



Spring bird migration as a dispersal mechanism for the hemlock woolly adelgid

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Abstract In eastern North America, the invasive hemlock woolly adelgid (*Adelges tsugae* Annand), has expanded northward at a pace that exceeds predictions from mechanistic models, suggesting successful long-distance dispersal despite the only viable dispersive phase being a flightless nymph, or “crawler.” We hypothesize that migrating birds may contribute to long-distance dispersal of crawlers by passively transporting them in their plumage during northward migration. We collected hemlock woolly adelgid crawlers from the plumage of wild birds in Connecticut hemlock forests in spring and summer 2016–2017 and evaluated the factors that influence crawler loads on wild birds. Of 456 birds examined, 40 individuals of 22 species carried adelgid crawlers. Crawler loads varied strongly over time, showing a mid-spring peak that mirrored the phenological pattern in crawler abundance. However, crawler load was not affected by either local crawler abundance at capture sites or the degree of bird species association with hemlock forests. To test whether dispersed crawlers could start new invasions, we

experimentally simulated avian-assisted dispersal of adelgids onto uninfested nursery hemlocks. Although rare, crawlers placed on birds did settle successfully on experimental branches during the adelgid’s summer generation. Our study confirms that birds carry hemlock woolly adelgid crawlers most often during the period of peak spring songbird migration, and that crawlers can move off bird plumage to settle on hemlock foliage. Bird-mediated, long-distance dispersal of crawlers likely has played a key role in hemlock woolly adelgid spread, and with warming temperatures, this mechanism may continue to be important for future range expansion.

Keywords *Adelges tsugae* · Biotic interactions · Phenology · Invasive species · Ectozoochory

Introduction

Birds contribute to the exchange of organisms among ecosystems by carrying plant and animal propagules on their bodies or in their digestive tracts during migration (Viana et al. 2013; Bauer and Hoye 2014). Numerous studies of species with disjunct ranges implicate migratory birds as dispersal vectors, especially in cases where species divergence times are anachronous with potentially explanatory geological events (Stevens and Hogg 2003; Popp et al. 2011; Lewis et al. 2014; Havill et al. 2016). Birds transport other organisms via two processes: endozoochory, or

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internal retention, and ectozoochory, or external adhesion. Unlike wind, birds can increase the dispersal success of propagules through deliberate, directed movement among suitable habitats, and over longer distances (Carlo et al. 2009; Carlo and Tewksbury 2013; Carlo and Morales 2016). To achieve bird-assisted long-distance migration, an organism or its propagules must interact with birds prior to or during migration, endure a migratory flight, and survive in suitable habitat post-dispersal.

As dispersers, migratory birds hold the potential to hasten biological invasions. One strong candidate for bird-assisted invasion is the hemlock woolly adelgid (*Adelges tsugae* Annand), a parasite of eastern and Carolina hemlock (*Tsuga canadensis* and *T. caroliniana*). Introduced to the eastern USA from Japan prior to 1951 (Stoetzel 2002), hemlock woolly adelgid feeds at the base of hemlock needles (Young et al. 1995). Severe adelgid infestations have caused widespread hemlock mortality throughout the Carolina hemlock's range, and in > 45% of the current range of the eastern hemlock, perhaps due to lack of competition, reduced host plant defenses, and/or lack of effective predators in its introduced range (Fig. 1; Morin et al. 2011; McKenzie et al. 2014). The eastern hemlock is considered a foundation species because it creates and maintains a moist, temperate climate necessary for the survival of obligate plant and animal species (Orwig et al. 2012; Ellison 2014). Hemlock mortality due to adelgid infestation eliminates the microclimates necessary for a host of organisms and can fundamentally transform the biotic communities living in eastern forests (Tingley et al. 2002; Rohr et al. 2009; Siderhurst et al. 2010; Toenies et al. 2018).

The life cycle of the hemlock woolly adelgid consists of two generations per year, largely dominated by flightless, asexual individuals (Fig. 2). The spring generation hatches from late April to late May in the Northeast USA, settles to feed throughout the spring, and gives rise to the summer generation crawlers toward the end of June. The summer generation then aestivates in late summer and early fall and resumes feeding during the winter (McClure 1989). A mobile "crawler" stage emerges in each generation. These individuals migrate to a feeding site where they insert their stylets and remain sessile for the rest of their lives. A density-dependent proportion of the spring generation can develop into

winged sexual adults which obligately reproduce on certain species of Asian spruce (*Picea* spp.; McClure 1991). The offspring of these winged migrants, however, are inviable in eastern North America because suitable spruce species do not exist in this region (McClure 1991). Dispersal of the hemlock woolly adelgid in the USA thus depends on vectors such as wind, humans, and wildlife to transport spring and summer generation crawlers (McClure 1990).

Since crawlers exhibit a first peak in abundance in the eastern USA between April and May—varying by location and year-to-year weather-dependent phenology (McClure 1987; Mausel et al. 2008)—it is plausible that directed, northward bird migration during the temperate North American spring has aided in the dispersal and expansion of this invasive species. McClure (1990) determined that wild birds can carry hemlock woolly adelgid eggs and crawlers on their feathers up to 1 km from an infested forest and suggested that dispersal potential could be greater during migration. Although this work documented that birds can carry ectozoochoric crawlers, mechanistic understanding is warranted to understand the potential for avian-assisted adelgid dispersal. Russo et al. (2016) found that the transfer of crawlers from hemlock branches onto bird surrogates is highest in May, when songbird migration peaks in northeastern USA (La Sorte et al. 2016). Additionally, Morin et al. (2009) determined that the spatial pattern of adelgid spread in North America over the past 60 years has been anisotropic, with expansion occurring disproportionately along a south-to-north trajectory, matching the direction of spring bird migration. Fitzpatrick et al. (2012) developed a model of hemlock woolly adelgid range expansion in the eastern USA that underestimated its northward expansion, which they attribute to the lack of knowledge about the mechanism or frequency of long-distance dispersal events. Havill et al. (2016) even speculated that hemlock woolly adelgid's introduction to western North America from Asia before the last glacial period was facilitated by long-distance bird flight across Beringia.

The ectozoochoric transport of crawlers, however, does not guarantee successful dispersal—for that to occur, adelgids must move off bird plumage and survive to settle, feed, and reproduce on hemlock trees. Many studies have documented the germination of seeds following endozoochoric dispersal by birds

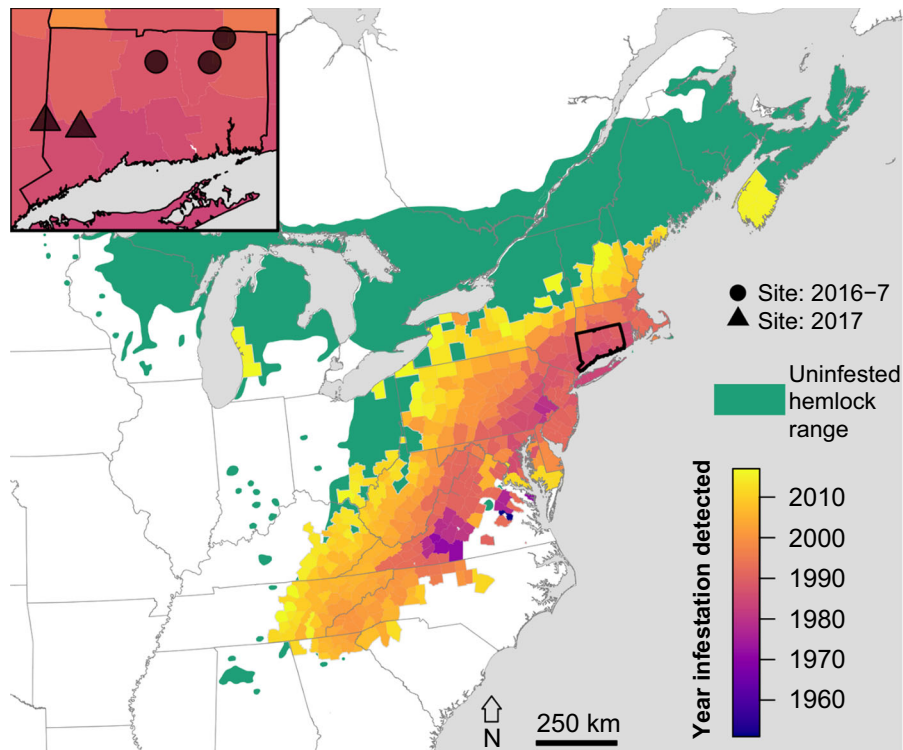


Fig. 1 Range of eastern hemlock and invasive hemlock woolly adelgid in eastern North America relative to sampling sites. Hemlock woolly adelgid was first detected in eastern North America in 1951 and has since spread throughout much of the range of the eastern hemlock—particularly northward and eastward. In 2016 and 2017, we sampled for adelgids on wild

birds caught at five sites in Connecticut, USA (inset; black outline on large map), where hemlock woolly adelgid first appeared in the 1980s. Map data on hemlock and adelgid range courtesy of USDA Forest Service, Northeastern Area State and Private Forestry, Forest Health Protection

(Charalambidou and Santamaria 2002; Charalambidou et al. 2003; van Leeuwen and van der Velde 2012), but few studies have tested the viability of ectozoochoric propagules dispersed by birds (Scharf and DePalma 1981; van Leeuwen and van der Velde 2012; Reynolds et al. 2015). Dispersal and subsequent viability of terrestrial arthropods dispersed by birds is generally unexplored (Lebedeva and Krivolutsky 2003; Suetsugu et al. 2018).

Here, we investigate the potential for birds to disperse hemlock woolly adelgids and initiate successful invasions on uninfested trees. We conducted a field study of the factors affecting the number of crawlers found on wild birds and a controlled experiment assessing adelgid settlement success following dispersal. We investigated the following questions: (1) at what point during the period of hemlock woolly adelgid crawler activity do wild birds carry the most crawlers; (2) how does ambient

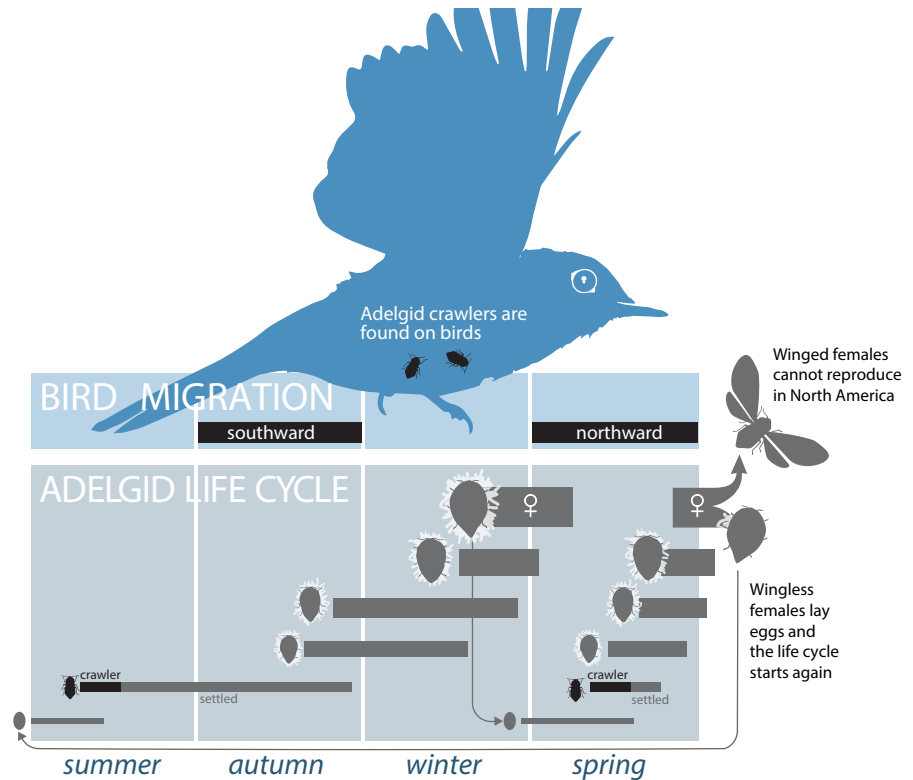
crawler abundance influence the crawler load of birds; (3) are hemlock-associated bird species more likely to carry, and thus spread, hemlock woolly adelgid crawlers; and, (4) are birds capable of depositing crawlers that subsequently settle on uninfested hemlocks?

Methods

Study area

We sampled the plumage of birds captured in five independent eastern hemlock (*Tsuga canadensis*) stands across Connecticut (Fig. 1). Hemlock woolly adelgid was first observed in Connecticut in 1985 (McClure 1987) and now occurs in all counties in the state. The eastern hemlock has a patchy distribution throughout Connecticut—generally growing in

Fig. 2 Schematic showing phenology of hemlock woolly adelgid life cycle and bird migration in eastern North America. The hemlock woolly adelgid has two generations per year, each with four instars, with mobile crawlers hatching in spring and summer. Birds have the potential to pick up dispersing crawlers whenever crawlers are present and active, but the greatest potential for long-distance dispersal occurs with the synchrony of the spring generation of crawlers with northward migrating birds. Adelgid crawlers and life stages are not drawn to scale. Graphic created by Vincent D'Amico (USDA Forest Service)



monotypic or mixed-deciduous stands—with Connecticut positioned approximately halfway along its north–south range (Fig. 1). Birds that breed in hemlock forests typically also breed in boreal forests north of the hemlock’s range, rendering Connecticut hemlock forests a likely stopover habitat for migrants.

Two of our five field sites were within mature hemlock forests of eastern Connecticut: the Moss Tract of UConn Forest in Willington (41°50′48.2″N 72°14′40.4″W) and the Myers Pond Road section of Yale-Myers Forest in Union. At Myers Pond Road, we sampled at two adjacent locations in 2016 (41°59′23.6″N 72°07′50.2″W and 41°59′16.4″N 72°07′48.7″W) but continued at only one location (41°59′16.4″N 72°07′48.7″W) in 2017. We also established a central Connecticut field site in the experimental hemlock stand at the Connecticut Agricultural Experiment Station in Windsor (41°51′00.4″N 72°39′48.7″W). In 2017, we added two additional sites in western Connecticut: one within a logged hemlock ravine at Great Hollow Ecological Research Center in New Fairfield (41°30′31.1″N 73°31′49.5″W) and another in a hemlock-dominated forest surrounding early-

successional habitat at Bent of the River Audubon Sanctuary in Southbury (41°27′41.2″N 73°15′20.7″W).

Crawler load of wild birds

We established four to seven mist net lanes in each hemlock stand and captured birds throughout the period of hemlock woolly adelgid crawler activity in 2016 and 2017. Total mist-net length at any site ranged from 48 to 72 m. We captured birds at each study site approximately once per week during the study period (09-May–12-Jul in 2016 and 15-Apr–27-Jul in 2017). At all sites in both years, we established mist net lanes in a variety of wetland, fluvial, forest interior and edge habitats within hemlock forests, choosing most sites close to or along the edge of a hemlock stand. At Windsor, we set up nets around the perimeter of a densely-planted hemlock stand of approximately 60 trees.

During the 2016 field season, we caught birds ad hoc with no preference for particular species. To increase our sample size for hemlock-associated birds in 2017 (Howe and Mossman 1995; Tingley et al.

2002; Becker et al. 2008), we used a waterproof speaker (Altec Lansing) to broadcast the song of conspecifics (specifically, black-throated green warbler *Setophaga virens*, blue-headed vireo *Vireo solitarius*, blackburnian warbler *Setophaga fusca*, hermit thrush *Catharus guttatus*, Louisiana water-thrush *Parkesia motacilla*, and brown creeper *Certhia americana*) near a mist net approximately four times on 1–5 banding days. We also used a recording of eastern screech owl (*Megascops asio*) songs and calls, accompanied by alarm calls of several songbird species typical of eastern woodlands. These methods can increase avian activity and bring canopy-dwelling birds closer to nets.

Upon extraction from a mist net, each bird was transported in a clean, unused cloth bag to a banding station where crawlers were removed from the plumage. Working quickly, we used compressed air to blow up and down each feather tract over a white collecting tray until we finished collecting biological material (i.e., crawlers or any other organisms; Russo et al. 2016). We wiped the tray clean prior to each trial. For all birds caught in 2016, and for all birds caught before 18-May in 2017, the collecting tray was left uncovered as the bird was banded and processed (1–3 min). Starting 20-May-2017, we modified the protocol so that the tray was covered completely during bird processing to avoid potential contamination of the tray by crawlers from non-avian sources (e.g., wind). In preliminary analyses employing the statistical framework described subsequently, we tested for an effect of contamination for trials conducted prior to 20-May-2017 using method as a binary predictor and found no evidence; we thus ignored this methodological shift in further analyses. Birds were captured under United States Geological Survey Permit 22664 and all methods approved under University of Connecticut Institutional Animal Care and Use Committee Protocol A16-004.

We collected all specimens from the collecting tray using a moistened paintbrush and preserved all material from each collection in 90% ethanol. We also inverted each carrying bag and collected its contents, in case any adelgids fell off the birds prior to compressed air treatment. We banded all birds with a United States Geological Survey-issued band prior to release. We examined all material collected for each trial under a dissecting microscope and isolated adelgid specimens. We stained and slide-mounted all

adelgid specimens and compared each to other candidate species in the adelgid collections at the United States Forest Service Northern Research Station in Hamden, CT, USA. As multiple adelgid species can be found in Connecticut, we confirmed species of collected specimens based on the dorsal wax pore pattern (Blackman and Eastop 1994). Voucher specimens were deposited in the Yale University Peabody Museum with voucher numbers ENT857015–ENT857025, and ENT943122–ENT943147.

Measuring ambient crawler activity

We hypothesized that a bird's crawler load would be influenced by the local density of active crawlers, so at each mist-netting site we estimated local crawler abundance throughout each field season by quantifying crawler activity directly on hemlock trees. At each site we selected five hemlock trees, one at each of the four corners of the netting area and one in the center. We then tied a 24 × 2.9 cm strip of pink vinyl flagging tape around one branch, approximately 1–2 m above the ground. We chose branches located at each of the four cardinal directions on each tree, resulting in 20 monitored hemlock branches per site. The two ends of the flagging hung at equal lengths on either side of the branch. Hemlock woolly adelgid crawlers regularly wandered off branches and onto the flagging. Since all flags had the same surface area, we used the raw number of crawlers on each flag as an index of crawler abundance. We also tied flagging around a control branch on a non-hemlock tree or shrub. All flags were monitored every 5–10 d from 25-May to 20-Jul in 2016 and 15-Apr to 27-Jul in 2017. On each visit, we removed and replaced any flagging that held crawlers.

We estimated ambient crawler abundance as the average number of crawlers per flag per week, which standardizes across variable numbers of days between samples and variable numbers of flags (e.g., when individual flags were lost). For every bird sampling day, we assigned an ambient abundance based on the closest monitoring period prior to or on the day of capture. If there was no monitoring for crawlers prior to or on the day of capture of a bird (e.g., on the first visit to each site in a year), then we used the ambient abundance for the first monitoring period after the day of capture.

Statistical analysis of crawler loads

We used a mixture of generalized additive models (GAMs) and generalized linear models (GLMs) to explore relationships between the number of crawlers found on birds (crawler load) and five a priori covariate predictors: (1) day of year; (2) site of capture; (3) year of capture; (4) ambient crawler abundance at the capture site; and (5) a categorical variable designating the strength of a bird species' association with hemlock. Species were designated as "strong," "facultative," or "weak" hemlock associates based on a literature review of hemlock forest use by breeding birds, focusing on studies that widely surveyed for birds using hemlock forests (Howe and Mossman 1995; Tingley et al. 2002; Becker et al. 2008). Species strongly associated with hemlock in any of the studies were designated as strong associates, those reported in at least two studies were designated as facultative, and those detected in fewer than two studies were designated as weak hemlock associates (Table 1). Most covariates (site, year, ambient abundance, and hemlock association) were modeled as strictly linear predictors of the number of crawlers found per bird. However, we looked for a non-linear effect of the day of year on crawler loads because we expected that the phenological pattern of abundance may have one or more peaks due to emergence cycles of different adelgid generations (McClure 1987; Russo et al. 2016). Consequently, day of year was modeled within the GAM framework via a non-linear smoother, while all models without day of year used a GLM framework. All GAM and GLM models assumed the response variable to be Poisson-distributed, with covariates modeled using a log-link (Zuur et al. 2009).

Our inferential goals were to assess the strength of support for our five main covariates in explaining observed abundances of crawlers on captured birds. We thus used an information theoretic approach to evaluate a full candidate set of 32 models, which comprised all additive relationships among covariates, as well as a null (intercept-only) model. We employed the small-sample corrected Akaike Information Criterion (AICc) to compare models (Burnham and Anderson, 2002). After confirming that the variance inflation factor (\hat{c}) of the full model was < 1 , we assumed that the data were not overdispersed (Arnold 2010). We ranked models by

difference in AICc (Δ_i) and calculated the weight of evidence in support of each model (w_i ; Burnham and Anderson 2002). We used the R programming language for all statistical analyses (R Core Team 2018), including the 'mgcv' package for GAM models (Wood 2010).

Post-dispersal settlement of crawlers

For the experimental test of whether crawlers can leave birds to start new infestations, we purchased ten nursery-raised, 1.0–1.5 m eastern hemlocks with no history of pesticide treatment or infestation and potted them at the Connecticut Agricultural Experiment Station in Windsor, CT, USA. The use of nursery hemlocks prevented the infestation of wild hemlocks. We performed three different types of experimental infestation trials: (1) placing 15 live crawlers on the belly feathers of a small, passerine bird mount (Canada warbler *Cardellina canadensis* or palm warbler *Setophaga palmarum*) and perching the mount upright on an uninfested branch tip, with feet and belly feathers touching the branch, for 1 min; (2) the same experimental setup but with perching time of 15 min; and (3) placing 15 crawlers directly onto the branch tip. We used the corner of a flat paintbrush to place crawlers onto bird mounts and branches. Each treatment was repeated 50 times, with 25 trials during the spring adelgid generation (treatments started 12-May-2017 to 23-May-2017) and 25 during the summer generation (all treatments started 05-Jul-2017). For both generations, we also performed ten trials each of two negative control treatments: (4) perching a bird mount without crawlers applied, and (5) using branches with no treatment at all. In total, 190 branches were used in the experiment (150 treatment, 40 control). In all cases, we selected and closely examined a 12 cm branch tip section before experimentation using a $2.75\times$ magnification jeweler's headset to confirm the absence of prior infestation. We collected all crawlers used in the experiment from infested trees on the property. For each branch (treatment and control), we tied a 24×24 cm fabric enclosure around the 12 cm tip, sealed the loose end with masking tape, and labeled with flagging immediately after concluding any treatment. We examined experimental branches after 2–4 weeks for signs of infestation indicated by the presence of settled first-instar adelgids. Crawlers typically settle

Table 1 Summary of bird captures in five Connecticut hemlock stands and total crawler specimen collection during the 2016 and 2017 field season, ordered by decreasing number of adelgids found on individuals per species

Common name	Scientific name	Hemlock association	Migration status	Number of captures	Number of adelgids	Number of birds with adelgids
Veery	<i>Catharus fuscescens</i>	Facultative	Neotropical migrant	67	13	11
Louisiana waterthrush	<i>Parkesia motacilla</i>	Facultative	Neotropical migrant	20	4	3
House sparrow	<i>Passer domesticus</i>	Weak	Resident	5	4	3
Gray catbird	<i>Dumetella caroliniana</i>	Facultative	Neotropical migrant	41	3	3
Rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	Facultative	Neotropical migrant	1	3	1
Northern cardinal	<i>Cardinalis cardinalis</i>	Facultative	Resident	11	2	1
Black-and-white warbler	<i>Mniotilta varia</i>	Facultative	Neotropical migrant	8	2	2
American goldfinch	<i>Spinus tristis</i>	Facultative	Temperate migrant	7	2	1
Song sparrow	<i>Melospiza melodia</i>	Weak	Temperate migrant	37	2	2
Blue-headed vireo	<i>Vireo solitarius</i>	Strong	Neotropical migrant	3	2	1
Brown-headed cowbird	<i>Molothrus ater</i>	Facultative	Temperate migrant	4	2	1
Hairy woodpecker	<i>Dryobates villosus</i>	Facultative	Resident	2	1	1
Black-throated green warbler	<i>Setophaga virens</i>	Strong	Neotropical migrant	6	1	1
Ovenbird	<i>Seiurus aurocapilla</i>	Facultative	Neotropical migrant	67	1	1
Wood thrush	<i>Hylocichla mustelina</i>	Facultative	Neotropical migrant	12	1	1
Eastern towhee	<i>Pipilo erythrophthalmus</i>	Facultative	Temperate migrant	11	1	1
Canada warbler	<i>Cardellina canadensis</i>	Facultative	Neotropical migrant	9	1	1
Magnolia warbler	<i>Setophaga magnolia</i>	Facultative	Neotropical migrant	1	1	1
Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>	Facultative	Temperate migrant	4	1	1
Tufted titmouse	<i>Baeolophus bicolor</i>	Facultative	Resident	4	1	1
Blue jay	<i>Cyanocitta cristata</i>	Facultative	Temperate migrant	4	1	1
White-breasted nuthatch	<i>Sitta carolinensis</i>	Facultative	Resident	2	1	1
Black-capped chickadee	<i>Poecile atricapillus</i>	Facultative	Resident	25	0	0
Black-throated blue warbler	<i>Setophaga caerulescens</i>	Facultative	Neotropical migrant	9	0	0
Eastern phoebe	<i>Sayornis phoebe</i>	Facultative	Temperate migrant	7	0	0
American robin	<i>Turdus migratorius</i>	Facultative	Temperate migrant	15	0	0
Chipping sparrow	<i>Spizella passerina</i>	Weak	Neotropical migrant	11	0	0
Red-eyed vireo	<i>Vireo olivaceus</i>	Facultative	Neotropical migrant	12	0	0
Pileated woodpecker	<i>Hylatomus pileatus</i>	Facultative	Resident	1	0	0
Common yellowthroat	<i>Geothlypis trichas</i>	Weak	Neotropical migrant	3	0	0
Great crested flycatcher	<i>Myiarchus crinitus</i>	Facultative	Neotropical migrant	4	0	0
Cedar waxwing	<i>Bombycilla cedrorum</i>	Facultative	Temperate migrant	4	0	0
Hermit thrush	<i>Catharus guttatus</i>	Strong	Temperate migrant	4	0	0
Downy woodpecker	<i>Picoides pubescens</i>	Facultative	Resident	4	0	0
Winter wren	<i>Troglodytes hiemalis</i>	Strong	Temperate migrant	1	0	0
Northern waterthrush	<i>Parkesia noveboracensis</i>	Facultative	Neotropical migrant	3	0	0
Pine warbler	<i>Setophaga pinus</i>	Facultative	Temperate migrant	3	0	0
Northern mockingbird	<i>Mimus polyglottos</i>	Weak	Resident	1	0	0
White-throated sparrow	<i>Zonotrichia albicollis</i>	Weak	Temperate migrant	1	0	0
European starling	<i>Sturnus vulgaris</i>	Weak	Temperate migrant	1	0	0
House finch	<i>Haemorhous mexicanus</i>	Weak	Temperate migrant	2	0	0
Swainson's thrush	<i>Catharus ustulatus</i>	Facultative	Neotropical migrant	1	0	0

Table 1 continued

Common name	Scientific name	Hemlock association	Migration status	Number of captures	Number of adelgids	Number of birds with adelgids
Yellow warbler	<i>Setophaga petechia</i>	Weak	Neotropical migrant	1	0	0
Hooded warbler	<i>Setophaga citrina</i>	Facultative	Neotropical migrant	1	0	0
Worm-eating warbler	<i>Helmitheros vermivorum</i>	Facultative	Neotropical migrant	2	0	0
Indigo bunting	<i>Passerina cyanea</i>	Weak	Neotropical migrant	4	0	0
Eastern wood-pewee	<i>Contopus virens</i>	Facultative	Neotropical migrant	1	0	0
Chestnut-sided warbler	<i>Setophaga pensylvanica</i>	Facultative	Neotropical migrant	1	0	0
Blue-winged warbler	<i>Vermivora cyanoptera</i>	Facultative	Neotropical migrant	5	0	0
Common grackle	<i>Quiscalus quiscula</i>	Facultative	Neotropical migrant	1	0	0
Red-breasted nuthatch	<i>Sitta canadensis</i>	Strong	Temperate migrant	1	0	0
Ruby-throated hummingbird	<i>Archilochus colubris</i>	Facultative	Neotropical migrant	1	0	0
Total				456	50	40

Species are classified based on hemlock association (Strong, Facultative, or Weak) and migration status: neotropical migrant species perform migrations to the neotropics; temperate migrants perform short-distance migrations within North America; and resident species typically do not migrate (Sauer et al. 1999; Zuckerberg et al. 2016). Many resident species, however, are capable of long-distance movements, and some individuals of species classified as temperate migrants do not migrate each year

within a few days after emergence (McClure 1992), so if crawlers had not settled after this time, we concluded that any infestation would fail. We performed a series of Fisher's exact tests to compare the probability of individual crawler settlement among all experimental conditions.

Results

Ambient crawler abundance

Over 2 years of field work, we collected 1914 samples of ambient crawler abundance at our five sites. Across all hemlock samples ($n=1847$), the median number of crawlers counted per sample was 0, with a maximum of 107. We did not find any crawlers on any of the 67 control samples collected from non-hemlock trees or shrubs. The abundance of ambient crawlers showed a strongly bi-modal pattern (Fig. 3a), consistent with the emergence of each adelgid generation.

Crawler load of wild birds

We captured 382 birds of 52 species and sampled crawler loads a total of 456 times, including 74

recaptures. Forty captures (8.8%), involving 22 species, yielded a total of 48 crawlers and two adelgid eggs (Table 1), with a median of 1 crawler found per carrying bird. The greatest number of crawlers ($n=3$) was collected from a female rose-breasted grosbeak (*Pheucticus ludovicianus*). Crawlers were typically found on 1–3 individual birds per species, except for the veery (*Catharus fuscescens*), upon which we found crawlers on 11 individuals out of 67 captures (16%). Other species with large sample sizes showed lower rates of carrying crawlers, including black-capped chickadee (*Poecile atricapillus*, 0 crawlers in 25 captures), gray catbird (*Dumetella carolinensis*, 3 out of 41 captures), ovenbird (*Seiurus aurocapilla*, 1 out of 67 captures), and song sparrow (*Melospiza melodia*, 2 out of 36 captures).

As multiple adelgid species can be found in Connecticut, we confirmed the species identity of 31 of the 48 crawlers as *Adelges tsugae*. The remaining 17 specimens were lost or destroyed in slide preparation, but since only one other adelgid species, pine bark adelgid (*Pineus strobi*), occurred at one field site at low density, we assumed the remaining adelgids to be *A. tsugae* and treat them as such in our analysis.

Table 2 Top 13 (of 32) generalized additive or generalized linear models examining the effect of candidate covariates on crawler carrying rate of birds in hemlock forests

Model	k	$\log(\mathcal{L})$	AIC_c	Δ_i	w_i
Day	1	-140.56	291.37	0.00	0.28
Day+abundance	2	-139.80	291.93	0.55	0.21
Day+year	3	-140.56	293.40	2.02	0.10
Day+species	4	-139.62	293.50	2.13	0.10
Day+year+abundance	4	-139.80	293.97	2.60	0.08
Day+abundance+species	5	-139.10	294.58	3.21	0.06
Day+year+species	6	-139.60	295.54	4.17	0.03
Day+site	5	-137.50	295.61	4.24	0.03
Day+year+site	7	-137.66	295.93	4.56	0.03
Day+year+abundance+species	7	-139.08	296.63	5.26	0.02
Day+year+abundance	6	-137.18	296.99	5.62	0.02
Day+site+species	8	-136.04	297.07	5.69	0.02
Day+year+abundance+site	8	-137.36	297.33	5.96	0.01

Covariate names: day=non-linear effect of day of year; abundance=ambient crawler abundance; species=categorical level of bird species association with eastern hemlock; year=year of study; site=categorical effect of study site. k =number of parameters in model; $\log(\mathcal{L})$ =log-likelihood of model; Δ_i =difference in AIC_c value from top model; w_i =model weight

The top thirteen models ($\Delta_i < 6$) explaining variation in adelgid load all contained day of year but varied greatly in other included covariates (Table 2). The top model ($w_i=0.28$) included only the smoothed effect of day of year, while the one other model with $\Delta_i < 2$ included both day of year and ambient crawler abundance ($w_i=0.21$). There was moderate support for the effect of year on crawler load of birds, and very little model support for crawler load varying across sites or based on the level of association between birds and hemlock habitat. Our global model explained 25.2% of deviance in the data, while the much simpler top model explained 21.8% of deviance.

All top models supported a strong nonlinear relationship between crawler load and day of year. The smoothed relationship showed that crawler carrying rates were highest near the beginning of the sampling period in late April and early May and decreased until approaching zero in late June (Fig. 3b). The periods of highest crawler load correspond to the emergence of spring and summer generations of crawlers (Fig. 3a), and the periods of decreasing crawler load correspond to periods of subsequent crawler settlement.

Post-dispersal settlement of crawlers

Of the 1125 spring generation crawlers applied to branch tips in experimental treatments, two settled. Both crawlers were from treatments that involved placement directly on a branch, and in both cases, the crawlers settled on the annual tree growth from the previous year. Of the 1125 summer generation crawlers applied, 92 settled (8.2%), all on foliage growth of the current year, which had lignified by this second phase of the experiment. Of these 92 crawlers, 31 (33.7%) were from trials in which a bird mount was perched on a branch, and the remaining 61 were placed directly on a branch (Fig. 4). We did not detect crawler settlement on either set of negative control branches ($n=40$, across both generations). Settlement likelihood of summer generation crawlers increased with perch duration (9 successes in 1-min trials, 22 successes in 15-min trials; Fisher's exact test, $p=0.03$), and direct placement of crawlers on branches led to significantly greater settlement success than all other experimental conditions (Fisher's exact test, $p < 0.001$ for all comparisons; Fig. 4). Settlement rates after direct placement or 15-min perch trials were both significantly greater than in negative control trials (Fisher's exact test, $p < 0.001$ and $p=0.001$, respectively). The crawler settlement of 1-min perch

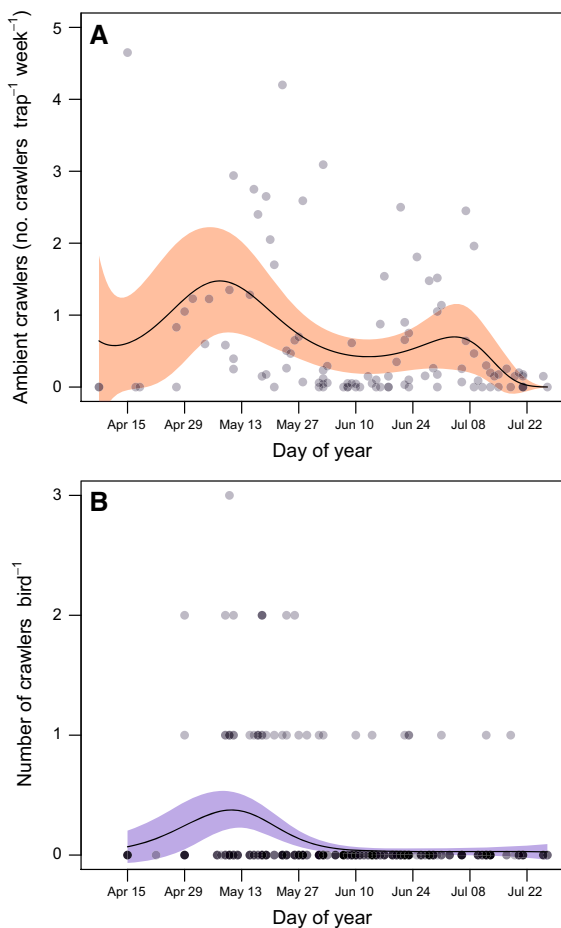


Fig. 3 Phenological trends in hemlock woolly adelgid across 5 hemlock forests in Connecticut. **a** Temporal variation in ambient crawler abundance on hemlock trees. Points correspond to the standardized number of crawlers per trap per week for each monitored location. A quasi-Poisson generalized linear model was fit to the data, using a flexible quintic polynomial as the functional form for the relationship to day of year. **b** Number of crawlers collected from birds in hemlock forests in relation to sampling date. The shaded area indicates the 95% confidence interval and mean (solid line) of the relationship to day of year, estimated using the top generalized additive model from the model set (Table 2). Darker-shaded points indicate a higher frequency of the crawler load count

trials was not significantly different from that of negative controls (Fisher's exact test, $p=0.066$).

Discussion

Our study of hemlock woolly adelgid dispersal by birds of eastern hemlock forests in Connecticut

demonstrates how the annual cycles of vectors and propagules can align to impact dispersal frequency and distance. We show through 2 years of data collection that wild birds carry dispersing adelgid crawlers in their plumage most often during periods of peak crawler abundance, which coincides with the period of spring bird migration in northeastern North America (late April–mid May). These results complement a previous study demonstrating that transfer of hemlock woolly adelgid crawlers from branches to birds also occurs most often during periods of peak crawler abundance (Russo et al. 2016). Confirming bird migration as a long-distance dispersal mechanism requires evidence that birds acquire propagules, that propagules are retained in the plumage during migratory flight, and that birds deposit viable propagules in suitable habitat (Viana et al. 2016). Although our study design cannot confirm that any long-distance dispersal events occurred, our results demonstrate not only that insect and bird phenology are important factors influencing crawler load on birds in hemlock forests, but also that crawlers are capable of actively moving off birds and settling onto uninfested hemlock foliage. Since hemlock woolly adelgids reproduce asexually, a single individual can be sufficient to establish an infestation (Tobin et al. 2013).

We expected birds strongly associated with hemlocks to have the greatest crawler loads, but the degree of association with hemlock was not a strong predictor of whether a bird carried the adelgid. We note, however, that since many hemlock-associated species inhabit higher foliage strata where they are less likely to be caught in mist nets, we have few representative individuals of some strong hemlock-associated species (Table 1). Still, we did find crawlers in the plumage of species strongly associated with hemlock cover, such as black-throated green warbler (*Setophaga virens*) and blue-headed vireo (*Vireo solitarius*; Tingley et al. 2002; Toenies et al. 2018). When McClure (1990) conducted preliminary work examining the adelgid load of birds in infested Connecticut forests, he found crawlers and eggs on birds with several different habitat associations, including ground-dwelling species that neither forage nor nest in hemlocks. Since crawlers are easily displaced from infested branches, wind may spread them to all strata within the forest (McClure 1990; Turner et al. 2011; Fidgen et al. 2015), so that birds

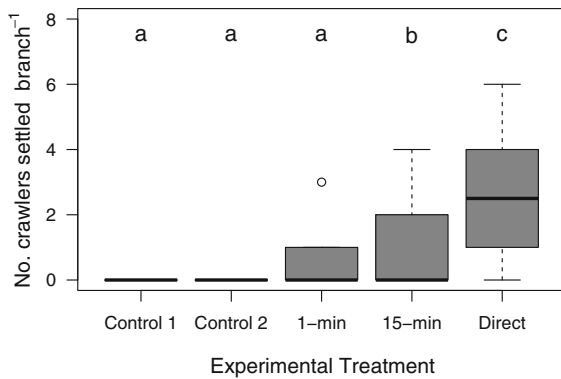


Fig. 4 Boxplots summarizing counts of settled summer-generation crawlers based on experiments where 15 crawlers were experimentally tested for their ability to settle on uninfested hemlock branches after 2–4 weeks. Experiments include two negative controls (control 1: a bird perched with no crawlers, $n=10$; control 2: no bird perched and no crawlers applied, $n=10$), tests where taxidermied birds with crawlers were perched on a branch for either 1 or 15 min ($n=25$ each), and direct placement of crawlers onto branches ($n=25$). Counts of settled crawlers with different letters indicate comparisons that are significantly different (Fisher's exact test, $p < 0.05$). Results of experiments with the spring generation are not shown because experiments only resulted in two successful settlements (see “Discussion”)

that rarely visit hemlocks may acquire crawlers from the air or ground.

Almost 9% of the 456 birds sampled were carrying crawlers or eggs in their plumage, which is nearly one tenth the frequency with which birds carried hemlock woolly adelgid in McClure's study (1990; 86% of 22 birds). Such a stark difference may reflect a decline in per-stand hemlock woolly adelgid density over the last 10–20 years in Connecticut (Preisser et al. 2007). Extremely cold winter weather the year before we began our work, which caused the most severe winter mortality ever recorded in Connecticut (Cheah 2016), may have also contributed our low adelgid collection total in comparison to McClure's study. Differences in sample size and collection procedure could also be important—our larger sample size may better indicate the true carrying frequency. McClure (1990) sampled at two sites in Connecticut, one site on 23 May and the other on 1, 8, and 15 June, and captured only 36 birds, representing 16 species. Our collection procedure may also have been less effective than McClure (1990), who immersed the birds in water with a drop of detergent. While we performed no systematic assessment of the efficacy of our

collecting method, multiple years of experimentation indicate that it is at least sufficient for generating an index of the number of non-parasitic arthropods on birds' plumage. Our method also gives greater consideration to the welfare of captured birds.

While the temporal pattern of crawler load on birds (Fig. 3b) generally followed the local phenology of ambient crawler abundance (Fig. 3a), we did not find evidence for a second peak in crawler loads coinciding with the emergence of the summer adelgid generation in late June and early July. Nearly twice as many adelgid eggs are produced during the spring adelgid generation as during the summer adelgid generation (McClure 1989), but given that transfer of crawlers onto bird surrogates during experiments did exhibit a second peak during the summer emergence (Russo et al. 2016), we expect that an even larger sample might reveal a second peak in crawler loads on wild birds. Behavioral factors also could explain this inconsistency, such as a difference in the tendency for crawlers of each generation to remain on a branch given a disturbance. Empirical tests of crawler behavior would be needed to assess potential differences in dispersal ability between generations.

We also found differences in crawler transfer and settlement across generations, where settlement increased 46-fold from the spring to the summer generation. Successful adelgid settlement benefits from the availability of higher quality, new annual hemlock foliage (McClure 1991). When we performed trials with spring generation crawlers, the annual growth on our nursery hemlocks was not yet lignified. It is likely that crawlers used in these trials may have attempted to settle on the immature growth and failed (C. Cheah, pers. comm.). All summer generation crawlers settled exclusively on the new annual growth, which had lignified by the time we performed the experiment. Since many birds migrate through the eastern USA when annual hemlock growth is either absent or unlignified, spring generation crawlers may need to settle on suboptimal foliage when dispersed by migrating birds.

A crawler's settlement behavior, however, might differ when transported in a live bird's feathers versus placement in the feathers of bird surrogates used in this experiment. In addition, experimental hemlocks in our study received prolonged exposure to full sunlight prior to experimentation, likely advancing their phenology compared to free-living hemlocks in

Connecticut forests, and potentially resulting in atypical settlement conditions for spring generation crawlers by offering immature foliage. Further research should therefore address settlement success of crawlers at each stage of annual hemlock foliage growth, and how dispersal phenology may or may not match with phenology of foliage growth. An experiment that retains branch enclosures through the period of aestivation and reproduction might confirm whether crawlers transferred from birds to branches truly cause a new infestation.

In our study, the dispersal of hemlock woolly adelgid by birds (8.8% of all captures) and the settlement of crawlers upon uninfested branches (4.2% of all trials involving birds) were seemingly rare. However, the sheer magnitude of bird migration in North America—about five billion migratory individuals (Reed et al. 2003)—indicates that bird-mediated dispersal could occur frequently enough to accelerate the adelgid's range expansion. Given the variety of species we found carrying hemlock woolly adelgid, our findings suggest that entire avian assemblages can contribute to the introduction of this destructive, invasive insect to uninfested hemlock forests. Hemlock woolly adelgid infests the Appalachian range of the eastern hemlock and Carolina hemlock (*T. caroliniana* Engelman), and is expected to cover the full northern extent of both species' ranges by 2100 in response to climate change (Paradis et al. 2008). Cold winter temperatures keep the adelgid's range in check, such that winter mortality in its northern extent is often greater than 90% (Cheah 2017). However, the adelgid has become increasingly cold-tolerant since its introduction to eastern North America (Butin et al. 2005). Although state lumber quarantines minimize northward long-distance dispersal of adelgids due to human activity (Gibbs 2002), the results of our study suggest that birds may complicate control efforts by providing long-distance dispersal services. Models of adelgid range expansion are limited by the lack of data documenting long-distance dispersal events (Fitzpatrick et al. 2012; Ferrari et al. 2013), but with further information on spatial variation in crawler loads on migratory birds, such models could be improved.

Migratory behavior leads to interactions between birds and other organisms in stopover habitat, which can facilitate the transport of these organisms or their

reproductive propagules to suitable habitat. Although bird-mediated dispersal is a natural process that contributes to gene flow and ecosystem functioning, it can also contribute to further spread of biological invasions caused by humans. Our study suggests that birds are capable of contributing to within-stand and inter-stand dispersal of an invasive species by carrying them in their feathers. The potential for invasive propagules to survive a long-distance bird flight, however, remains largely unexplored (Anastácio et al. 2013). Insights on the ability of hemlock woolly adelgid to use bird migration for its own dispersal can be used to inform management to prevent further spread of forest insect invasions, such as identifying target areas for invasion monitoring based on knowledge of migratory routes. As our investigations of avian dispersal of invasive insects are restricted to Connecticut, we suggest further research to compare rates of dispersal throughout the adelgid's range, especially on the invasion front and in areas with higher ambient adelgid concentrations. Indeed, researchers in Nova Scotia, Canada have recently reported an isolated population of hemlock woolly adelgid > 100 km from the nearest infestation site and are distributing material to inform all stakeholders about the potential for bird-mediated dispersal (Emilson et al. 2018). The dispersal of the hemlock woolly adelgid shows that biological invasions of organisms that can be passively dispersed by migratory birds could be especially difficult to eradicate, and projections of range expansions should account for infrequent, long-distance dispersal events.

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Author contributions NJR and MWT conceived and designed the experiments. NJR performed the experiments with assistance of CSE and NPH. NJR and MWT analyzed the

data. NJR wrote the first draft of the manuscript; all authors contributed to the final version.

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