

Effects of Hemlock Woolly Adelgid on Breeding Birds at Fort Indiantown Gap, Pennsylvania

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Abstract - To determine how *Tsuga canadensis* (eastern hemlock) decline caused by *Adelges tsugae* (hemlock woolly adelgid) affects bird communities in Pennsylvania, we surveyed breeding birds in hemlock and forested non-hemlock habitats in 2003 and 2004 at Fort Indiantown Gap, PA and monitored nesting *Empidonax virescens* (Acadian Flycatcher), a hemlock specialist in Pennsylvania. Of the nine species more abundant in hemlocks than other forested habitats, only two, the Acadian Flycatcher and *Dendroica virens* (Black-throated Green Warbler), were positively associated with living hemlocks. *Contopus virens* (Eastern Wood-pewee), *Myiarchus crinitus* (Great-crested Flycatcher), and *Hylocichla mustelina* (Wood Thrush) were negatively associated with the amount of living hemlocks and were apparently benefiting from the increased number of dead trees and canopy gaps associated with the adelgid infestation. Acadian Flycatcher nest sites had more living hemlocks and were less impacted by adelgid than random sites. Nest success did not differ by habitat variables. Initially, hemlock decline will negatively impact hemlock specialists while providing habitat for opportunistic species. Some specialist species might persist by shifting habitats, but long-term studies are needed.

Introduction

Exotic pests and pathogens can have major impacts on forested ecosystems and the wildlife communities they support as evidenced by the loss of *Castanea dentata* (Marshall) Borkh. (American chestnut) to *Cryphonectria parasitica* (chestnut blight) and *Ulmus americana* L. (American elm) to *Ophiostoma ulmi* (Dutch elm disease) (Ickes 1992). The current invasion by *Adelges tsugae* Annand (hemlock woolly adelgid [HWA]) threatens the health and survival of *Tsuga canadensis* (L.) Carr. (eastern hemlock) in the eastern United States. The aphid-like adelgid was introduced near Richmond Virginia from Japan in the early 1950s (Miller 1988) and has spread to 16 states (Cheah et al. 2004). HWA was first observed in southeastern Pennsylvania in 1967 and had infested 44 counties by 2005 (Pennsylvania Department of Conservation and Natural Resources 2006). Due to its rapid reproductive rate (McClure 1989) and effective dispersal ability (McClure 1990), HWA continues to spread unimpeded northward and westward, approximately 8 km per year across Pennsylvania and the eastern United States (Evans and Gregoire 2006).

Upon infestation, HWA feed on the parenchyma cells of the hemlock's xylem (Young et al. 1995), causing desiccation and often mortality within

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four years (McClure 1991). The severity of damage, however, can vary from stand to stand (Orwig and Foster 1998). The eastern hemlock has no natural resistance (McClure 1995), and HWA can attack and kill all sizes and age classes (Orwig 2002).

The eastern hemlock fills a unique ecological role within eastern forests due to its dense coniferous structure, extreme shade tolerance, and longevity, and provides important habitat for a variety of animals, particularly birds (Mitchell 1999, Tingley et al. 2002). Over the long-term, HWA-induced hemlock mortality may adversely impact these species by increasing forest homogeneity as hemlock or mixed-hemlock forests shift to common hardwood forest types (Jenkins et al. 2000, Orwig et al. 2002). Compared to pure stands, floristic differences between conifers and hardwoods in mixed forests lead to higher avian diversity (Gates and Giffen 1991). Structurally, hemlocks also differ from other conifers due to the retention of their lower branches. By retaining those branches, foliage is available at a greater range of heights, providing more feeding and nesting sites (Haapanen 1965) and allowing greater vertical specialization by species, both of which lead to higher avian diversity (Martin 1988).

While a great deal of research has been conducted on the biology of the HWA and its impact on the forest plant community (e.g., McClure 1987, McClure et al. 2001, Orwig and Kizlinski 2002), very few studies have analyzed how this decline impacts the avian community (Ross et al. 2004, Tingley et al. 2002). As part of a larger bird inventory, we studied avian response to the impacts of HWA starting 3 years post-infestation in hemlock habitats in eastern Pennsylvania. Our objectives were to: (1) compare species abundances in hemlock versus hardwood stands; (2) identify specific habitat variables associated with bird species more abundant within hemlock stands; and (3) test whether nest success of the *Empidonax vireescens* Vieillot (Acadian Flycatcher), a species that commonly nests in hemlocks in central and northern Pennsylvania (McWilliams and Brauning 2000), was influenced by hemlock decline.

Materials and Methods

Study area

We conducted this study during the summers of 2003 and 2004 on the 6942-ha Fort Indiantown Gap National Guard Training Center (FIG), Fort Indiantown Gap, PA, and on the riparian hemlock habitats along Rausch and Stony Creeks within the adjacent State Game Lands (SGL) 211. Both sites are located about 40 km northeast of Harrisburg in the Ridge and Valley region of the state. As part of a forestry inventory completed during our research at FIG, McQuaide et al. (2003) established 2320 sampling points as a grid across forested habitats at FIG, of which 32% contained hemlock. On average, stands with hemlocks contained 69.2 small hemlocks per ha (<8 cm DBH; range = 3.2-423.0), 40.2 medium hemlocks per ha (8–23 cm DBH; range = 1.2-204.1), 11.8 large hemlocks per ha (23–38 cm DBH; range = 0.7-68.0), and 5.8 extra large hemlocks per ha (>38 cm DBH; range = 0.3-34.1; McQuaide et

al., 2003). Because trees sorted by DBH were only broken down into species at the stand level and not at the individual point, we used this inventory data primarily for descriptive purposes and not in our point-level statistical analysis. HWA initially infested FIG during 2000, 3 years prior to this study and has impacted hemlock stands to varying degrees.

Point counts

We randomly chose 237 bird survey points from the preexisting forest inventory point grid based on two criteria. Initially, we limited selection to only those points located between 50 m and 250 m from roads, 82% of the total area, to maximize area covered while minimizing travel time between points. Then, in 2004, we added additional points in hemlock stands outside this buffer. Second, all survey points were separated by at least 250 m. Overall, we sampled 237 forested points (135 in 2003, 102 in 2004) as part of the larger bird inventory of FIG (Becker 2005). We then classified the 237 forested point counts into 71 points without hemlocks, 115 points with at least one hemlock, and 137 points at which $\geq 10\%$ of trees within 50 m were hemlock. In 2004, we re-sampled all points surveyed in 2003 in which $\geq 10\%$ of the trees within 50 m were hemlocks ($n = 57$). For these points surveyed in more than 1 year, we randomly selected a single year's data to include in analyses resulting in 80 points in which $\geq 10\%$ of the trees within 50 m were hemlock.

During May and June in 2003 and 2004, two observers conducted point counts (Hutto et al. 1986) between 0600 and 1000, initiating counts 2 minutes after arrival at the point to allow time for the birds to acclimate to the observer. We did not conduct counts on days with rain or strong wind. We recorded all individuals heard or observed within a 50-m radius within a 10-minute time span. We surveyed each point twice, once per observer, with at least 3 weeks between replicates. We used the maximum number recorded from the two replicates for each point and species in our analyses.

Nest searching and monitoring

We searched for Acadian Flycatcher nests on all detected territories. Each hemlock stand was searched at least twice weekly. Upon discovery of a nest, the observer determined the nest stage and contents using a mirror attached to an extendable pole, marked the general location using flagging, and recorded the exact location with a GPS unit. Nests were re-checked every 36 days until completion, with the exception of a one-week period in 2003 in which the base was not accessible due to military maneuvers. Females were not flushed to check nests except to check initial contents and to verify hatching success.

Vegetation

Initially, we had planned to use the DBH results from the forest inventory (McQuaide et al. 2003), but this was not possible because the DBH results by tree species were only available at the stand level. Instead, we measured six habitat variables at each hemlock survey point and at all nest sites (Table 1). Within 50 m of the point or nest, we estimated the percentage of trees that

were hemlock (% TREES_HEM), the percentage of these hemlocks that were living (% HEM_LIVING), the percentage of hemlocks reaching the overstory (% MATURE), and the presence/absence of water or a wetland (WATER). We also measured the average percentage of terminal buds with HWA present (AVG_HWA) and the average percentage of terminal buds with new growth (AVG_NG) by sampling a random branch from five hemlocks at each location, one near the point or nest and one 50 m away in each of the four cardinal directions. Branches were selected at eye level or slightly higher if an eye-level branch was not available. On each branch, we counted the terminal buds, terminal buds with HWA, and terminal buds with new growth, determined the percentage of the buds with adelgid or new growth, and then averaged the results over the five trees for each location. If five trees were not present within a location, then measurements were taken from the maximum number of hemlocks available within 50 m.

In addition to measuring average percentage of terminal buds with HWA, the overall impact of HWA at each location was classified as “none,” “low,” “moderate,” “high,” or “dead” within 50 m of the point or nest. “None” referred to stands that showed no mortality or die-back from HWA. “Low” stands had only scattered needle loss and limb die-off. “Moderate” stands had significant limb die-off, but <50% of the trees were affected. “High” impact stands contained limb die-off affecting $\geq 50\%$ of the trees, with needles only remaining in the crowns of most trees. “Dead” stands had complete hemlock mortality.

Analyses

To describe the bird community associated with hemlock habitats, we calculated the mean relative abundance for all birds recorded at points with $\geq 10\%$ hemlock. For birds with at least 5 detections within these habitats, we used a Mann-Whitney test with a 95% confidence interval and $\alpha = 0.05$

Table 1. Hemlock habitat variables measured at point counts with hemlocks (n = 115) and at Acadian Flycatcher nest sites (n = 74) at Fort Indiantown Gap, 2003–2004.

Variable ^A	Point count		Nest site		t ^B	p
	Mean \pm SE	Min–max	Mean \pm SE	Min–max		
% TREES_HEM	24 \pm 2	1–90	40 \pm 3	0–85	4.66	<0.001
% HEM_LIVING	65 \pm 4	0–100	93 \pm 2	0–100	9.06	<0.001
% MATURE	66 \pm 3	1–100	66 \pm 2	0–100	0.13	0.9
AVG_HWA	20 \pm 2	0–81	8 \pm 1	0–53	6.41	<0.001
AVG_NG	15 \pm 2	0–76	10 \pm 1	0–47	2.12	0.036
WATER	37%		88%			

^A% TREES_HEM: Percentage of trees within 50 m that were hemlock.

% HEM_LIVING: Percentage of hemlocks within 50 m that were living.

% MATURE: Percentage of hemlocks within 50 m that were in the overstory.

AVG_HWA: Average percentage of terminal buds per branch with hemlock woolly adelgid.

AVG_NG: Average percentage of terminal buds per branch with new growth.

WATER: Percentage of points or nests with a stream or wetland within 50 m, min-max not included because the variable was presence/absence.

^BOne-sided two-sample t-test.

to determine whether a species was significantly more abundant within hemlock habitats than forested non-hemlock habitats. For all species determined to be more abundant in hemlock habitats (hereafter, hemlock associates), we further used logistic regression analyses to determine which habitat variables significantly predicted each species occurrence. These analyses were used to determine whether each hemlock associate was more abundant in hemlock habitats because it was attracted to healthy hemlock stands or because of changes in forest structure due to hemlock decline.

Prior to running the logistic regression analyses, we calculated Pearson correlation coefficients for all hemlock variables (Table 2). Many of the variables were significantly correlated. For example, % TREES_HEM was positively correlated with water and the percentage of hemlocks that were mature, and negatively correlated with AVG_HWA. After reviewing the correlation analyses, for correlated pairs ($p \leq 0.05$), we selected the most biologically significant variables resulting in two non-correlated variables (% TREES_HEM and % HEM_LIVING) for our analysis. Although AVG_NG was not correlated with other variables, we did not include it because results were not available for 23 points due to our inability to reach branches. We employed backward selection using an alpha level of 0.15 to exit the model and tested model fit using a Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989).

In order to determine whether Acadian Flycatchers preferentially selected sites with higher densities of hemlocks, lower HWA impact, or higher densities of mature hemlocks, we compared these hemlock variables at nest sites versus the randomly positioned survey points. Because Acadian Flycatchers nest near streams (Bushman and Therres 1988), and hemlocks tend to be healthier near streams (Mayer et al. 2002), we compared the same variables between Acadian Flycatcher nests and the subset of points associated with water. We also compared the proportion of stands by HWA impact (none, low, moderate, high, dead) at all hemlock points, hemlock points with water, and nest sites.

We calculated Acadian Flycatcher nest success using the Mayfield method (Mayfield 1961, 1975). We classified a nest as successful if at least one young fledged. If a nest failed between checks, the median day was used

Table 2. Pearson correlation coefficients of hemlock habitat variables[^] at Fort Indiantown Gap, 2003–2004.

	%TREES_ HEM	%HEM_ LIVING	%MATURE	AVG_HWA	AVG_ NG
%HEM_LIVING	0.045				
%MATURE	0.32**	-0.42**			
AVG_HWA	-0.045	-0.25*	-0.03		
AVG_NG	0.13	-0.12	0.2	-0.15	
WATER	0.32**	0.36**	0.04	-0.32**	-0.03

[^]See Table 1 for variable descriptions.

* $P < 0.05$.

** $P < 0.001$.

in calculating exposure (Mayfield 1961). We calculated Mayfield estimates for all nests combined, but also calculated success based on the following nest-habitat variables to evaluate factors that may affect nest success: HWA impact (none, low, moderate, high/dead), nest substrate (hemlock, non-hemlock), percentage of trees within 50 m that were hemlock (0–25%, 26–50%, >50%), and hemlock maturity (0–50%, 51–75%, 76–100%). We used the program CONTRAST (Hines and Sauer 1989) to test for differences among these groups. This program tests whether nest success is equal among groups using an asymptotically chi-square quadratic form suggested by Sauer and Williams (1989). The null hypothesis, that nest success in all groups are equal, was rejected if $p \leq 0.05$.

Results

Hemlock health

HWA was present in most stands. Adelgid was present at >98% of sampled points with the average sampled branch having HWA on 20% of terminal buds (Table 1). On average, 65% of hemlocks were living. The variables % HEM_LIVING, % MATURE, WATER, and AVG HWA were correlated; Hemlock were healthier near water, where there were also fewer adelgids (Table 2). Mature hemlocks were negatively correlated with the percentage of hemlocks that were living, but not with the percent of terminal buds with adelgids.

Bird community

During point counts, we detected 63 species of which 48 were found in stands with hemlock comprising $\geq 10\%$ of total trees (Table 3). Of these 48 species, we identified 9 species with greater abundance in hemlock than non-hemlock habitats (Table 4). Probability of occurrence of the Acadian Flycatcher was positively related to both the % TREES_HEM and % HEM_LIVING (Table 5). Probabilities of occurrence of the Eastern Wood-Pewee, Great-crested Flycatcher, and Wood Thrush were all negatively related to % HEM_LIVING, while Black-throated Green Warbler occurrence was negatively related to % TREES_HEM. Probability of occurrence of Louisiana Waterthrush was not related to any variables; however, all detections occurred at points adjacent to water. Finally, Downy Woodpecker, Hairy Woodpecker, and Scarlet Tanager occurrence was not significantly related to any of the hemlock variables (Table 5).

Acadian Flycatcher nest success

We located and monitored 74 Acadian Flycatcher nests, 26 in 2003 and 48 in 2004. Eighty-four percent of the nests were in hemlock, 11% were in *Hamamelis virginiana* L. (witch hazel), and the remaining 5% were in *Nyssa sylvatica* Marshall (black gum), *Carya* spp. (hickory), and *Betula lenta* L. (black birch). Compared to the randomly placed survey points in hemlock habitats, nest sites had significantly greater % TREES_HEM ($t = 4.66$, $P = <0.001$), greater % HEM_LIVING ($t = 9.06$, $P = <0.001$), lower AVG_NG

($t = 2.12$, $P = 0.036$), and lower AVG_HWA ($t = 6.41$, $P = <0.001$) (Table 1). Also, based on the impact of HWA on the stand, Acadian Flycatchers nested

Table 3. Relative abundance of bird species at points with $\geq 10\%$ hemlocks ($n = 80$) at Fort Indiantown Gap, 2003–2004.

Species	Mean birds/10 ha \pm SE
Sharp-shinned Hawk (<i>Accipiter striatus</i> Vieillot)	0.16 \pm 0.16
Mourning Dove (<i>Zenaida macroura</i> Linnaeus)	0.16 \pm 0.16
Yellow-billed Cuckoo (<i>Coccyzus americanus</i> Linnaeus)	0.48 \pm 0.27
Ruby-throated Hummingbird (<i>Archilochus colubris</i> Linnaeus)	0.16 \pm 0.16
Red-bellied Woodpecker (<i>Melanerpes carolinus</i> Linnaeus)	0.80 \pm 0.41
Downy Woodpecker (<i>Picoides pubescens</i> Linnaeus)	1.43 \pm 0.45
Hairy Woodpecker (<i>P. villosus</i> Linnaeus)	2.23 \pm 0.59
Pileated Woodpecker (<i>Dryocopus pileatus</i> Linnaeus)	1.27 \pm 0.49
Acadian Flycatcher (<i>Empidonax vireescens</i> Vieillot)	5.73 \pm 1.01
Eastern Wood-pewee (<i>Contopus virens</i> Linnaeus)	3.98 \pm 0.77
Great-crested Flycatcher (<i>Myiarchus crinitus</i> Linnaeus)	2.23 \pm 0.63
Eastern Kingbird (<i>Tyrannus tyrannus</i> Linnaeus)	0.32 \pm 0.32
Blue-headed Vireo (<i>Vireo solitarius</i> Wilson)	1.59 \pm 0.53
Red-eyed Vireo (<i>Vireo olivaceus</i> Linnaeus)	15.61 \pm 0.91
Blue Jay (<i>Cyanocitta cristata</i> Linnaeus)	0.96 \pm 0.44
American Crow (<i>Corvus brachyrhynchos</i> Brehm)	0.16 \pm 0.16
Black-capped Chickadee (<i>Poecile atricapilla</i> Linnaeus)	1.27 \pm 0.62
Tufted Titmouse (<i>Baeolophus bicolor</i> Linnaeus)	0.80 \pm 0.41
White-breasted Nuthatch (<i>Sitta carolinensis</i> Latham)	0.80 \pm 0.41
Carolina Wren (<i>Thryothorus ludovicianus</i> Latham)	0.32 \pm 0.22
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i> Linnaeus)	0.80 \pm 0.35
Veery (<i>Catharus fuscescens</i> Stephens)	0.48 \pm 0.27
Wood Thrush (<i>Hylocichla mustelina</i> Gmelin)	3.50 \pm 0.75
American Robin (<i>Turdus migratorius</i> Linnaeus)	0.32 \pm 0.22
Gray Catbird (<i>Dumetella carolinensis</i> Linnaeus)	0.80 \pm 0.52
Cedar Waxwing (<i>Bombicilla cedrorum</i> Vieillot)	1.59 \pm 0.53
Northern Parula (<i>Parula americana</i> Linnaeus)	0.16 \pm 0.16
Yellow Warbler (<i>Dendroica petechia</i> Linnaeus)	0.16 \pm 0.16
Black-throated Blue Warbler (<i>D. caerulescens</i> Gmelin)	0.16 \pm 0.16
Black-throated Green Warbler (<i>D. virens</i> Gmelin)	2.71 \pm 0.63
Blackburnian Warbler (<i>D. fusca</i> Muller)	0.16 \pm 0.16
Pine Warbler (<i>D. pinus</i> Wilson)	0.48 \pm 0.27
Prairie Warbler (<i>D. discolor</i> Vieillot)	0.16 \pm 0.16
Black-and-white Warbler (<i>Mniotilta varia</i> Linnaeus)	2.39 \pm 0.60
Worm-eating Warbler (<i>Helmitheros vermivora</i> Gmelin)	0.32 \pm 0.22
Ovenbird (<i>Seiurus aurocapilla</i> Linnaeus)	15.76 \pm 1.14
Louisiana Waterthrush (<i>Seiurus motacilla</i> Vieillot)	0.96 \pm 0.38
Common Yellowthroat (<i>Geothlypis trichas</i> Linnaeus)	0.96 \pm 0.38
Hooded Warbler (<i>Wilsonia citrine</i> Boddaert)	1.91 \pm 0.60
Scarlet Tanager (<i>Piranga olivacea</i> Gmelin)	6.21 \pm 0.85
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i> Linnaeus)	0.48 \pm 0.35
Indigo Bunting (<i>Passerina cyanea</i> Linnaeus)	1.43 \pm 0.51
Northern Cardinal (<i>Cardinalis cardinalis</i> Linnaeus)	0.16 \pm 0.16
Eastern Towhee (<i>Pipilo erythrophthalmus</i> Linnaeus)	0.16 \pm 0.16
Chipping Sparrow (<i>Spizella passerina</i> Bechstein)	0.32 \pm 0.22
Baltimore Oriole (<i>Icterus galbula</i> Linnaeus)	0.32 \pm 0.22
Brown-headed Cowbird (<i>Molothrus ater</i> Boddaert)	0.80 \pm 0.35
American Goldfinch (<i>Carduelis tristis</i> Linnaeus)	0.32 \pm 0.32

in stands with no impact more often than expected, and “moderate” and “high/dead” stands less often than expected compared to the randomly placed survey points in all hemlock habitats ($\chi^2 = 54.586$, $df = 3$, $P = <0.001$), and compared to the subset of survey points in hemlock habitats associated with water ($\chi^2 = 12.908$, $df = 3$, $P = 0.005$) (Table 6).

Overall, 52% of nests with known fate ($n = 73$) were successful. Nest success was 0.43 ± 0.06 , with most nest failures due to predation. Nest success did not differ between stands with different levels of HWA impact ($\chi^2 = 0.56$, $df = 2$, $P = 0.76$), with varying percents of hemlock ($\chi^2 = 2.529$, $df = 2$, $P = 0.282$), with varying degrees of maturity ($\chi^2 = 0.807$, $df = 2$, $P = 0.668$), or with different nesting substrates (success in non-hemlock substrates: 0.56 ± 0.16 , $n = 12$; success in hemlock: 0.42 ± 0.07 , $n = 61$; $\chi^2 = 0.607$, $df = 1$, $P = 0.436$).

Table 4. Relative abundance of bird species more abundant in hemlocks at Fort Indiantown Gap, 2003–2004.

Species	Mean birds/10 ha \pm SE (n)		W ^B	P
	Hemlock (80) ^A	Non-Hemlock (71)		
Downy Woodpecker	1.43 \pm 0.45	0.36 \pm 0.25	5157	0.024
Hairy Woodpecker	2.23 \pm 0.59	0.89 \pm 0.39	5132	0.041
Acadian Flycatcher	5.73 \pm 1.01	0.00 \pm 0.00	4500	<0.001
Eastern Wood-pewee	3.98 \pm 0.77	1.80 \pm 0.54	5000	0.019
Great-crested Flycatcher	2.23 \pm 0.63	0.71 \pm 0.43	5093	0.015
Wood Thrush	3.50 \pm 0.75	1.62 \pm 0.51	5068	0.035
Black-throated Green Warbler	2.71 \pm 0.63	0.18 \pm 0.18	4868	<0.001
Louisiana Waterthrush	0.96 \pm 0.38	0.18 \pm 0.18	5223	0.039
Scarlet Tanager	6.21 \pm 0.85	3.94 \pm 0.75	4969	0.030

^APoints at which $\geq 10\%$ of trees were hemlocks.

^BMann-Whitney Test.

Table 5. Logistic regression results showing factors influencing probability of occurrence for selected species^A within hemlock habitats ($n = 80$) at Fort Indiantown Gap, 2003–2004.

Species	%Trees_Hem ^B			%Hem_Living ^C		
	coef (SE)	Odds ratio	P ^D	coef (SE)	Odds ratio	P
Downy Woodpecker	-0.02 (0.02)	0.98	NS	-0.01 (0.01)	0.99	NS
Hairy Woodpecker	-0.03 (0.02)	0.97	NS	-0.004 (0.01)	0.99	NS
Acadian Flycatcher	0.04 (0.01)	1.04	0.005	0.04 (0.01)	1.04	0.004
Eastern Wood-pewee	0.01 (0.01)	1.01	NS	-0.03 (0.01)	0.97	<0.001
Great-crested Flycatcher	0.01 (0.01)	1.01	NS	-0.02 (0.01)	0.98	0.01
Wood Thrush	0.01 (0.02)	1.01	NS	0.02 (0.01)	0.98	0.005
Black-throated Green Warbler	-0.03 (0.02)	0.96	0.05	0.02 (0.01)	1.02	NS
Louisiana Waterthrush	0.02 (0.07)	1.00	NS	0.03 (0.03)	1.03	NS
Scarlet Tanager	-0.01 (0.01)	0.99	NS	-0.01 (0.01)	0.99	NS

^AAll species were significantly more abundant in hemlock than non-hemlock habitats (see Table 4).

^BTrees_Hem percentage of trees within 50 m that were hemlock.

^CHem_Living percentage of hemlocks within 50 m that were living.

^DNS = Not significant, $P > 0.05$.

Discussion

Three years post infestation, HWA had spread to almost all stands on FIG, but 65% of hemlocks were still living. Thus, there was typically a mix of living and dead hemlocks within stands, with healthier stands located near streams. Many of the dead hemlocks were larger mature trees, which may have simply resulted from older trees taking longer to decay and fall than smaller trees, as there was no correlation between maturity and number of adelgids. We identified nine bird species with greater abundance in hemlock stands. This group included species that were associated with living hemlocks and would be considered true hemlock associates and others that instead likely benefited from the effects of HWA infestation because of the increased number of dead trees and/or canopy gaps within the forest.

The Acadian Flycatcher was a true riparian hemlock associate in this region and has been similarly linked to living hemlocks in other studies (Mitchell 1999, Ross et al. 2004, Tingley et al. 2002). Acadian Flycatchers often breed in habitats associated with streams and prefer closed canopies with relatively little understory (Bushman and Therres 1988), characteristics typical of hemlock stands less impacted by HWA on our site. Compared to randomly placed hemlock survey points, nest sites were found in habitats with a greater percentage of living hemlocks, hemlocks less impacted by HWA, and lower percentage of terminal buds with HWA. Acadian Flycatchers forage in openings in the mid-canopy and may prefer less impacted hemlock stands because canopy openings created by hemlock decline eventually lead to the loss of these mid-canopy openings as understory vegetation increases (Gates and Giffin 1991). This pattern may also partially result from the flycatcher's tendency to nest near streams, as hemlocks tended to be less impacted by HWA near water. However, this pattern held up even when we compared nest sites to random hemlock sites near water, suggesting that Acadian Flycatchers truly prefer less impacted stands.

Table 6. Habitat availability by hemlock woolly adelgid (HWA) impact^A at hemlock point count locations (n = 80), hemlock point count locations near water (n = 42), and Acadian Flycatcher nest sites (n = 73^B) as determined by the degree to which the stand has been impacted by HWA at Fort Indiantown Gap, 2003–2004.

HWA_impact ^A	All hemlock_points(%)	Points with_water (%)	Nest sites (%)
None	24.3	52.4	69.9
Low	18.3	16.7	19.2
Moderate	24.3	23.8	6.8
High	20.9	7.1	2.7
Dead	12.2	0	1.4

^ANone: stands showed no negative impact from HWA; Low: stands had only scattered needle loss and limb die-off; Moderate: stands had significant die-off but <50% of the trees were affected; High: stands contained limb die-off affecting ≥50% of the trees, with needles only remaining in the crowns of most of trees; Dead: stands had complete hemlock mortality.

^BOne nest was excluded because it was not within 50 m of any hemlock.

Most of the Acadian Flycatcher nests were built in hemlocks in agreement with other studies that have found Acadian Flycatchers favor hemlock for nesting (Ross et al. 2004, Sheehan 2003). Both Sheehan (2003) and Benzinger (1994) suggested that nesting in hemlocks could reduce predator effectiveness due to the abundance of potential nesting sites. Further, hemlock branches in the understory catch debris, creating structures similar in appearance to flycatcher nests, further increasing predator search times. These benefits would be associated with living trees only. We did not find a difference in nest success among stands with different levels of HWA impact. However, our determination of significant differences was hindered by the difficulty in finding a large-enough sample of nests in stands highly impacted by HWA. The majority of flycatcher nests were in stands with low or no HWA impact.

While the Acadian Flycatcher preferred hemlock habitats in this study, this preference is not the case throughout its breeding range. In the southern portion of its range, this species prefers swampy woodlands, especially *Taxodium distichum* L.C. Rich. (bald cypress), shifting to mature deciduous and western mesophytic forest near the center of its distribution (Whitehead and Taylor 2002). In stands with considerable hemlock decline, we found flycatchers using non-hemlock nesting substrates, especially witch hazel. One nest was built in deciduous habitat with no hemlocks within 50 m. In addition, we found no difference in success rates between nests in hemlocks and hardwoods. This ability to shift to other nesting substrates suggests that Acadian Flycatchers might persist at FIG following hemlock loss by shifting to other habitats, similar to how Baltimore Orioles shifted to sycamores and willows following elm decline (Ickes 1992). It is unknown, however, whether flycatcher densities would remain the same in the absence of hemlock.

The Black-throated Green Warbler was more abundant in stands with some hemlock than in hardwood stands with no hemlock. This species prefers mixed hardwood/hemlock forests with high volumes of mid-level foraging substrates (Benzinger 1994). These foraging substrates decline in stands dominated only by overstory hemlocks. In our study, Black-throated Green Warbler abundance within hemlock stands was negatively related to the abundance of hemlocks, highlighting this species preference for mixed stands. While Black-throated Green Warblers will also occupy deciduous habitats (Collins 1983), reduced abundances have been associated with hemlock decline in other studies (Tingley et al. 2002).

The Louisiana Waterthrush was detected only near water. This species is not an exclusive hemlock specialist, but rather prefers high-quality headwater streams surrounded by mature forests (McCracken 1991, Prosser and Brooks 1998). At FIG, mature hemlocks dominated streamside habitats. Due to water availability, riparian hemlocks are better able to delay the effects of HWA infestation (Mayer et al. 2002) and were able to remain healthier on FIG. Deterioration of waterthrush breeding habitat is possible as riparian hemlocks eventually succumb to infestation, resulting in reduced stream

quality and the loss of mature trees until colonizing hardwood species eventually mature (Evans 2002, Yorks 2002).

Unfortunately, this study was initiated three years after the initial HWA infestation, making it impossible to compare current findings with the pre-infestation bird community. Without baseline data, we could not determine whether the rarity or absence of other expected hemlock associates (e.g., Blackburnian Warbler, *Sitta canadensis* Linnaeus [Red-breasted Nuthatch], *Certhia americana* Bonaparte [Brown Creeper], *Troglodytes troglodytes* Linnaeus [Winter Wren], and *Dendroica magnolia* Wilson [Magnolia Warbler]) were the result of hemlock decline or were due to a natural absence of these species from our site. We do know, however, that Winter Wrens have been recorded as breeding on FIG in recent years. Further, we detected at least one breeding Magnolia Warbler and numerous territorial Blackburnian Warblers in large tracts of hemlock in the adjacent SGL during this study. A concern is that the eventual decline or complete loss of hemlock from eastern forests will likely cause declines in populations of some hemlock-associated bird species and, possibly, local extinctions and range contractions.

Although hemlock decline has apparently had a negative impact on some species, other species appear to have benefited. In its initial stages, hemlock decline creates forest gaps that increase avian species diversity due to an influx of early successional species, aerial foragers, or cavity nesters (Canterbury and Blockstein 1997). In our study, Great-crested Flycatcher, Eastern Wood-pewee, and Wood Thrush were more abundant in hemlock stands where die-off had occurred. Hemlock mortality may have benefited the two flycatchers by creating high-quality foraging habitat. Both of these species capture prey by sallying from exposed perches in the upper canopy and would benefit from increased snag availability and gaps in the upper canopy created by hemlock deaths. Wood Thrush likely benefited from the denser understory structure that often follows initial hemlock decline, as this species prefers a well-developed deciduous understory for nesting and foraging (Roth et al. 1996). The Downy Woodpecker and Hairy Woodpecker also probably benefited from hemlock mortality as the resultant snags would provide cavity sites and foraging substrates for these species.

Finally, our models were unable to determine why the Scarlet Tanager was more abundant in hemlock habitats. Scarlet Tanagers are associated with mature forests and may have been more abundant within hemlock stands because of the presence of large trees. Perhaps the tanagers benefit from temporary changes in habitat structure associated with hemlock decline; however, their high abundance at non-hemlock points indicates that the species is not closely tied to this habitat type.

In our study, the initial stages of hemlock decline due to HWA had either negative or positive effects on a bird species depending on its habitat associations. Winners include Eastern Wood-pewee, Great-crested Flycatcher, Wood Thrush, and some of the cavity nesters, while hemlock specialists were apparent losers. As hemlocks die, species such as the Acadian Flycatcher that

breed within stands of living hemlock and use living hemlock as their primary nest site will likely decline in number unless they are able to shift to other habitats. The effects of hemlock loss on the abundance and distribution of this species and other hemlock specialists are unknown. Long-term research monitoring bird populations from pre-infestation to complete hemlock elimination is needed to better evaluate the impacts of hemlock decline.

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Literature Cited

- Becker, D.A. 2005. The abundance and diversity of breeding birds at Fort Indiantown Gap National Guard Training Center. M.Sc. Thesis. The Pennsylvania State University, University Park, PA. 130 pp.
- Benzinger, J. 1994. Hemlock decline and breeding birds II. Effects of habitat change. *Records of New Jersey Birds* 20:34–51.
- Bushman, E.S., and G.D. Therres. 1988. Habitat management guidelines for forest interior breeding birds of coastal Maryland. Wildlife Technical Publication 88-1. Maryland Department of Natural Resources, Forest, Park, and Wildlife Service, Annapolis, MD. 50 pp.
- Canterbury, G.E., and D.E. Blockstein. 1997. Local changes in a breeding-bird community following forest disturbance. *Journal of Field Ornithology* 68:537–546.
- Cheah, C., M.E. Montgomery, S. Salom, B.L. Parker, S. Costa, and M. Skinner. 2004. Biological control of hemlock woolly adelgid. USDA Forest Service, Morgantown, WV. FHTET-2004-04, Reardon, R., and B. Onken (Technical Coordinators). 22 pp.
- Collins, S.L. 1983. Geographic variation in habitat structure of the Black-throated Green Warbler (*Dendroica virens*). *Auk* 100:382–389.
- Evans, A.M., and T.G. Gregoire. 2006. A geographically variable model of hemlock woolly adelgid spread. *Biological Invasions* 8:1–14.
- Evans, R.A. 2002. An ecosystem unraveling? Pp. 23–33, *In* R.C. Reardon, B.P. Onken, and J. Lashomb (Eds.). Proceedings: Symposium on the Hemlock Woolly Adelgid in the Eastern United States. 57 February, East Brunswick, New Jersey. New Jersey Agricultural Experiment Station, Rutgers University, East Brunswick, NJ. 403 pp.
- Gates, J., and N. Giffen. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. *Wilson Bulletin* 103:204–217.
- Haapanen, A. 1965. Bird fauna of Finnish forests in relation to forest succession. *Annales Zooloci Fennici* 2:153–196.
- Hines, J.E., and J.R. Sauer. 1989. Program CONTRAST: - A general program for the analysis of several survival or recovery rate estimates. US Fish and Wildlife Service Fish and Wildlife Technical Report 24. Washington, DC.
- Hosmer, D.W., and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, Inc., New York, NY. 672 pp.
- Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point-count method for nonbreeding and breeding season use. *Auk* 103:593–602.

- Ickes, R. 1992. Northern Oriole, *Icterus galbula*. Pp. 410–411, *In* D.W. Brauning (Ed.). Atlas of Breeding Birds in Pennsylvania. University of Pittsburgh Press, Pittsburgh, PA. 484 pp.
- Jenkins, J.C., C.D. Canham, and B.K. Barten. 2000. Predicting long-term forest development following hemlock mortality. Pp. 62–75, *In* K.A. McManus, K.S. Shields, and D.R. Souto (Eds.). Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. US Department of Agriculture General Technical Report 267. Newtown Square, PA. 237 pp.
- Martin, T. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? *Ecology* 69:74–84.
- Mayer, M., R. Chianese, T. Scudder, J. White, K. Vongpaseuth, and R. Ward. 2002. Thirteen years of monitoring the hemlock woolly adelgid in New Jersey forests. Pp. 50–60, *In* R.C. Reardon, B.P. Onken, and J. Lashomb (Eds.). Proceedings: Symposium on the Hemlock Woolly Adelgid in the Eastern United States. 57 February, East Brunswick, New Jersey. New Jersey Agricultural Experiment Station, Rutgers University, East Brunswick, NJ. 403 pp.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73: 255–261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87: 456–466.
- McClure, M.S. 1987. Biology and control of hemlock woolly adelgid. Bulletin no. 851. Connecticut Agricultural Experiment Station, New Haven, CT. 9 pp.
- McClure, M.S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomology Society of America* 82:50–54.
- McClure, M.S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology* 19: 36–43.
- McClure, M.S. 1991. Density dependant feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20:258–264.
- McClure, M.S. 1995. Managing hemlock woolly adelgid in ornamental landscapes. Bulletin of Connecticut Agricultural Experimental Station 925. 7 pp.
- McClure, M.S., S.M. Salom, and K.S. Shields. 2001. Hemlock woolly adelgid. Forest Health Technology Enterprise Team Report 3, Morgantown, WV. 14 pp.
- McCracken, J.D. 1991. Status report on the Louisiana Waterthrush *Seiurus motacilla* in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, ON, Canada. 22 pp.
- McQuaide, J., T. Bowersox, J. Harding, B. and Harding. 2003. Fort Indiantown Gap Forest Inventory. Unpublished report. Fort Indiantown Gap National Guard Training Center.
- McWilliams, G.M., and D.W. Brauning. 2000. The Birds of Pennsylvania. Cornell University Press, Ithaca, NY. 479 pp.
- Miller, H.S., Jr. 1988. Hemlock woolly adelgid report. Virginia Department of Agriculture and Consumer Services, Division of Product and Industry Regulations, Richmond, VA. Internal report. 2/10/88. 2 pp.
- Mitchell, J.M. 1999. Habitat relationships of five northern bird species breeding in hemlock ravines in Ohio, USA. *Natural Areas Journal* 19:3–11.

- Orwig, D.A. 2002. Stand dynamics associated with chronic hemlock woolly adelgid infestations in southern New England. Pp. 36–47, *In* R.C. Reardon, B.P. Onken, and J. Lashomb (Eds.). Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium. 57 February, East Brunswick, New Jersey. New Jersey Agricultural Experimental Station Publication. New Brunswick, NJ. 403 pp.
- Orwig, D.A., and D.R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of Torrey Botanical Society* 125:60–73.
- Orwig, D.A., and M.L. Kizlinski. 2002. Vegetation response following hemlock woolly adelgid infestation, hemlock decline, and hemlock salvage logging. Pp. 106–117, *In* R.C. Reardon, B.P. Onken, and J. Lashomb (Eds.). Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium. 57 February, East Brunswick, New Jersey. Harvard Forest, Harvard University, Petersham, MA, 403 pp.
- Orwig, D.A., D.R. Foster, and D.L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29:1475–1487.
- Pennsylvania Department of Conservation and Natural Resources. 2006. Forest health fact sheet: Hemlock woolly adelgid. Available online at <http://www.dcnr.state.pa.us/forestry/leaflets/wooley.htm>. Accessed December 6, 2006.
- Prosser, D.J., and R.P. Brooks. 1998. A verified habitat-suitability index for the Louisiana Waterthrush. *Journal of Field Ornithology* 69:288–298.
- Ross, R.M., L.A. Redell, R.M. Bennett, and J.A. Young. 2004. Mesohabitat use of threatened hemlock forests by breeding birds of the Delaware River basin in northeastern United States. *Natural Areas Journal* 24:307–315.
- Roth, R.R., M.S. Johnson, and T.J. Underwood. 1996. Wood Thrush, No. 246. *In* A. Poole and F. Gill (Eds.). *The Birds of North America*. Vol. 7. Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- Sauer, J.R., and B.K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *Journal of Wildlife Management* 53:137–142.
- Sheehan, J. 2003. Habitat selection in the Acadian Flycatcher: The potential impact of hemlock woolly adelgid infestations and other anthropogenic stressors. M.Sc. Thesis. East Stroudsburg University, East Stroudsburg, PA
- Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: Consequences of hemlock woolly adelgid infestations. *Journal of Biogeography* 29:1505–1516.
- Whitehead, D.R., and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*), No. 614. *In* A. Poole and F. Gill (Eds.). *The Birds of North America*, The Birds of North America, Inc., Philadelphia, PA.
- Yorks, T.E. 2002. Influence of hemlock mortality on soil water chemistry and ground flora. Pp. 47–49, *In* R.C. Reardon, B.P. Onken, and J. Lashomb (Eds.). Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, 57 February, East Brunswick, New Jersey. U.S. Department of Agriculture, Forest Service, Newtown Square, Pennsylvania, 403 pp.
- Young, R.F., K.S. Shields, and G.P. Berlyn. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): Stylet bundle insertion and feeding sites. *Annals of the Entomological Society of America* 88:827–835.