except richness.

Abundance and density were measured for total arthropods. Abundance, relative abundance, and density were measured for arthropod orders, focal bird prey guilds, and herbivorous insect guilds. To examine the second hypothesis regarding the effects of imidacloprid on arthropod diversity and food availability for insectivores, paired *t*-tests (two tailed, $\alpha = 0.05$) were used to test for differences in order richness and metrics of total arthropods, orders, focal bird prey guilds, and herbivorous insect guilds between treated and untreated sites. Order richness and abundance were also examined through non-metric multidimensional scaling (NMS) ordination (PC-ORD, Version 5, McCune and Mefford 2005). Site clustering and gradients were evaluated for treated-untreated, elevation, hemlock DBH, and hemlock branch foliage mass. Multi-response permutation procedure (MRPP) using two distance measures, Sorensen (Bray-Curtis; abundance) and Jaccard (presence-absence), was used to test differences in composition between treated and untreated sites ($\alpha = 0.05$). Monte Carlo test of significance was used to test for significant indicator taxa (in this case, orders) in treated versus untreated sites ($\alpha = 0.05$).

To evaluate HWA infestation, paired *t*-tests (two tailed, $\alpha = 0.05$) were used to test for differences in abundance and density of HWA ovisacs and winged HWA between treated and untreated sites.

A Posteriori Examination of Hemlock Foliage Density

Other research within GSMNP and observations of park scientists revealed a trend of heavy HWA infestation and subsequent hemlock stress in the southeastern region of GSMNP (Kincaid and Parker 2008) including within treated HCAs (T. Remaley, pers. comm.). To explore *a posteriori* the potential effects of HWA-induced defoliation in living hemlocks on hemlock-associated birds in GSMNP, density of focal birds was compared between the five northern study sites (lesser HWA impact) and the six southern sites (greater HWA impact); one site that fell between the north-south clusters was not included in location comparisons (Figure 1). Site and branch characteristics and focal bird prey guilds were also compared between northern and southern sites to evaluate habitat quality and food availability for birds in the two locations. Treated-untreated site pairing was disregarded in these location comparisons. To further explore effects of defoliation on hemlock-associated birds, relationships between focal bird territory density and hemlock foliage density were examined in all 12 sites.

A Posteriori Data Analysis

To evaluate habitat quality by location, two-sample *t*-tests (two-tailed, $\alpha = 0.05$) were used to test for differences between northern and southern sites for the following site and branch characteristics: elevation, slope, proportion of northern aspect, hemlock cover, hemlock DBH, foliage mass, foliage ratio, and percent dead woody material. GIS cover classes were not statistically tested. To compare bird density between locations, two-sample *t*-tests (two-tailed, $\alpha = 0.05$) were used to test for differences in focal bird density between northern and southern sites. Linear regression ($\alpha = 0.05$) was used to test for relationships between bird density (dependent variable) and the hemlock foliage density metrics branch foliage mass, foliage ratio, and percent dead woody material (independent variables). To compare food availability between locations, two-sample *t*-tests (two-tailed, $\alpha = 0.05$) were used to test for differences in relative abundance of the three focal bird prey guilds between northern and southern sites.

Results

Study Site and Branch Characteristics

There were no significant differences between treated and untreated sites for any site or branch characteristic (Table 1). Sites averaged 7.3 ± 2.9 ha in size and were at mid-elevations in GSMNP ranging from 515 to 1076 m ($\bar{x}$ = 811 ± 166 m). Slope steepness varied from 12 to 56% ($\bar{x}$ = 29 ± 14%) with predominantly north-facing aspects ($\bar{x}$ = 77 ± 23%). GIS forest cover classes were similar between treated and untreated stands with hemlock-cove forest accounting for nearly 40% and mixed-hardwoods forest approximately 50% of the overstory in both treatments (Table 2). Hemlock cover around bird foraging hemlocks ranged from 30 to 80% with a mean of 50 (± 6%). Hemlock diameters of all sampled trees ranged from 7.9 to 122.1 cm and averaged 60.4 (± 19.0 cm). Although the average diameter of hemlocks sampled for arthropods did not vary between treated and untreated sites, hemlock diameters in treated sites tended to be larger than in untreated sites. The average diameter of hemlocks where birds foraged also did not differ from the nearest hemlock where additional arthropods were collected. Sample hemlock branches were similarly foliated between treated and untreated paired sites.

Study sites located in the northern study area of GSMNP had similar site characteristics to sites sampled in the southern area, although the average elevation of northern stands was significantly lower versus southern stands (673 vs. 912 m, p = 0.011) (Tables 1-2). In addition, branches from hemlocks sampled in the north had significantly more foliage mass, higher foliage ratios, and less dead woody material than branches sampled from the south.

Table 1. Site and branch characteristics of hemlock study sites sampled in Great Smoky Mountains National Park.

	Insecticide treatment[a]			Location[b]		
	Treated	Untreated		Northern	Southern	
Characteristic	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*
Site variables						
elevation (m)	777 ± 215	845 ± 107	0.350	673 ± 142	912 ± 107	**0.011**
slope (%)	20 ± 10	39 ± 12	0.062	27 ± 18	30 ± 14	0.728
northern aspect[c]	83 ± 22	71 ± 26	0.434	77 ± 24	81 ± 23	0.788
hemlock cover[d]	53 ± 7	48 ± 4	0.292	51 ± 8	50 ± 5	0.928
DBH[e]	73.4 ± 13.3	47.5 ± 9.8	0.057	62.7 ± 17.9	59.6 ± 22.9	0.813
Branch variables						
foliage mass (g)	32.9 ± 4.8	33.9 ± 7.6	0.780	42.7 ± 7.3	27.1 ± 5.7	**0.003**
foliage ratio[f]	0.24 ± 0.06	0.24 ± 0.07	0.883	0.29 ± 0.05	0.21 ± 0.04	**0.028**
dead woody[g]	20 ± 10	20 ± 10	0.818	12 ± 6	24 ± 6	**0.009**

[a] Six sites per treatment, df = 5

[b] Five northern and six southern sites, df = 9

[c] Area-weighted percent of N-facing slopes out of 2 classes: N and S

[d] Percent hemlock cover (mid- to overstory) at bird foraging locations

[e] Diameter at breast height (cm) of hemlocks sampled for arthropods

[f] Ratio of foliage mass to total branch mass

[g] Percent of non-foliated (dead) twigs on branches

Table 2. GIS-based cover classifications of hemlock study sites sampled in Great Smoky Mountains National Park.

	Insecticide treatment[a]		Location[b]	
GIS cover classifications (%)[c]	Treated	Untreated	Northern	Southern
Mixed hemlock-cove forest	37	39	37	34
Mixed hardwood forest	47	54	63	45
Mixed pine forest	15	5	0	18
Other (field, water, road, human use)	2	2	0	3

[a] Six sites per treatment

[b] Five northern and six southern sites

[c] Area-weighted percents of forest cover classifications in pooled treatments

Focal Bird Density

A total of 81 focal bird territories were mapped over the 12 study sites. Bird density ranged from 2.8 to 7.7 territories per 5 ha ($\bar{x}$ = 4.7 ± 1.5), and there was no difference between insecticide treatments (Figure 2). However, territory density was significantly higher in northern versus southern sites (5.9 vs. 3.8 per 5 ha, $p = 0.015$). Bird territory density also increased significantly as foliage mass increased, and decreased significantly as dead woody material increased on branches ($p = 0.017$ and 0.027, respectively) (Figure 3).

Arthropod Diversity, Food Availability, and Adelgid Infestation

A total of 906 (non-HWA) arthropods were collected and analyzed, 425 in treated sites and 481 in untreated sites. There were no differences between insecticide treatments for total arthropod abundance or density (Table 3). There were no differences between insecticide treatments for abundance, relative abundance, or density of the two focal bird prey guilds arthropods ≥ 3 mm ($n = 571$) and larvae ≥ 3 mm ($n = 217$) (Table 3). There were no differences between northern and southern sites for relative abundance of the two focal bird prey guilds arthropods ≥ 3 mm ($\bar{x}$ = 0.66 ± 0.16, df = 9, $p = 0.109$) and larvae ≥ 3 mm ($\bar{x}$ = 0.23 ± 0.12, df = 9, $p = 0.637$).

A total of 16 taxonomic orders in three classes were identified (Table 4), 15 in treated sites and 15 in untreated sites. Order richness averaged 10 (± 2) per site with no difference between insecticide treatments. The four most common orders collected ($n >$ 100) were Psocoptera, Araneae, Hemiptera, and Lepidoptera. There were no differences between insecticide treatments for abundance, relative abundance, or density of Psocoptera, Araneae, or Hemiptera (Table 5). In contrast, Lepidoptera relative abundance was significantly lower in treated stands versus untreated stands

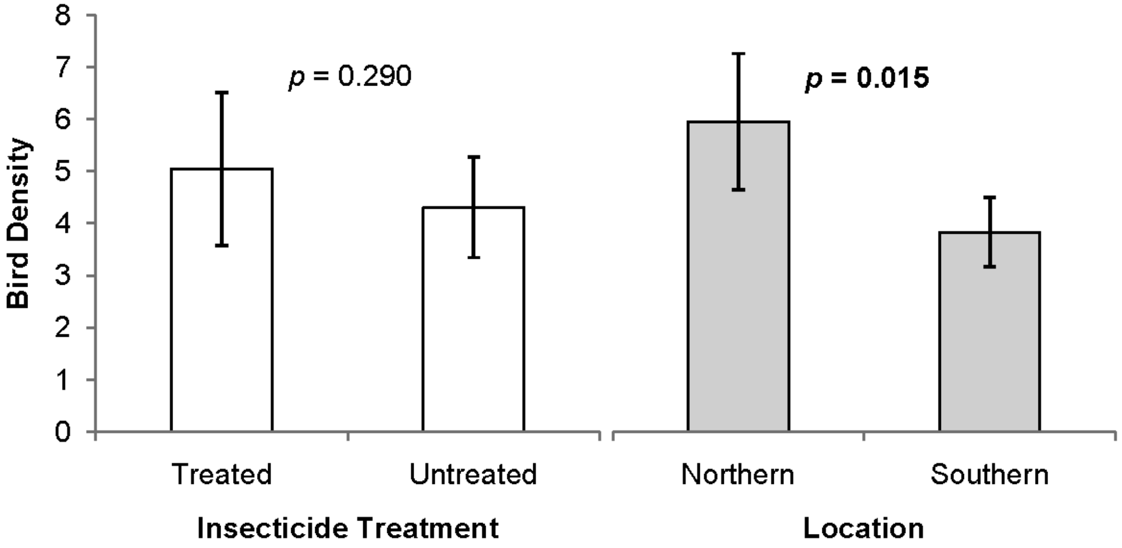

Figure 2. Focal bird density (territories per 5 ha) in hemlock study sites in Great Smoky Mountains National Park. Error bars are 95% confidence intervals.

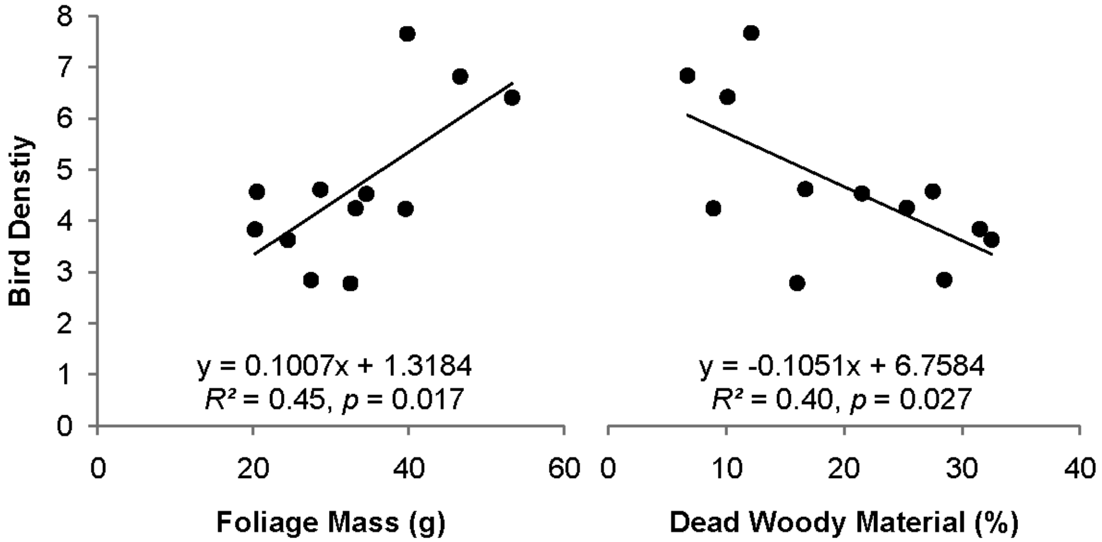

Figure 3. Relationships between focal bird density (territories per 5 ha) and branch foliage mass or percent dead woody material in hemlock study sites in Great Smoky Mountains National Park.

Table 3. Diversity of total arthropods and two focal bird prey guilds in hemlock study sites in Great Smoky Mountains National Park.

	Insecticide treatment[a]		
	Treated	Untreated	
Variable[b]	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*
Total arthropods			
abundance	7.1 ± 3.0	8.0 ± 4.2	0.498
density	24.5 ± 16.8	24.9 ± 13.1	0.936
Arthropods ≥ 3 mm			
abundance	4.8 ± 2.5	4.8 ± 2.6	0.980
relative abundance	0.67 ± 0.15	0.63 ± 0.17	0.410
density	17.1 ± 14.1	15.3 ± 10.3	0.446
Larvae ≥ 3 mm			
abundance	1.7 ± 1.3	2.0 ± 1.6	0.379
relative abundance	0.21 ± 0.13	0.25 ± 0.11	0.462
density	5.6 ± 4.5	5.8 ± 3.5	0.860

[a] Six sites per treatment, df = 5

[b] Abundance = numbers per branch; relative abundance = ratio of guild abundance to total arthropod abundance; density = abundance per 100 g foliage

Table 4. Diversity of arthropod orders found on hemlock branches in Great Smoky Mountains National Park.

Class	Order	Common name	Total
Arachnida	Araneae	Spiders	197
	Opiliones	Harvestmen	22
	Sarcoptiformes	Oribatid mites and allies	6
	Trombidiformes	Velvet mites and allies	48
Diplopoda	Opisthospermophora	Millepedes	2
Insecta	Coleoptera	Beetles	56
	Diptera	Flies, mosquitoes, and allies	52
	Ephemeroptera	Mayflies	2
	Hemiptera	True bugs, hoppers, aphids, and allies	125
	Hymenoptera	Ants, wasps, and allies	13
	Lepidoptera	Butterfiles and moths	121
	Neuroptera	Lacewings and allies	8
	Orthoptera	Grasshoppers and allies	4
	Plecoptera	Stoneflies	10
	Psocoptera	Barklice and allies	232
	Thysanoptera	Thrips	8
Total			906

Table 5. Diversity of the four most common arthropod orders in hemlock study sites in Great Smoky Mountains National Park.

	Insecticide treatment[a]		
	Treated	Untreated	
Variable[b]	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*
Psocoptera			
abundance	1.7 ± 1.4	1.7 ± 1.6	0.382
relative abundance	0.30 ± 0.10	0.21 ± 0.19	0.125
density	7.9 ± 8.1	6.0 ± 6.6	0.278
Araneae			
abundance	1.5 ± 0.9	1.8 ± 1.2	0.258
relative abundance	0.19 ± 0.07	0.22 ± 0.06	0.297
density	5.0 ± 4.3	5.6 ± 3.2	0.585
Hemiptera			
abundance	1.1 ± 0.8	1.0 ± 0.5	0.427
relative abundance	0.16 ± 0.08	0.15 ± 0.12	0.886
density	3.8 ± 2.7	2.8 ± 0.7	0.301
Lepidoptera			
abundance	0.8 ± 0.7	1.3 ± 1.3	0.176
relative abundance	0.09 ± 0.07	0.13 ± 0.06	**0.009**
density	2.7 ± 2.6	3.5 ± 2.5	0.222

[a] Six sites per treatment, df = 5

[b] Abundance = numbers per branch; relative abundance = ratio of order abundance to total arthropod abundance; density = abundance per 100 g foliage

(0.09 vs. 0.13, *p* = 0.009).

NMS ordination of study sites according to arthropod order composition demonstrated no patterns related to insecticide treatments, elevation, hemlock DBH, or hemlock branch foliage mass (dimensions = 2, stress = 9.06) (Figure 4). Treated sites were compositionally similar to their paired untreated site. MRPP showed no differences between insecticide treatments (Sorenson *p* = 0.909, Jaccard *p* = 0.910), and there were no significant indicator orders for insecticide treatments.

Three Hemiptera suborders were identified (Table 6). The two suborders Auchenorrhyncha and Sternorrhyncha comprised the herbivorous insect guild herbivorous Hemiptera (pooled *n* = 60). Relative abundance of herbivorous Hemiptera was significantly lower in treated sites versus untreated sites (0.06 vs. 0.10, *p* = 0.048) (Table 7). Relative abundance of larval Lepidoptera (*n* = 113), both an herbivorous guild and the third focal bird prey guild, was also significantly lower in treated sites versus untreated sites (0.07 vs. 0.13, *p* = 0.004). There was no difference between northern and southern sites for larval Lepidoptera relative abundance ($\bar{x}$ =0.11 ± 0.07, df = 9, *p* = 0.968).

A total of 9566 HWA ovisacs were counted and 653 winged HWA collected. There were no differences between insecticide-treated and untreated sites for abundance or density of HWA ovisacs or winged HWA (Table 8).

Discussion

Focal Bird Density, Food Availability, and Hemlock Foliage Density

Paired treated-untreated study sites were similar in site characteristics and amount of foliage on sampled hemlock branches. Densities of hemlock-associated insectivorous foliage-gleaning birds were also similar in imidacloprid-treated and

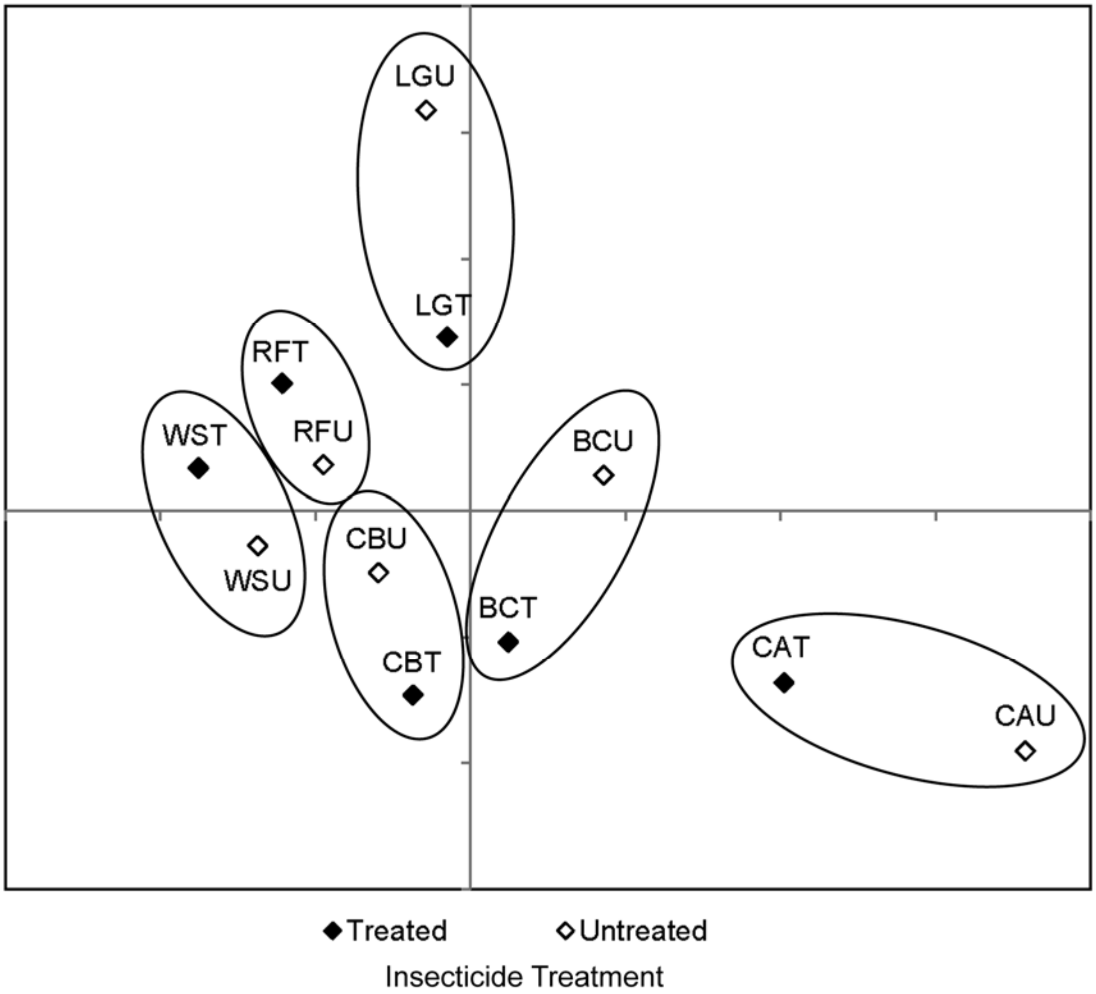

Figure 4. Non-metric multidimensional scaling ordination according to arthropod order composition of hemlock study sites in Great Smoky Mountains National Park. Geographically paired insecticide-treated and untreated sites were compositionally similar (in ellipses).

Table 6. Diversity and feeding guilds of Hemiptera suborders found on hemlock branches in Great Smoky Mountains National Park.

Suborder	Common name	Feeding guild	Total
Auchenorrhyncha	Leafhoppers, treehoppers, and allies	Herbivores	35
Sternorrhyncha	Aphids, scales, and allies	Herbivores	25
Heteroptera	Assassin bugs, coreids, mirids, shield bugs, stink bugs, and allies	Herbivores, predators, other	65
Total			125

Table 7. Diversity of herbivorous insect guilds in hemlock study sites in Great Smoky Mountains National Park. Larval Lepidoptera were also a focal bird prey guild.

	Insecticide treatment[a]		
	Treated	Untreated	
Variable[b]	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*
Herbivorous Hemiptera[c]			
abundance	0.4 ± 0.2	0.7 ± 0.5	0.261
relative abundance	0.06 ± 0.06	0.10 ± 0.08	**0.048**
density	1.4 ± 0.8	1.6 ± 1.2	0.764
Larval Lepidoptera			
abundance	0.7 ± 0.7	1.2 ± 1.3	0.194
relative abundance	0.09 ± 0.07	0.13 ± 0.07	**0.004**
density	2.5 ± 2.4	3.3 ± 2.6	0.181

[a] Six sites per treatment, df = 5

[b] Abundance = numbers per branch; relative abundance = ratio of guild abundance to total arthropod abundance; density = abundance per 100 g foliage

[c] Suborders Auchenorrhyncha and Sternorrhyncha

Table 8. Winged and non-winged hemlock woolly adelgid (HWA) in hemlock study sites in Great Smoky Mountains National Park.

	Insecticide treatment[a]		
	Treated	Untreated	
Variable[b]	$\bar{x}$ ± s.d.	$\bar{x}$ ± s.d.	*p*
HWA ovisacs[c]			
abundance	72 ± 74	87 ± 82	0.520
density	223 ± 197	247 ± 196	0.771
Winged HWA[d]			
abundance	6 ± 3	5 ± 4	0.787
density	17 ± 8	15 ± 7	0.606

[a] Six sites per treatment, df = 5

[b] Abundance = numbers per branch, density = abundance per 100 g foliage

[c] Ovisacs of non-winged HWA counted on branches

[d] Winged form of HWA collected from branches

untreated sites, as were the two arthropod prey guilds for these birds based on size and life stage. However, their favored prey guild, larval Lepidoptera (MacArthur 1958, Robinson and Holmes 1982, Holmes 1990, Jones et al. 2003), showed significant declines in treated hemlocks. These results imply that while a major food source was reduced in hemlocks, overall habitat and resources in paired treated and untreated sites were equivalent for focal birds. All three bird species will also forage in deciduous trees (Hamel 1992) which comprised a large proportion of tree cover in these mixed hemlock stands, and these potential deciduous foliage-dwelling prey resources may have compensated for caterpillar reductions in hemlocks. An insecticide-compromised lepidopteran prey guild in more dense, monotypic hemlock stands might negatively impact territory densities for this specialized guild of birds based on the food value theory of territories (Mariani and Manuwal 1990, Haney 1999, Jones et al. 2003, Barber et al. 2008). In contrast, gypsy moth treatments in mixed-deciduous forests have affected insectivorous foliage-gleaning birds by inducing dietary shifts to proportionately fewer caterpillars (Sample et al. 1993b) and by negatively impacting productivity (Holmes 1998, Nagy and Smith 1997). However, authors noted the insectivores' adaptability to insecticide-caused changes in food resources, and avian hemlock associates using imidacloprid-treated hemlock forests may also shift from favored prey and foraging substrates.

Hemlock-associated focal birds were more abundant in northern sites than in southern sites, suggesting that this specialized guild of birds preferred some resource or combination of resources in the north. While there were no differences in measured food availability in northern versus southern stands, hemlock branches collected from northern sites were significantly more foliated than southern branches, and focal bird densities significantly increased with foliar density. These results suggest that breeding avian hemlock associates prefer healthier hemlock trees within mixed hemlock-deciduous stands in GSMNP. Numbers of breeding hemlock-associated birds have been shown to decline as hemlock health deteriorates in response to HWA in the northeastern US (Tingley et al. 2002). Similarly, Rabenold et al. (1998) documented the decline of breeding Neotropical migrant conifer associates including black-throated green warblers and the blue-headed vireos in GSMNP spruce-fir forests negatively impacted by balsam woolly adelgid (*Adelges piceae* [Ratzeburg]). Avian insectivores associated with closed-canopy forests have also been shown to decline from gypsy moth defoliation; however, this foraging and habitat guild returned over time as deciduous trees re-foliated (Gale et al. 2001). More densely foliated trees may satisfy multiple resource needs in breeding birds including better cover from predators and better nest substrate (Marshall and Cooper 2004). Studies have also shown that structural cues in the habitat, such as foliar density, that relate to overall resource availability and habitat quality may serve to calibrate territory size on the breeding grounds rather than direct assessment by breeding birds of food availability (Smith and Shugart 1987, Marshall and Cooper 2004).

Arthropod Diversity and Adelgid Infestation

Numbers of total arthropods were no different in treated and untreated hemlocks, nor was order richness, with 15 orders in each treatment out of 16 total identified, indicating that imidacloprid did not impact overall arthropod abundance or diversity. Furthermore, ordination of study sites according to arthropod order composition demonstrated that geography of paired sites influenced overall arthropod diversity more than effects of insecticide treatments. The two most abundant orders, Psocoptera and Araneae, do not feed on directly on treated hemlock tissue and were no different in treated and untreated stands. Similarly, in another study non-target predators and scavengers in associated litter communities where systemic imidacloprid was applied showed little negative impact from treatments (Sánchez-Bayo et al. 2007). However, in my study herbivorous insect guilds including caterpillars and herbivorous hemipterans were significantly reduced in treated sites. Native insect herbivores may be displaced by non-native insect congeners and other herbivores with similar resource requirements (Wagner 2008, Kenis et al. 2009), indicating that hemlock insect herbivores may compete for resources with herbivorous HWA in HWA-infested trees. Surprisingly, HWA infestation in my study did not differ between insecticide treatments; therefore, competition with HWA was similar between insecticide treatments for non-target herbivores, implicating imidacloprid as the cause of the declines in herbivorous insect guilds. In contrast to my study, imidacloprid has been found in other studies to reduce overall arthropod abundance in crop systems but to have little impact on richness or on non-target herbivores (Marquini et al. 2002, Sánchez-Bayo et al. 2007). By comparison, gypsy moth chemical control has been found to significantly reduce both diversity and abundance of foliage-dwelling arthropods in treated deciduous forests (Butler et al. 1997a), and caterpillars have been especially vulnerable to various gypsy moth insecticide treatments (Sample et al. 1993b, Sample et al. 1996, Butler et al. 1997b, Marshall et al. 2002). Butler et al. (1997a) observed that over half of the most abundant canopy arthropod families which showed reductions from gypsy moth insecticide treatments were univoltine, and authors suggested this reproductive strategy may delay recolonization compared to taxa with multiple generations produced per year. Marquini et al. (2002) also concluded that impacts of imidacloprid on non-target crop taxa may cause changes in the trophic webs of arthropod assemblages in part because of the timing of recolonization by different taxa. In my study, HWA produces multiple yearly generations and likely recolonized faster than native herbivores after imidacloprid treatments.

Management Implications

While forests may recover from other insect pest infestations such as gypsy moth, lack of eastern hemlock resistance to HWA prohibits natural recovery in hemlock forests of the eastern US (Lovett et al. 2006). Systemic imidacloprid treatments may conserve eastern hemlock habitat and thus sustain habitat for hemlock-associated birds. Black-throated green warblers and blue-headed vireos in this study may serve as useful bioindicators of hemlock habitat quality in the mid-elevations of Southern Appalachians because of their affinity for hemlocks in this region (Kendeigh and Fawver 1981, Wilcove 1988, Shriner 2001) and because their numbers decline in hemlock forests in as hemlock health deteriorates from HWA (Tingley et al. 2002).

Similar HWA infestation levels in treated and untreated hemlocks in my study implies that systemic imidacloprid applications, which should have a prolonged insecticidal effect and a delayed peak in strength (Webb et al. 2003, Sánchez-Bayo et al. 2007), were not at peak efficacy when arthropods were sampled. If herbivores were sampled before peak imidacloprid strength, then herbivore declines at the peak would likely be greater than reported here. If herbivores were sampled after peak imidacloprid strength, then these results suggest that HWA recovers faster than other herbivores. If these imidacloprid treatments were lacking in overall efficacy, then herbivore declines might be greater than measured in my study under more effective treatments. In all three scenarios, repeated treatments over the long term may successively depress non-target herbivores that have not recovered from previous treatments. When using systemic imidacloprid in hemlock forests, monitoring of herbivorous insect guilds is recommended to detect changes in native hemlock canopy arthropod diversity and safeguard avian food resources.

Conclusions

Systemic imidacloprid soil application may be a viable conservation tool to sustain hemlock groves and save this unique ecosystem in the Southern Appalachian region and beyond. However, potential harmful effects of imidacloprid must also be considered when using this control method.

Canopies of imidacloprid-treated hemlock trees had reduced herbivorous canopy arthropods including larval Lepidoptera, which are an important food resource for many bird species. However, densities of hemlock-associated insectivorous birds were similar between the treated and untreated sites, suggesting that birds may find adequate resources despite food reductions in these mixed hemlock-deciduous stands. Hemlock associates were denser in stands with healthier hemlocks in GSMNP, regardless of insecticide treatment.

In this study, despite indications that arthropods were not sampled at peak imidacloprid efficacy, herbivorous insects declined from imidacloprid treatments. In the short term imidacloprid treatments may benefit hemlock-associated birds by maintaining vigorous hemlocks. However, in the long term with repeated application, systemic imidacloprid may cause compounding declines in herbivorous insects such as larval Lepidoptera. Therefore, continued research is warranted on the effects of imidacloprid on herbivorous canopy arthropods over the full systemic imidacloprid treatment cycle and through multiple treatments. Research is also warranted on the direct effects of HWA on hemlock canopy arthropod diversity over full gradients of HWA infestation and HWA-induced hemlock defoliation. Coupling canopy arthropod sampling with bird foraging rates and tree species selection during foraging in treated versus untreated stands would yield both direct and indirect measures of hemlock-associated avian insectivore food availability. Impacts on the productivity of hemlock-associated insectivorous birds, such as time spent away from nests during the feeding of young, proportion of caterpillars brought to nestlings, and number and vigor of nestlings produced, should also be examined in imidacloprid-treated hemlock stands.

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APPENDIX A: STUDY SITE LOCATIONS

Table A1. Locations of hemlock study sites in Great Smoky Mountains National Park. Coordinates are in Universal Transverse Mercator (UTM) coordinate system, North American Datum of 1983.

			UTM zone 17 N	
Site pair[a]	Treatment	Site landmark	m North	m South
BC	Treated	Big Creek Trail	308471	3957637
	Untreated	Little Cataloochee Trail	310984	3950019
CA	Treated	East of Cataloochee Valley	313986	3946228
	Untreated	Road to Cataloochee Valley	313021	3945662
CB	Treated	Chestnut Branch Trail	309446	3959238
	Untreated	Chestnut Branch Trail	308251	3959287
LG	Treated	Low Gap Trail	300946	3958543
	Untreated	Snake Den Ridge Trail	299496	3957963
RF	Treated	Rough Fork Trail	307111	3941939
	Untreated	Mossy Branch	309114	3945195
WS	Treated	Cataloochee Creek	312014	3946162
	Untreated	Winding Stair Branch	312256	3946522

[a] Insecticide treated-untreated pairs of study sites