Responses of Acadian Flycatchers (Empidonax virescens) to Hemlock Woolly Adelgid (Adelges tsugae) Infestation in Ap....

4 authors:

Michael C Allen
New Jersey Audubon Society

8 PUBLICATIONS **24** CITATIONS

SEE PROFILE

James Sheehan
West Virginia University

17 PUBLICATIONS **78** CITATIONS

SEE PROFILE

Terry Master
East Stroudsburg University

27 PUBLICATIONS **151** CITATIONS

SEE PROFILE

Robert S. Mulvihill
National Aviary

40 PUBLICATIONS **819** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Project Ecomorphology Wing Shape View project

Project Second Atlas of Breeding Birds in Pennsylvania View project

RESPONSES OF ACADIAN FLYCATCHERS (*EMPIDONAX VIRESCENS*) TO HEMLOCK WOOLLY ADELGID (*ADELGES TSUGAE*) INFESTATION IN APPALACHIAN RIPARIAN FORESTS

MICHAEL C. ALLEN,[1] JAMES SHEEHAN, JR.,[1] TERRY L. MASTER,[1,3] AND ROBERT S. MULVIHILL[2]

[1]*Department of Biological Sciences, East Stroudsburg University, 200 Prospect Street, East Stroudsburg, Pennsylvania 18301, USA; and*
[2]*Powdermill Nature Reserve, Carnegie Museum of Natural History, Rector, Pennsylvania 15677, USA*

ABSTRACT.—Invasive insects pose a significant threat to biodiversity, often affecting entire communities through the destruction of foundation species. Eastern Hemlock (*Tsuga canadensis* [L.] Carr.) forests, which are unique habitats in eastern North America, are threatened by an introduced insect, the Hemlock Woolly Adelgid (*Adelges tsugae* Annand). Previous studies have found declines in the abundance of some forest bird species, including the Acadian Flycatcher (*Empidonax virescens*), with increasing infestation by Hemlock Woolly Adelgids. To identify potential mechanisms behind these declines, we studied abundance, breeding biology, and habitat selection of Acadian Flycatchers in 11 Eastern Hemlock-dominated riparian sites in Pennsylvania and New Jersey, representing a continuum of infestation levels, in 2001–2002 and 2006–2007. Eastern Hemlock supported 90% of all nests and was used more as a nesting substrate than expected at most sites. We found ~70% fewer breeding pairs at heavily infested sites, though nest survival rates were not affected. The results suggest that Acadian Flycatcher populations in Eastern Hemlock forests may decrease with continued decline of Eastern Hemlocks. Populations in the Appalachian Highlands, where the species' association with Eastern Hemlock is most pronounced, may be at greatest risk. *Received 28 April 2008, accepted 25 January 2009.*

Key words: Acadian Flycatcher, *Adelges tsugae,* Eastern Hemlock, *Empidonax virescens,* Hemlock Woolly Adelgid, productivity, *Tsuga canadensis.*

Respuestas de *Empidonax virescens* a la Infestación por *Adelges tsugae* en Bosques Ribereños de los Apalaches

RESUMEN.—Las especies invasoras representan una amenaza significativa para la biodiversidad y a menudo afectan comunidades enteras mediante la destrucción de especies clave. Los bosques de *Tsuga canadensis* [L.] Carr., que son ambientes únicos en el este de América del Norte, están amenazados por un insecto introducido, el adélgido *Adelges tsugae* Annand. Estudios previos han encontrado disminuciones en la abundancia de algunas especies de aves de bosque, incluyendo a *Empidonax virescens*, con aumentos en los niveles de infestación por *A. tsugae*. Para identificar los potenciales mecanismos que están detrás de esas disminuciones, en 2001–2002 y 2006–2007 estudiamos la abundancia, la biología reproductiva y la selección de hábitat de *E. virescens* en 11 localidades ribereñas dominadas por *T. canadensis* en Pensilvania y Nueva Jersey, las cuales representaban un continuo de niveles de infestación. Los árboles de *T. canadensis* soportaron el 90% de todos los nidos y fueron usados como sustrato de anidación de forma mayor a la esperada en la mayoría de los sitios. Encontramos ~70% menos parejas reproductivas en los lugares fuertemente infestados, pero las tasas de superviencia de los nidos no fueron afectadas. Los resultados sugieren que las poblaciones de *E. virescens* de los bosques de *T. canadensis* podrían disminuir con el declive continuado de estos árboles. Las poblaciones de las tierras altas de los Apalaches, en donde la asociación de la especie con *T. canadensis* es más pronunciada, podrían presentar el mayor riesgo.

INTRODUCED INSECTS REPRESENT one of the most serious threats to forests in eastern North America and worldwide (Castello et al. 1995, Ellison et al. 2005). They alter the structure and dynamics of stands by killing dominant tree species and creating gaps in the canopy, which may facilitate further disturbances (Mack and D'Antonio 1998). Introduced insects have contributed to declines in ecologically important eastern forest trees such as American Elm (*Ulmus americana* L.), American Beech (*Fagus grandifolia* Ehrh.), and Fraser Fir (*Abies fraseri* [Pursh] Poir.; Rabenold et al. 1997, Lovett et al. 2006). They have the potential to dramatically affect flora and fauna even in protected areas that are free from other anthropogenic threats (e.g., Rabenold et al. 1997).

Although several studies have documented changes in avian communities in response to forest pathogens (Osborne 1985, Rabenold et al. 1997, Bell and Whitmore 2000, Matsuoka et al. 2001, Tingley et al. 2002), few have examined the mechanisms that drive declines of individual species.

Eastern Hemlock (*Tsuga canadensis* [L.] Carr.; hereafter "hemlock") forests are unique ecosystems in eastern North America, with characteristically low light penetration, persistent shade-tolerant branches, and sparse groundcover (Kizlinski et al. 2002, Small et al. 2005). Because of these ecological attributes, and the fact that they are the only conifer-dominated habitat in many regions, hemlock forests contain regionally distinct avian communities, as well as other characteristic fauna (Benzinger 1994, Snyder et al. 2002, Ross et al. 2003). Birds commonly associated with hemlock forests in the Northeast include Black-throated Green Warbler (*Dendroica virens*), Blackburnian Warbler (*D. fusca*), Blue-headed Vireo (*Vireo solitarius*), and Acadian Flycatcher (*Empidonax virescens*), among others (Haney 1999, Tingley et al. 2002, Ross et al. 2004, Swartzentruber 2004). Although these species occur in other habitats to varying degrees, significant portions of their populations inhabit hemlock stands (Ross et al. 2004).

Large-scale timber cutting was responsible for historical loss of hemlock forests throughout eastern North America (Whitney 1990), but the greatest current threat to this habitat is an introduced insect, the Hemlock Woolly Adelgid (HWA; *Adelges tsugae* Annand). Infestation by HWA causes defoliation and death of individual trees, usually within 4–10 years. The most severe infestations can result in complete stand mortality and dramatic changes to canopy and understory structure (Kizlinski et al. 2002, Small et al. 2005). The insect currently occupies nearly half of the hemlock's native range, and it continues to spread at a rate of ~20 km year^{-1} (Orwig et al. 2002; U.S. Department of Agriculture, Forest Service, HWA website [see Acknowledgments]; Fig. 1). Relatively few studies have examined the effects of HWA on the abundance of hemlock-associated birds as a group (Tingley et al. 2002, Swartzentruber 2004) and none, to our knowledge, has examined the productivity of individual sensitive species under varying levels of infestation. This may be especially important, given that the reasons for potential population declines are likely to be species-specific (Tingley et al. 2002).

Among hemlock-associated birds, Acadian Flycatchers have several desirable characteristics as a study species: they are relatively abundant, are vocally conspicuous, and build low nests that are comparatively easy to locate and monitor. Several studies indicate an association of this species with hemlock habitats (Shriner 2001, Ross et al. 2004, Becker et al. 2008) in the Northeast and elsewhere in the Appalachian Highlands. Anecdotal accounts from other sources corroborate these findings (Eaton 1988, Zeranski and Baptist 1990, Brauning 1992, Benzinger 1994).

Tingley et al. (2002) found that Acadian Flycatcher, along with other hemlock-associated species, was less abundant in heavily infested hemlock stands. Because Acadian Flycatchers prefer open microhabitats (Wilson and Cooper 1998, Bell and Whitmore 2000), preferentially nest in hemlock branches (Table 1), and tend to nest on lower branches, which are more susceptible to HWA, they should respond in measurable ways to a loss of suitable nest sites following infestation.

To better understand the consequences of HWA infestation, we undertook a detailed study of Acadian Flycatcher breeding biology in two locations: an area infested since 1989 and an area on the leading edge of the HWA range where infestation is imminent or very recent (Fig. 1). We examined differences in nest substrate, breeding density, and breeding productivity along a continuum of infested to noninfested hemlock stands using a nest-census and habitat-analysis approach. We sought to determine (1) the nature of the species' relationship to hemlock, both as a nesting substrate and as breeding habitat; (2) the effects of HWA infestation on the species' demographics and breeding biology; and (3) the likelihood that the Acadian Flycatcher will persist as a breeding species in regions where hemlock is lost because of HWA. Finally, we aimed to document baseline conditions in soon-to-be infested and long-infested stands for future monitoring.

Methods

Study sites.—We studied Acadian Flycatchers at 11 sites in two regions in the Appalachian Mountains: (1) northeastern Pennsylvania–northwestern New Jersey, in and around Delaware Water Gap National Recreation Area (DEWA; 41°9′N, 74°55′W); and (2) southwestern Pennsylvania, in and around Powdermill Nature Reserve (PNR; 40°9′N, 79°14′W), field station of the Carnegie Museum of Natural History (Fig. 1). Study sites were linear (0.9–1.9 km long, ~150 m wide) and were centered on small, first- to third-order headwater streams (about 2–5 m wide) within wooded ravines, a preferred habitat of Acadian Flycatchers in the region (Brauning 1992, Ross et al. 2004). Sites were roughly similar in habitat attributes, including stream size, stand maturity, topography (narrow "floodplains" flanked by steep slopes), and surrounding landscape characteristics (mainly forested with northern hardwoods; Table 2).

The DEWA sites included six hemlock ravines with varying levels of infestation (see Sheehan 2003). Hemlock Woolly Adelgid was first reported here in 1989 and has caused severe defoliation in many ravines (Evans 2004). The PNR sites included five hemlock stands located on four streams at the leading edge of the HWA range (see Allen 2008). Three of the five PNR sites contained low densities of HWA, which was first reported in Westmoreland County in 2006 during our study (U.S. Department of Agriculture, Forest Service, HWA website [see Acknowledgments]). Field work was performed at DEWA sites in 2001 and 2002 and at PNR sites in 2006 and 2007. All but two sites (Vancampens and McCullen) were studied for two consecutive years.

Infestation level and hemlock health.—We used a derivation of a protocol developed at Delaware Water Gap National Recreation Area (R. Evans pers. comm.) to assess the average infestation level at sites. In May and June, when new growth on twigs was discernible from older growth on the basis of needle color, we established a transect along the center of the stream at each site. Every 50 m, on a random side of the stream, we surveyed the lowest live branch of each of the four nearest hemlocks. We examined the terminal 30 cm of the branch and calculated the proportion of last year's twigs containing HWA (an index of HWA abundance) and the proportion sprouting new growth (an index of branch health; Evans 2004). The sampling period and design are consistent with more recently developed protocols (Costa and Onken 2006). To
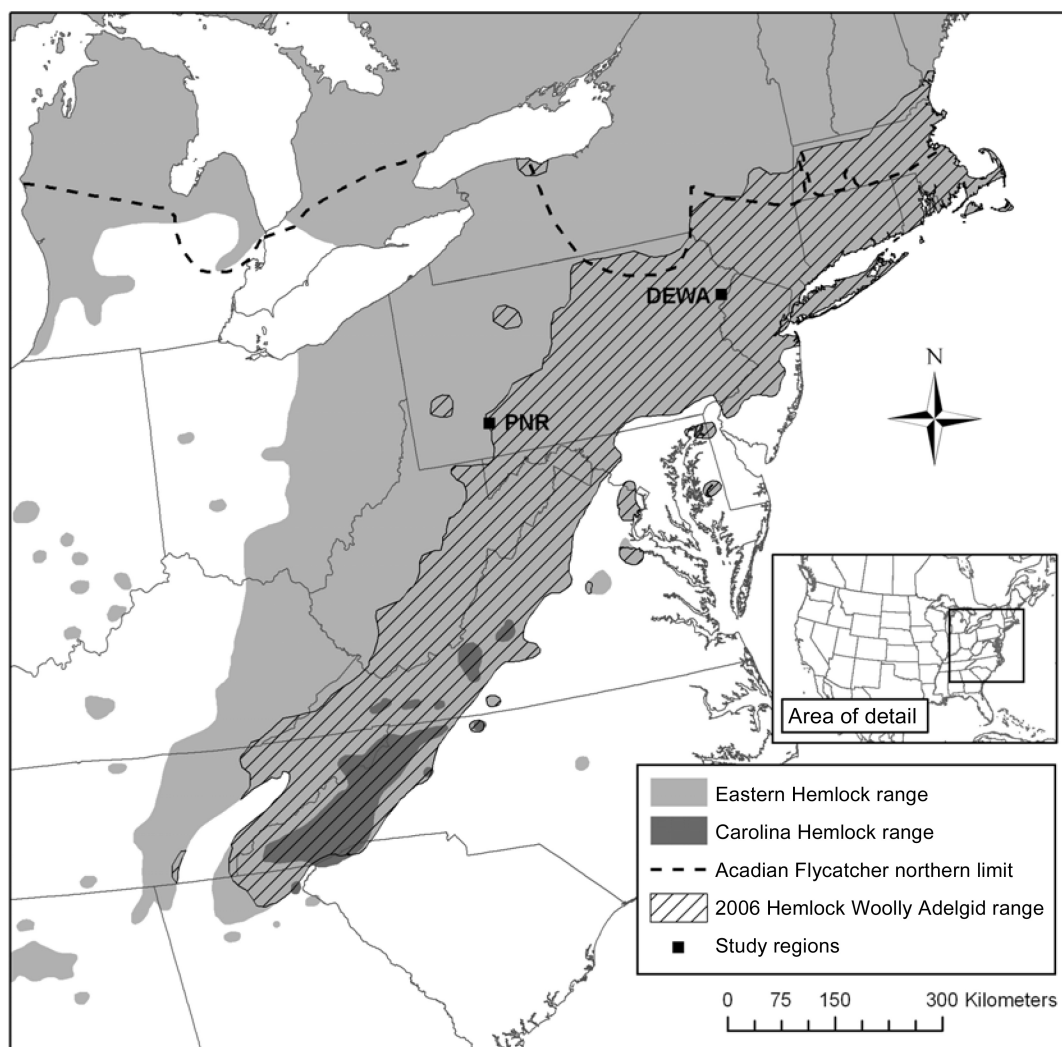
FIG. 1. Extent of Hemlock Woolly Adelgid infestation in 2006 in relation to the range of Eastern Hemlock and Carolina Hemlock (*Tsuga caroliniana* Engelm.) and the breeding range of Acadian Flycatchers. Locations of the two study regions are shown, including the long-infested Delaware Water Gap area (DEWA) and the recently infested Powdermill area (PNR). (Data sources: U.S. Department of Agriculture, Forest Service; Whitehead and Taylor 2002; Natureserve [see Acknowledgments].)

TABLE 1. Reports of Acadian Flycatcher use of Eastern Hemlock as a nesting substrate. All but the Michigan site are located in the Appalachian Mountains.

State	County	Use (%)	Availability (%)	Number of nests	Reference
Michigan	Muskegon	64	26	47	Walkinshaw 1966
Massachusetts	Franklin and Hampshire	100	54	13	Lyons and Livingston 1997
Pennsylvania	Lebanon	84	40	73	Becker et al. 2008
West Virginia	Grant and Hardy	18	ND	45	Shearer 1990
Virginia	Rockbridge	75	ND	37	Lewis 1999
Virginia	Rockbridge	33	ND	141	Fauth and Cabe 2005
Virginia	ND	86	ND	21	Wilson and Cooper 1998 (unpubl. data cited therein)

Notes: Use = percentage of nests in Eastern Hemlocks. Availability = abundance of Eastern Hemlocks, where data were provided. ND = no data provided.

TABLE 2. Measurements (± SD) of Hemlock Woolly Adelgid (HWA) infestation and vegetation-structure.

| Site | Region[b] | Length (km) | HWA[a] | | | | Vegetation structure | | | | |
			Infestation	Defoliation	New growth	n	Trees ha^{-1}	Live Eastern Hemlocks ha^{-1}	Percent Eastern Hemlock mortality[c]	Saplings ha^{-1}	n
Linn	P	0.91	0 ± 0	1.6 ± 6.3	65.8 ± 7.2	16	563 ± 124	120 ± 200	0 ± 0	2623 ± 2871	5
McCullen	P	1.10	0 ± 0	0 ± 0	71.6 ± 6.6	20	674 ± 127	269 ± 141	7 ± 9	573 ± 601	10
Powdermill	P	0.99	0.1 ± 0.4	1.3 ± 5.6	76.6 ± 4.7	20	455 ± 153	61 ± 76	0 ± 0	648 ± 866	11
Rolling Rock 1	P	1.63	2.3 ± 5.9	0.7 ± 4.3	69.9 ± 9.9	34	357 ± 215	95 ± 79	6 ± 9	266 ± 329	11
Rolling Rock 2	P	1.63	6.0 ± 13.5	2.2 ± 9.5	69.3 ± 14.3	34	383 ± 157	64 ± 75	3 ± 6	424 ± 476	9
Spruce	D	1.30	2.3 ± 4.4	2.8 ± 10.6	45.1 ± 10.1	27	747 ± 220	353 ± 211	5 ± 8	323 ± 872	28
Marshalls	D	1.89	18.7 ± 11.7	19.9 ± 30.9	40.3 ± 14.8	29	719 ± 289	411 ± 257	5 ± 8	233 ± 434	41
Dunnfield	D	1.56	20.6 ± 13.8	25.0 ± 24.3	64.7 ± 7.6	35	376 ± 160	88 ± 65	15 ± 24	123 ± 215	28
VanCampens	D	1.15	26.3 ± 9.6	23.6 ± 32.6	43.1 ± 14.1	18	463 ± 198	207 ± 143	4 ± 8	217 ± 345	17
Toms	D	1.65	30.5 ± 12.9	62.1 ± 31.3	29.0 ± 17.6	33	548 ± 184	280 ± 240	13 ± 14	427 ± 448	14
Hornbecks	D	1.63	35.6 ± 15.5	61.7 ± 36.4	27.5 ± 31.3	30	502 ± 202	237 ± 208	7 ± 8	302 ± 304	8

[a] Infestation = percentage of twigs with HWA; defoliation = percentage defoliated branches; new growth = percentage of twigs with new shoots present.
[b] Study region: P = PNR, D = DEWA.
[c] Percent Eastern Hemlock mortality = (number of dead Eastern Hemlocks in plot/number of live and dead Eastern Hemlocks in plot)*100.

further assess hemlock lower-branch health, we classified the condition of the lowest live branch of each surveyed tree as either "good," "fair," or "poor" according to the condition of the foliage (i.e., largely intact, somewhat defoliated, or severely defoliated). Because of the low frequency of "fair" branches, in our analyses we combined this category with "poor" (i.e., "affected" branches). Site-infestation and branch-health indices were calculated by first averaging each parameter for the four trees and then averaging these values across the site.

Habitat selection and vegetation structure.—We measured habitat characteristics using nest-centered and randomly located 0.04-ha plots (11.3 m radius; after Martin et al. 1997). Methods for locating "random" plots differed somewhat by region. At DEWA, they were placed 35 m from each nest in a random direction (1–3 plots nest^{-1}); at PNR, they were placed at randomly generated points within 75 m of the stream. Within each plot, the diameter at breast height (dbh) and species were recorded for all live and dead stems ≥5 cm dbh (hereafter "trees"). Woody stems <5 cm dbh and >1.4 m tall (hereafter "saplings") were counted within a concentric 5-m-radius circle. Vegetation characteristics at the stand level (including percent composition) were estimated by averaging all random plots in a site.

Nest-substrate preferences.—An index of nest-substrate preference was calculated at each site as the percent use of a tree species minus the percent availability (after Wilson and Cooper 1998). Preferences were evaluated by comparing observed frequencies of nest substrate use with expected use (based on mean percent composition) using chi-square goodness-of-fit tests.

Nest placement.—Nest height was measured (to 10 cm) using a graduated 7-m pole or, for higher nests, a clinometer at a known distance from the nest. Diameter at breast height of nest trees was measured using a dbh tape. Only hemlock nest trees were used for analysis of nest-placement characteristics.

Breeding density, productivity, and nest survival.—Sites were searched thoroughly for nests every two to four days by walking up one side of the stream and down the other, listening and looking for singing males and calling females. Nests were often located by following calling females to the nest during construction or incubation. We visited nests every two to four days (more often as fledging approached) to determine contents–stage and final outcome, either using a pole-mounted mirror or by remotely observing adult behavior. A nest was considered successful if it was empty on or after the expected fledge date (14 days after hatching; Mumford 1964) and (on most occasions) adults and fledglings were located in the vicinity. The number of pairs at a study site was determined by the number of territories at which nests were found. Each site was searched 25–35 times year^{-1}, and we believe this left few, if any, nests undiscovered. Pair density was calculated as number of pairs per kilometer of study site per year.

Nest survival at each site was calculated as the daily survival probability (Mayfield 1961) raised to the power of 30 to estimate the probability of surviving the entire nest cycle (16-day egg-laying–incubation, 14-day nestling period; Mumford 1964). Exposure days were calculated using the "last active—A" approach of Manolis et al. (2000).

To estimate the number of fledglings produced at each site ("productivity"), we summed the brood sizes (i.e., number of young observed at last nest-check) of all successful nests. If brood size was

Table 3. Model rankings for Acadian Flycatcher demographic parameters based on Akaike's information criterion corrected for small sample size (AIC_c) and Akaike weights (w_i).

Region	Dependent variable	Model[a]	K [b]	AIC_c	ΔAIC_c	w_i
DEWA	Pair density	Defoliation	3	10.7	0.0	0.96
		Null	2	17.2	6.5	0.04
		Saplings ha^{-1}	3	23.8	13.1	0.00
		Trees ha^{-1}	3	26.9	16.2	0.00
		Live Eastern Hemlocks ha^{-1}	3	27.2	16.5	0.00
	Productivity	Defoliation	3	27.2	0.0	0.51
		Null	2	27.3	0.1	0.48
		Saplings ha^{-1}	3	36.0	8.8	0.01
		Trees ha^{-1}	3	37.1	10.0	0.00
		Live Eastern Hemlocks ha^{-1}	3	37.3	10.1	0.00
	Nest survival	Null	2	290.2	0.0	0.24
		Trees ha^{-1}	3	290.4	0.2	0.22
		Live Eastern Hemlocks ha^{-1}	3	290.4	0.2	0.22
		Defoliation	3	291.1	0.9	0.15
		Year	3	292.1	1.9	0.09
		Saplings ha^{-1}	3	292.3	2.0	0.09
PNR	Pair density	Null	2	13.2	0.0	1.00
		Defoliation	3	29.4	16.2	0.00
		Saplings ha^{-1}	3	32.9	19.7	0.00
		Live Eastern Hemlocks ha^{-1}	3	32.9	19.7	0.00
		Trees ha^{-1}	3	33.0	19.8	0.00
	Productivity	Null	2	26.3	0.0	1.00
		Saplings ha^{-1}	3	42.7	16.4	0.00
		Defoliation	3	45.7	19.3	0.00
		Trees ha^{-1}	3	45.9	19.5	0.00
		Live Hemlocks ha^{-1}	3	46.2	19.9	0.00
	Nest survival	Saplings ha^{-1}	3	354.5	0.0	0.85
		Trees ha^{-1}	3	359.4	4.9	0.07
		Null	2	361.4	6.9	0.03
		Live Eastern Hemlocks ha^{-1}	3	361.5	7.0	0.03
		Year	3	362.4	7.9	0.02
		Defoliation	3	362.9	8.4	0.01

[a] The independent variable used in the model, except: null—intercept only.
[b] The number of model parameters, including the intercept and an error term.

unknown ($n = 10$ of 57 successful nests at DEWA, $n = 12$ of 35 at PNR), the average size at each region (2.8 for each) was used. All but one accessible nest had two or three offspring, and brood size appeared to be unrelated to nest height (t-tests of nests with 2 or 3 young, $P \geq 0.41$). Our default brood size, therefore, is not likely biased by using only lower nests. Productivity was calculated as the number of fledglings produced per kilometer of study site per year.

Statistical analyses.—To avoid confounding the effects of time or region with infestation, data from PNR and DEWA were analyzed separately. To assess habitat selection, two multivariate analyses of variance (MANOVAs) were run initially to test for differences between nest and random plots in (1) vegetation structure and (2) nest-substrate species composition (PROC GLM; SAS Institute 2004). Vegetation variables were then evaluated individually using analysis of variance (ANOVA; i.e., a protected ANOVA approach; Scheiner 1993). Site was included as a blocking factor, as was the site*plot-type interaction (both random effects; Potvin 1993). Dependent variables for vegetation structure were trees per hectare, live hemlocks per hectare, percent hemlock mortality, and saplings per hectare (see Table 2 for descriptions); for nest-substrate composition, variables were the percent compositions of six tree or shrub species used during the study (see below). Variables were log or (for proportions) arcsine square-root transformed as needed to normalize residuals. Results are not reported for site (the blocking factor), because individual sites are expected to differ in vegetation structure and composition. An alpha level of 0.05 was used.

Factors affecting pair density and productivity within each region were evaluated using linear regression. Years were averaged for this analysis, because no significant year effects were observed (paired t-tests, $P \geq 0.23$). Five candidate models were compared: two vegetation-structure models, two hemlock-related models, and a null model (see Table 3 for model variables). More complex models (e.g., multiple–quadratic regression) were not attempted because limited sample sizes precluded calculation of selection criteria (see below). Daily nest survival rates were modeled using Mayfield logistic regression (Hazler 2004). For this, the five models above were used, plus a "study year" model. For each dependent variable, the best-supported model(s) given the data were selected using relative differences in Akaike's information criterion adjusted for small sample sizes (AIC_c) and Akaike weights (w_i). Models with $\Delta AIC_c \leq 2$ were considered equally supported (Burnham and Anderson 2002). All means are presented ± SD.

RESULTS

Infestation level and hemlock health.—Hemlock Woolly Adelgids were found at 9 of 11 sites. Mean percentage of twigs with HWA (hereafter "infestation") ranged from 0 to 36% (Table 2) and was strongly correlated with measures of branch health (Fig. 2A). Mean percentage of branches with significant needle loss ranged from 0 to 62% among sites and increased with infestation (linear regression, $F = 61.56$, df = 1 and 9, $r^2 = 87\%$). Mean percentage of twigs with new growth ranged from 28% to 77% and decreased with infestation ($F = 18.80$, df = 1 and 9, $r^2 = 68\%$). Hemlock mortality (percentage of dead hemlocks) ranged from 1% to 15% and showed a weak positive relationship with infestation ($F = 3.63$, df = 1 and 9, $r^2 = 29\%$; Fig. 2B). No other measures of vegetation structure were correlated with infestation.

Habitat selection and vegetation structure.—Vegetation structure did not differ, overall, between nest and random plots at DEWA (MANOVA, Wilks's $\Lambda = 0.99$, $P = 0.633$) or at PNR ($\Lambda = 0.98$, $P = 0.674$). However, there was evidence of a difference in hemlock mortality by plot type at DEWA sites (ANOVA, $F = 4.68$, df = 1 and 33, $P = 0.038$; nest: 4.8 ± 3.5%, random: 8.1 ± 4.7%, $n = 6$ sites). Composition of nest-substrate species did not differ by plot type at DEWA ($\Lambda = 0.98$, $P = 0.732$) or at PNR ($\Lambda = 0.93$, $P = 0.264$), and no interaction effects were observed ($\Lambda \geq 0.82$, $P \geq 0.485$).

Nest-substrate preferences.—Of 180 nests found during the study, 98.9% were placed in four tree or shrub species: (1) Eastern Hemlock (90.0%); (2) American Beech (4.4%); (3) American Witchhazel (*Hamamelis virginiana*; 2.2%); and (4) rhododendron (*Rhododendron* sp.; 2.2%). Sugar Maple (*Acer saccharum*) and Red Maple (*A. rubrum*) were also used (one nest each). Hemlock

use was relatively high at all sites, ranging from 66.7% to 100% at DEWA sites (mean: 83.1 ± 16.0%) and from 73.7% to 100% at PNR sites (88.8 ± 10.8%; Table 4). American Beech, American Witchhazel, and rhododendron use were generally much lower, averaging 7.1%, 2.7%, and 3.3%, respectively, across all sites.

Hemlock preference values averaged 40.0 ± 20.6 at DEWA sites and 59.2 ± 3.0 at PNR sites (Table 4). By contrast, averages for American Beech, American Witchhazel, and rhododendron were 1.8, −0.2, and −0.4 across all sites, respectively. Chi-square goodness-of-fit tests indicated that hemlock was used more than expected at eight sites, American Beech at one site, American Witchhazel at no sites, and rhododendron at one site (Table 4).

Nest placement.—Height above the ground for nests in hemlocks averaged 5.8 ± 2.8 m at DEWA ($n = 91$) and 6.2 ± 2.9 m at PNR ($n = 69$) (pooled mean = 6.0 ± 2.8 m, range: 1.5–16.1 m). Mean diameter of hemlock nest trees was 32.7 ± 14.0 cm at DEWA and 40.1 ± 16.5 cm at PNR (pooled mean = 35.9 ± 15.5 cm, range: 6–81 cm).

Breeding density, productivity, and nest survival.—Pair density at the 11 sites varied from 1.2 to 7.7 pairs km⁻¹ year⁻¹ and was relatively consistent between years (mean absolute difference = 1.0 ± 1.0 pairs km⁻¹, $n = 9$; Table 5). At DEWA, variation in pair density was best explained by the model including hemlock defoliation ($w_i = 0.96$; Table 3). Pair density was negatively associated with defoliation during both study years (Fig. 3A). At PNR, the null model was by far the best supported of the candidate models ($w_i = 1.0$).

Site productivity ranged from 0 to 17.2 fledglings km⁻¹ year⁻¹ and exhibited low between-year variation (mean absolute difference = 2.4 ± 2.0 fledglings km⁻¹; Table 5). For productivity, the defoliation model ranked highest at DEWA sites, though the null model was nearly equally supported ($\Delta AIC_c = 0.14$). Productivity
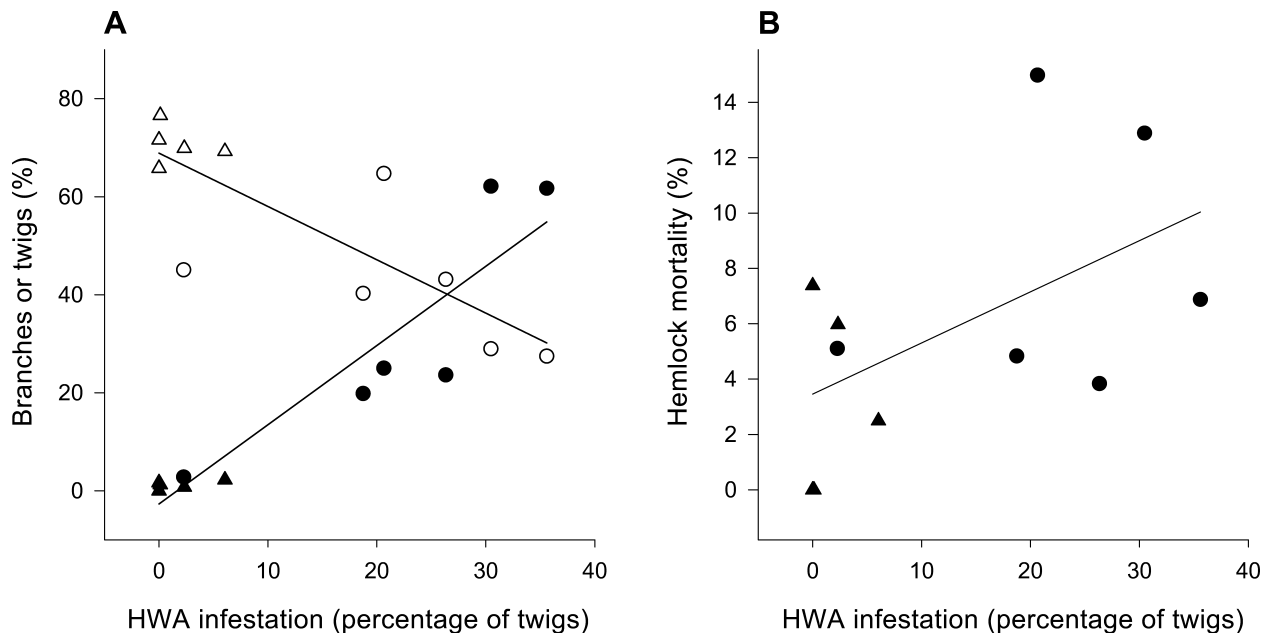

FIG. 2. Relationships between Hemlock Woolly Adelgid (HWA) infestation measurements. (A) Average defoliation (percentage of branches with moderate-to-severe needle loss; closed symbols) and new growth (percentage of twigs with fresh green shoots; open symbols) in relation to the site infestation level (percentage of twigs with HWA; x-axis). (B) Eastern Hemlock mortality (percent dead Eastern Hemlocks) in relation to the site infestation level. Triangles are Delaware Water Gap (DEWA) sites, and circles are Powdermill (PNR) sites.

TABLE 4. Nesting substrate use in relation to availability.

Site	Eastern Hemlock				American Beech				American Witchhazel				Rhododendron				n
	U	A	P	χ^2	U	A	P	χ^2	U	A	P	χ^2	U	A	P	χ^2	
Linn	81.8	20.1	61.7	26.1*	0.0	6.6	–6.6	0.8	18.2	11.7	6.5	0.5	0.0	11.4	–11.4	1.4	11
McCullen	100	39.8	60.2	15.1*	0.0	1.0	–1.0	0.1	0.0	2.0	–2.0	0.2	0.0	2.8	–2.8	0.3	10
Powdermill	73.7	15.6	58.1	48.7*	15.8	12.1	3.7	0.2	0.0	4.7	–4.7	0.9	5.3	0.0	NA	NA	19
Rolling Rock 1	96.0	30.1	65.9	51.6*	4.0	5.0	–1.0	0.1	0.0	1.3	–1.3	0.3	0.0	7.8	–7.8	2.1	25
Rolling Rock 2	92.3	20.9	71.4	40.1*	0.0	6.3	–6.3	0.9	7.7	3.6	4.1	0.6	0.0	1.8	–1.8	0.2	13
Spruce	96.3	44.9	51.4	28.8*	0.0	1.4	–1.4	0.4	0.0	0.3	–0.3	0.1	0.0	0.0	NA	NA	27
Marshalls	96.4	54.1	42.3	20.2*	0.0	1.3	–1.3	0.4	3.6	1.3	2.3	1.1	0.0	0.0	NA	NA	28
Dunnfield	100	25.6	74.4	69.8*	0.0	7.1	–7.1	1.8	0.0	5.0	–5.0	1.3	0.0	9.2	–9.2	2.4	24
VanCampens	66.7	46.2	20.5	1.5	11.1	3.2	7.9	1.8	0.0	0.8	–0.8	0.1	22.2	12.6	9.6	0.8	9
Toms	72.7	44.9	27.8	3.4	18.2	7.7	10.5	1.7	0.0	2.0	–2.0	0.2	9.1	0.3	8.8	29.5*	11
Hornbecks	66.7	43.4	23.3	0.7	33.3	4.7	28.6	5.5*	0.0	2.1	–2.1	0.1	0.0	0.0	NA	NA	3

Notes: U = percentage of nests placed in substrate species. A = percent availability at site. P = an index of substrate preference, calculated as U–A. Values marked with an asterisk are significant at P < 0.05 (df = 1). NA = not calculable because of 0% availability. n = number of nests.

exhibited a negative relationship with defoliation in both years (Fig. 3B). The null model was best supported for productivity at PNR sites ($w_i = 1.0$).

Nest survival probabilities ranged from 44% to 79% at DEWA sites (pooled: 61.2%, 1,785 exposure days) and from 4% to 61% at PNR (pooled: 40.2%, 1,336 exposure days; Table 5). At DEWA, several logistic regression models of daily survival rates (including the null) were equally plausible ($\Delta AIC_c \leq 2$), and all had low Akaike weights ($w_i \leq 0.24$; Table 3). At PNR, the logistic model including sapling density as an independent variable was best supported ($w_i = 0.85$; $\beta_0 = -3.957 \pm 0.235$ [SE], $\beta_1 = 0.000581 \pm 0.000168$).

DISCUSSION

Disturbances to forest structure caused by insect infestations have been shown to affect the abundance of a variety of avian species in diverse locations (Rabenold et al. 1997, Bell and Whitmore 2000, Matsuoka et al. 2001, Tingley et al. 2002). Less clear, however, is whether declines or increases in individual species are accompanied by changes in reproductive and survival rates. In the present study, we observed a negative relationship between Acadian Flycatcher pair density and HWA-induced defoliation during both study years at our long-infested DEWA sites, but not at our recently infested PNR sites. Nest survival rates were not related to defoliation. Together with previous studies, our results suggest that Acadian Flycatchers breeding in declining hemlock forests will likely be faced with increasingly undesirable habitat structure, even as their nesting success may remain unimpaired.

Infestation level and hemlock health.—The decreased abundance of Acadian Flycatchers at heavily infested DEWA sites is presumably attributable to some change in habitat structure. The study sites exhibited a broad range of infestation levels and branch condition, yet we did not detect a corresponding increase in sapling densities (*contra* Kizlinski et al. 2002, Small et al. 2005) or in any other habitat variable. This is likely attributable to comparatively low rates of hemlock mortality at our sites (1–15%), which still had generally intact canopies. Reports from hemlock forests in New England range from 0–3% mortality in healthy stands to 31–87% in heavily infested stands (Kizlinski et al. 2002, Tingley et al. 2002, Small et al. 2005). Sapling densities at even our most infested sites were within the range of those reported from healthy stands (about 100–600 ha⁻¹) and well below those of severely damaged stands (to 5,500 ha⁻¹; Kizlinski et al. 2002, Small et al. 2005). The relatively high sapling-density value at our "Linn" site (PNR, 2,623 ha⁻¹) is attributable mainly to thickets of shade-tolerant rhododendron (Table 2). Although mortality levels at our DEWA sites are relatively low, the sites have suffered extensive ecological changes since the arrival of HWA in 1989 (reviewed in Evans 2004), the most visible of which is extensive defoliation below the canopy.

Habitat selection and vegetation structure.—In the only other study, to our knowledge, that has assessed avian abundance across an HWA-infestation gradient, Acadian Flycatchers in Connecticut were absent from sites with high hemlock mortality (31–87%, *n* = 7) and relatively common in low-mortality sites (0%, *n* = 5; Tingley et al. 2002). The greater density of Black Birch (*Betula lenta* L.) saplings at the infested sites (~20× more) suggests a possible cause. Acadian Flycatchers declined in abundance and chose nest

Table 5. Abundance, nest survival, and productivity of Acadian Flycatchers.[a]

Site	Pair density[b] (pairs km⁻¹)		Mayfield nest survival[c] (%)		Productivity[d] (fledglings km⁻¹)		Number of nests
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1/2
Linn	3.3	6.6	4	11.1	0	0	5/6
McCullen	ND	6.4	ND	30.3	ND	7.8	ND/10
Powdermill	7.1	7.1	61.1	49.9	17.1	13.0	10/9
Rolling Rock 1	7.4	6.1	52.9	49.7	11.9	10.0	14/11
Rolling Rock 2	3.1	3.7	44.9	32.3	4.8	5.3	6/7
Spruce	6.2	7.7	71.8	59.6	15.2	18.0	10/17
Marshalls	5.8	5.8	57.9	44.3	11.1	7.7	14/14
Dunnfield	5.8	7.1	57.4	67.4	11.4	15.1	10/14
VanCampens	ND	6.1	ND	75.1	ND	13.9	ND/9
Toms	1.8	2.4	74.3	79.4	3.6	9.0	4/6
Hornbecks	1.8	1.2			3.7	0.0	2/2

[a] ND = no data. Year 1 is 2001 for DEWA sites, and 2006 for PNR sites.

[b] Breeding pairs per kilometer of stream reach.

[c] Mayfield (1961) nest survival, calculated as 100*(daily survival rate)[30]. Toms and Hornbecks were pooled because of low sample sizes and similarity of habitat.

[d] Number of fledglings produced per kilometer of stream reach.

sites with fewer shrubs and saplings following severe gypsy moth infestation in West Virginia (Bell and Whitmore 2000). Therefore, although we did not observe increased shrub and sapling growth at our sites, future hemlock mortality has the potential to exacerbate population declines by creating increasingly undesirable habitat structure.

There is some evidence that Acadian Flycatchers preferentially select less-infested areas for nest sites within declining hemlock stands. In central Pennsylvania, hemlocks near Acadian Flycatcher nests had less HWA infestation and lower mortality than those throughout the stand (Becker et al. 2008). This agrees with our finding that hemlock mortality was lower in nest plots (4.8%) than in random plots (8.1%) at DEWA, though Becker et al. (2008) observed a much greater discrepancy (7% vs. 35%).

Nest-substrate preferences and nest placement.—Our finding that hemlock branches were a highly preferred nest substrate is supported by several other studies (Table 1). Given that HWA was not yet heavily influencing shrub and sapling growth at our sites, it is possible that Acadian Flycatchers were responding to a loss of suitable nest sites. The height of nests recorded in the present
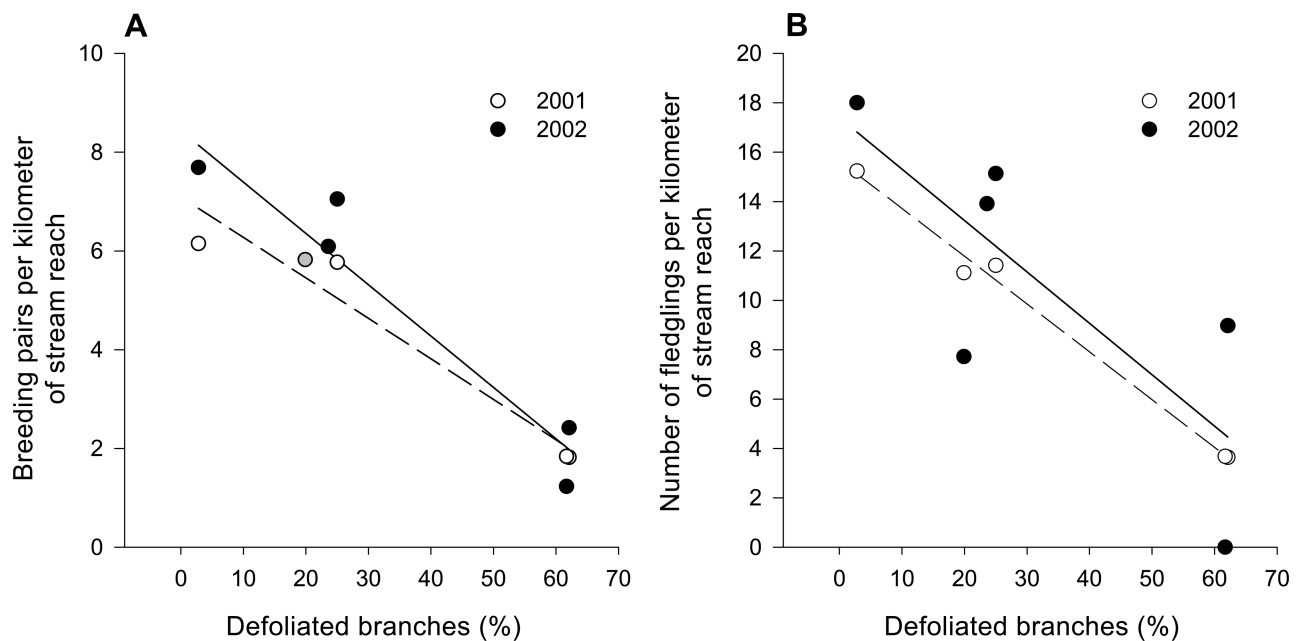

Fig. 3. Relationship of Acadian Flycatcher pair density and breeding productivity to lower-branch health (percent defoliated branches) at the Delaware Water Gap (DEWA) sites. (A) Number of breeding pairs per kilometer of study site. (B) Number of young fledged per kilometer of study site. Gray symbol represents a site that is identical for 2001 and 2002.

study (range: 1.5–16.1 m) corresponds closely with the hemlock lower canopy, which tends to be first affected by HWA (T. Master pers. obs.). Our sites varied widely in the extent of hemlock lower-branch defoliation (0–62%). Also supporting a nest-site-limitation hypothesis is the observation that hemlock preference values were lower at our two most-infested sites, where American Beech preference values were correspondingly higher (Table 4). More data are needed, however, because use estimates from these sites are based on relatively few nests.

Alternatively, Acadian Flycatchers may be responding to some unmeasured habitat variable correlated with defoliation. For example, it is possible that insect prey availability decreases along with foliage volume as infestation progresses. Published studies of insect abundance in relation to HWA infestation are lacking.

Breeding density, productivity, and nest survival.—Variation in pair density of Acadian Flycatchers along Appalachian streams is likely attributable to several factors, including competition, predation, and landscape characteristics (Whitehead and Taylor 2002), none of which was measured in the present study. Our results are based on relatively few sites (necessitated by a nest-searching study design), which limits the inferences that can be drawn. Nevertheless, hemlock defoliation was clearly the best-performing of the candidate models evaluated at DEWA sites and explained 92–94% of the variation observed (r^2) during both study years. Also, sites in the lightly infested PNR region, though perhaps not directly comparable, had pair densities similar to those of less-infested DEWA sites (Table 5). Site-level productivity measurements exhibited a similar negative trend with defoliation at DEWA sites but were more variable, partly because of variation in nesting success.

Nest survival rates were substantially higher at DEWA than at PNR sites (means: 66% vs. 37%). Three other studies in the region averaged 47% (range: 43–55; Bell and Whitmore 2000, Fauth and Cabe 2005, Becker et al. 2008). Because survival rates were not related to defoliation within DEWA sites, the relatively high rates at those sites are perhaps more likely a result of regional differences than of HWA infestation (e.g., fewer predators in defoliated stands). At PNR sites, sapling density best explained variation in nest survival. Although deserving of further study, this result is likely influenced by the Linn site, which had exceptionally high sapling densities and poor nest survival (Tables 2 and 5).

Regional patterns of habitat preference.—Although Acadian Flycatchers are associated with a wide variety of habitats throughout their range (Whitehead and Taylor 2002), hemlock appears to be an important habitat in the Northeast and much of the Appalachian Highlands. For example, 85% of territories from 22 hardwood and hemlock ravines near our DEWA study area occurred in hemlock habitat (Ross et al. 2004). Hemlock has been noted as a characteristic habitat for the species in northern Pennsylvania (Brauning 1992), western New York (Eaton 1988), northern New Jersey (Benzinger 1994), and southern New England (Zeranski and Baptist 1990, Lyons and Livingston 1997). Use of hemlock habitat is also reported farther south in the Appalachians (Wilcove 1988, Murray and Stauffer 1995, Fauth and Cabe 2005), and it is a preferred habitat in Great Smoky Mountains National Park (Shriner 2001). It is unclear whether these associations reflect an explicit preference for hemlock habitat or for the sheltered ravine habitats in which hemlocks grow. Regardless, large numbers of Acadian Flycatcher pairs likely occur in hemlock forests throughout the eastern United States.

Hemlock mortality and long-term habitat changes.—Long-term studies of HWA infestation predict ultimate replacement by hardwoods such as Black Birch and oaks (*Quercus* spp.; Small et al. 2005, Eschtruth et al. 2006). The degree to which Acadian Flycatcher populations can adapt to these changes is unknown. At the stand level, tree and shrub species commonly used for nesting in hardwood habitats (e.g., American Beech, American Witchhazel) will likely be available in replacement forests. However, given the habitat specificity apparent in the northeastern portion of their range (Tingley et al. 2002, Ross et al. 2004) and their history of range retractions in the area (Whitehead and Taylor 2002), the likelihood of adaptation is far from certain. In addition, emerging invasive forest pathogens such as beech bark disease (*Nectria* sp.; Runkle 2005) and the Asian Long-horned Beetle (*Anoplophora glabripennis* Mot.; Haack et al. 1997) have the potential to compound disturbance in many preferred habitats.

It is possible that the ultimate loss of the ~1 million ha of hemlock-dominated forest in the eastern United States (Ellison et al. 2005) could result in population declines and range contractions of Acadian Flycatchers. The mechanism of decline appears to be habitat avoidance in response to defoliation, whether because of a lack of nest sites, a lack of insect prey, or some other factor. This warrants further study, and it may be relevant to other bird species or other forest pathogens.

Temporal trends across multiple sites can be especially valuable in elucidating cause and effect in studies of forest pathogens (e.g., Rabenold et al. 1997). We recommend continued monitoring of Acadian Flycatchers and other sensitive species, especially in as-yet-uninfested habitats. Such baseline data will be needed to fully understand the consequences of hemlock decline on biodiversity.

Literature Cited

Allen, M. C. 2008. Potential effects of hemlock decline on Acadian Flycatcher populations in Pennsylvania with implications for the northeastern U.S. M.S. thesis, East Stroudsburg University, East Stroudsburg, Pennsylvania.

Becker, D. A., M. C. Brittingham, and C. B. Goguen. 2008. Effects of hemlock woolly adelgid on breeding birds at Fort Indiantown Gap, Pennsylvania. Northeastern Naturalist 15:227–240.

Bell, J. L., and R. C. Whitmore. 2000. Bird nesting ecology in a forest defoliated by gypsy moths. Wilson Bulletin 112:524–531.

Benzinger, J. 1994. Hemlock decline and breeding birds. II. Effects of habitat change. Records of New Jersey Birds 20:34–51.

Brauning, D. W. 1992. Acadian Flycatcher (*Empidonax virescens*). Pages 200–201 *in* Atlas of Breeding Birds in Pennsylvania (D. W. Brauning, Ed.). University of Pittsburgh Press, Pittsburgh, Pennsylvania.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Castello, J. D., D. J. Leopold, and P. J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience 45:16–24.

Costa, S., and B. Onken. 2006. Standardized Sampling for Detection and Monitoring of Hemlock Woolly Adelgid in Eastern Hemlock Forests. FHTET-2006-16. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Washington, D.C.

Eaton, S. W. 1988. Acadian Flycatcher *Empidonax virescens*. Pages 250–251 *in* The Atlas of Breeding Birds in New York State (R. F. Andrle and J. R. Carroll, Eds.). Cornell University Press, Ithaca, New York.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, and others. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36:1435–1450.

Evans, R. A. 2004. Hemlock woolly adelgid and the disintegration of eastern hemlock ecosystems. Park Science 22:53–56.

Fauth, P. T., and P. R. Cabe. 2005. Reproductive success of Acadian Flycatchers in the Blue Ridge Mountains of Virginia. Journal of Field Ornithology 76:150–157.

Haack, R. A., K. R. Law, V. C. Mastro, H. S. Ossenbruggen, and B. J. Raimo. 1997. New York's battle with the Asian longhorned beetle. Journal of Forestry 95:11–15.

Haney, J. C. 1999. Hierarchical comparisons of breeding birds in old-growth conifer-hardwood forest on the Appalachian Plateau. Wilson Bulletin 111:89–99.

Hazler, K. R. 2004. Mayfield logistic regression: A practical approach for analysis of nest survival. Auk 121:707–716.

Kizlinski, M. L., D. A. Orwig, R. C. Cobb, and D. R. Foster. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. Journal of Biogeography 29:1489–1503.

Lewis, J. 1999. Nest-site selection and productivity of the Acadian Flycatcher (*Empidonax virescens*) in the southwestern Appalachian Mountains. M.S. thesis, Ball State University, Muncie, Indiana.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395–405.

Lyons, P. J., and J. E. Livingston. 1997. Identification and characterization of Acadian Flycatcher breeding habitat on Quabbin Reservation. Silvio O. Conte National Fish and Wildlife Refuge, Department of Conservation and Recreation, Belchertown, Massachusetts.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13:195–198.

Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. Auk 117:615–626.

Martin, T. E., C. R. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.

Matsuoka, S. M., C. M. Handel, and D. R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. Canadian Journal of Zoology 79:1678–1690.

Mayfield, H. [F.] 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Mumford, R. E. 1964. The breeding biology of the Acadian Flycatcher. Miscellaneous Publications of the Museum of Zoology, no. 125. University of Michigan, Ann Arbor.

Murray, N. L., and D. F. Stauffer. 1995. Nongame bird use of habitat in central Appalachian riparian forests. Journal of Wildlife Management 59:78–88.

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.

Osborne, P. 1985. Some effects of Dutch elm disease on the birds of a Dorset dairy farm. Journal of Applied Ecology 22:681–691.

Potvin, C. 1993. ANOVA: Experiments in controlled environments. Pages 46–68 *in* Design and Analysis of Ecological Experiments (S. M. Scheiner and J. Gurevitch, Eds.). Chapman & Hall, New York.

Rabenold, K. N., P. T. Fauth, B. W. Goodner, J. A. Sadowski, and P. G. Parker. 1997. Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. Conservation Biology 12:177–189.

Ross, R. M., R. M. Bennett, C. D. Snyder, J. A. Young, D. R. Smith, and D. P. Lemarie. 2003. Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. Ecology of Freshwater Fish 12:60–65.

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.

Runkle, J. R. 2005. Twenty-four years of change in an old *Tsuga canadensis* woods affected by beech bark disease. Journal of the Torrey Botanical Society 132:483–491.

SAS Institute. 2004. SAS/STAT 9.1 User's Guide. SAS Institute, Cary, North Carolina.

Scheiner, S. M. 1993. MANOVA: Multiple response variables and multispecies interactions. Pages 94–112 *in* Design and Analysis

of Ecological Experiments (S. M. Scheiner and J. Gurevitch, Eds.). Chapman & Hall, New York.

Shearer, J. A. 1990. Studies of the Acadian Flycatcher (*Empidonax virescens*): Responses to Dimilin treatments and nest site selection. M.S. thesis, West Virginia University, Morgantown.

Sheehan, J., Jr. 2003. Habitat selection in the Acadian Flycatcher: The potential impact of hemlock woolly adelgid infestations and other anthropogenic stressors. M.S. thesis, East Stroudsburg University, East Stroudsburg, Pennsylvania.

Shriner, S. A. 2001. Distribution of breeding birds in Great Smoky Mountains National Park. Ph.D. dissertation, North Carolina State University, Raleigh.

Small, M. J., C. J. Small, and G. D. Dreyer. 2005. Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. Journal of the Torrey Botanical Society 132:458–470.

Snyder, C. D., J. A. Young, D. P. Lemarié, and D. R. Smith. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences 59:262–275.

Swartzentruber, B. 2004. The effects of hemlock woolly adelgid on breeding populations of three species of eastern hemlock dependent songbirds. M.S. thesis, East Stroudsburg University, East Stroudsburg, Pennslyvania.

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.

Walkinshaw, L. H. 1966. Studies of the Acadian Flycatcher in Michigan. Bird-Banding 37:227–257.

Whitehead, D. R., and T. Taylor. 2002. Acadian Flycatcher (*Empidonax virescens*). *In* The Birds of North America, no. 614 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Whitney, G. G. 1990. The history and status of the hemlock-hardwood forests of the Allegheny Plateau. Journal of Ecology 78:443–458.

Wilcove, D. S. 1988. Changes in the avifauna of the Great Smoky Mountains: 1947–1983. Wilson Bulletin 100:256–271.

Wilson, R. R., and R. J. Cooper. 1998. Acadian Flycatcher nest placement: Does placement influence reproductive success? Condor 100:673–679.

Zeranski, J. D., and T. R. Baptist. 1990. Connecticut Birds. University Press of New England, Hanover, Connecticut.

Associate Editor: A. D. Rodewald