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Mercury exposure in songbird communities within *Sphagnum* bog and upland forest ecosystems in the Adirondack Park (New York, USA)

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Abstract

Mercury (Hg) is a potent neurotoxin that biomagnifies within both aquatic and terrestrial food webs resulting in adverse physiological and reproductive effects on impacted wildlife populations, including songbird communities. Due to reducing conditions, wetland ecosystems promote the formation of methylmercury. Regional studies have documented elevated blood mercury concentrations in songbird species within these habitat types. The overall goal of this research was to examine spatial and seasonal patterns of Hg exposure for targeted songbird species within *Sphagnum* bog wetland systems and compare these patterns with adjacent upland forests in the Adirondack Park of New York State. Project sampling was conducted at study plots within four Sphagnum bog and associated upland forest sites from May - August during the 2008, 2009, and 2011 field seasons. The overall results documented: (1) blood Hg concentrations were elevated in songbird species inhabiting Sphagnum bog habitats as compared to nearby upland forest species; (2) target species within each habitat type exhibited consistent specieslevel patterns in blood Hg concentrations at each study site; and (3) no seasonal change in blood Hg concentrations within Sphagnum bog habitats was documented, but an increasing, followed by a decreasing seasonal pattern in mercury exposure was detected for upland forest species. Habitat type was demonstrated to influence avian Hg exposure levels. Moreover, Sphagnum bog ecosystems may be contributing to elevated Hg concentrations in biota within the surrounding environment. Seasonal patterns for blood Hg concentrations were found to vary between habitat type and are likely related to a combination of variables including habitat-driven Hg concentrations in prey items, seasonal dietary shifts, and annual molting cycles. This project emphasizes the importance of prioritizing future research efforts within identified high Hg habitat types, specifically wetland systems, to better characterize associated avian exposure levels, estimate the spatial extent of wetland systems on the surrounding environment, and identify locations of potential biological hotspots across the Adirondack Park.

Keywords Mercury · Songbird · Sphagnum bog · Upland forest · Adirondack Park

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Introduction

Mercury (Hg) is a widespread and potent neurotoxin that has been linked to adverse effects within wildlife populations (Evers and Clair 2005; Bank et al. 2007; Evers et al. 2007). Due to the ability of Hg to be atmospherically transported across great distances, Hg is a regional as well as a global contaminant. Domestic efforts, such as the Mercury and Air Toxics Standard (MATS), and international initiatives, such as the Minamata Convention, are aimed at reducing anthropogenic releases of Hg to the environment. While natural sources of Hg, such as volcanic activity and soil weathering, account for a portion of Hg emissions, the primary contributors to atmospheric Hg are direct anthropogenic emissions from sources, including coal-fired power plants and mining, and re-emissions (Driscoll et al. 2013). Atmospheric deposition is the major source of Hg inputs to remote ecosystems (Fitzgerald et al. 1998), but deposition patterns upon the landscape vary due to a number of factors, such as distance from point sources, elevation, land cover and meteorological patterns (Miller et al. 2005). Once deposited, inorganic Hg can be converted by bacteria and archaea into the toxic form of Hg, methylmercury (MeHg; Benoit et al. 2002; Podar et al. 2015), which is available for uptake and bioaccumulation within individuals. Through the processes of trophic transfer, methylmercury biomagnifies within aquatic and terrestrial food webs to levels where adverse physiological and reproductive impacts become evident (Watras et al. 2018).

The dynamics of Hg cycling and patterns in wildlife exposure have been well-established for aquatic ecosystems, particularly within fish communities (Chen et al. 2005; Kamman et al. 2005) and piscivorous species, such as the common loon (Gavia immer; Evers et al. 2005; Schoch et al. 2014, 2019). However, it is also critical to establish the extent of Hg contamination within terrestrial ecosystems (Driscoll et al. 2007). Numerous studies have identified sublethal effects of Hg across a variety of terrestrial wildlife species (Wolfe et al. 1998; Whitney and Cristol 2017a; Evers 2018). Songbirds, which are well-distributed across the landscape, have the ability bioaccumulate MeHg within blood and feather tissue (Jackson et al. 2011b) and are increasingly utilized as indicators of Hg contamination across terrestrial ecosystems (Jackson et al. 2015; Adams et al. 2019). Investigations have documented the detrimental effects of elevated Hg exposure on avian behavior (Hallinger et al. 2010), immune function (Hawley et al. 2009; Lewis et al. 2013) and reproductive success (Brasso and Cristol 2008; Evers et al. 2008; Hallinger and Cristol 2011; Jackson et al. 2011a; Varian-Ramos et al. 2014). Therefore, research efforts are necessary to further quantify baseline Hg exposure levels, sensitivity thresholds and associated impacts for avian species across a variety of terrestrial habitat types.

The Adirondack Park of New York State is characterized by moderate atmospheric Hg deposition, an abundance of forest and wetland land cover that promote net deposition, transport via drainage and the methylation of Hg, and biotic Hg concentrations that exceed established adverse threshold levels (Driscoll et al. 2007; Evers et al. 2007). As a result, the region has been designated as a "biological mercury hotspot" (Evers et al. 2007). Wetlands, a habitat type prevalent in the Adirondack Park, have been widely associated with elevated Hg concentrations due to reducing conditions which promote the formation and transport of MeHg (Ullrich et al. 2001; Selvendiran et al. 2008; Wang et al. 2019) and also possess complex food webs that facilitate the biomagnification of MeHg (Cristol et al. 2008). Regional research efforts have identified elevated blood Hg concentrations in wetland songbirds. Species, particularly those foraging on insects during the breeding season, are at the greatest risk to the impacts of Hg contamination (Evers et al. 2005; Edmonds et al. 2010, 2012; Lane et al. 2011, 2019; Jackson et al. 2015; Adams et al. 2019). Further, a synthesis of Northeastern songbirds documented elevated blood Hg concentrations in freshwater wetland species when compared to upland forest species, suggesting differences in Hg cycling and bioavailability between habitat types (Jackson et al. 2015). There have been relatively few observations documenting Hg exposure in Adirondack songbirds, specifically within wetland habitats, such as Sphagnum bogs, which are prevalent and known to sequester atmospherically deposited Hg (Grigal et al. 2003; Yu et al. 2010). Therefore, this research will serve to further characterize Hg concentrations in avian communities and improve understanding of MeHg bioavailability across distinct habitat types.

The objectives of this study were to document spatial, seasonal and species patterns of Hg exposure for songbirds inhabiting Sphagnum bog habitats and compare these observations with adjacent upland forest habitats in the Adirondack Park of New York State. To achieve these objectives, blood Hg concentrations were analyzed from songbird species within four Sphagnum bog and adjacent upland forest study sites over the course of two breeding seasons. A subset of data, from related research examining songbird Hg exposure at low elevations on Whiteface Mountain in the Adirondack Park, was utilized for comparative analysis with the same target species in upland habitats adjacent to bog wetlands. The results of this research will ultimately provide valuable baseline data relating to Hg bioavailability and exposure levels for avian communities within sensitive habitat types in the Adirondack Park.

Methods

Study site descriptions

Four *Sphagnum* bog and adjacent upland forest study sites were selected for sample collection in the Adirondack Park of New York State (Supplementary information Fig. 1). Massawepie Mire (44.23°N, 74.66°W), located on the Massawepie Boy Scout Camp property in the town of Piercefield, is the largest boreal peatland bog complex in New York State with an estimated area of 2020 hectares (ha), including 360 ha of open peatland. Spring Pond Bog (44.37°N, 74.50°W), owned by The Nature Conservancy-Adirondack Chapter and located in the town of Altamont, is the second largest *Sphagnum* bog in New York State at 200 ha with a total complex area of 1700 ha. Madawaska

Flow (44.51°N, 74.40°W), located on New York State Department of Environmental Conservation (NYSDEC) Conservation Easement property in the town of Santa Clara, contains a series of open bogs within an estimated 1210 ha wetland complex. Bloomingdale Bog (44.38°N, 74.14°W), also managed by NYSDEC in the town of St. Armand, is a large bog complex that encompasses approximately 630 ha and contains a mix of open peatland and forested community types. All study sites contain extensive wetland systems and provide essential habitat for a wide variety of resident and migratory boreal songbird species.

Research approach and study design

Project sampling to evaluate spatial, seasonal and species exposure patterns in songbird communities using blood Hg concentrations was conducted at study plots within four Sphagnum bog and adjacent upland forest sites from May - August during the 2008, 2009, and 2011 field seasons. During this period, each site was sampled over the course of two complete breeding seasons. Sampling events were timed to correspond with periods of peak breeding activity for songbirds in the northeastern United States. Study plots were repeatedly sampled within each breeding season to examine seasonal patterns in blood Hg concentrations. Additionally, fluctuations in blood Hg concentrations were documented for a limited number of individuals that were recaptured both within and between breeding seasons. Detailed information for these individuals is included in Supporting Information (Supplementary information Table 1).

To document overall patterns of Hg exposure, project results are presented for all species sampled, which included target species as well individuals that were captured opportunistically. Six avian species were specifically targeted in this study to examine differences in blood Hg concentrations between Sphagnum bog and upland forests. Targeted species were common among all study sites, shared similar foraging strategies, and served as a representative species for each habitat type. Yellow palm warbler (Setophaga palmarum), Lincoln's sparrow (Melospiza lincolnii), and Nashville warbler (Leiothlypis ruficapilla) were selected as Sphagnum bog species. Hermit thrush (Catharus guttatus), ovenbird (Seiurus aurocapilla), and red-eyed vireo (Vireo olivaceus) served as the representative species for upland forests. Upland forest species were sampled at least 75 m away from the interface of wetland habitat and in locations with intact forest canopy cover.

During 2009–2010, a contemporaneous field study was conducted on Whiteface Mountain to examine spatial and seasonal Hg patterns in songbird species within montane Adirondack habitats (Sauer et al. 2019). Whiteface Mountain $(44.36^{\circ}N, 73.90^{\circ}W)$ is located in the

Wilmington Wild Forest and McKenzie Mountain Wilderness of the Adirondack High Peaks Region and is the fifth highest peak (1483 m) in New York State. To supplement the wetland study and better understand patterns of habitat, species-level and seasonal Hg exposure across the Adirondack landscape, a comparative analysis was conducted utilizing subsets of data from low-elevation sites (450–900 m) on Whiteface Mountain with the upland forest sites adjacent to wetlands from the current study. To standardize species across study sites, data subsets for each project were comprised of target forest songbirds which included ovenbirds, hermit thrushes and red-eyed vireos. All songbird capture and tissue sampling methodologies were the same between project locations.

Songbird capture and tissue sampling

Songbirds were captured using nonlethal methods, which included mist netting techniques, decoy displays, and recordings of conspecific vocalizations. At each study site, 6and 12-m (36-mm black nylon mesh) mist nets were temporarily erected, along with decoys, and playback of vocalizations were used to elicit a territorial response for each target species. Once captured, each bird was fitted with a uniquely-numbered aluminum U.S. Geological Survey (USGS) band. Reproductive status, age and sex were determined for each individual, and morphometric measurements, including wing chord and tail length, were recorded.

Blood samples were collected via venipuncture of the ulnar vein, using a sterile, 27-gauge needle. Approximately $30-50 \mu l$ of sampled blood was collected within heparinized, micro-hematocrit capillary tubes, which were sealed and stored in plastic vacutainers. After collection, blood samples were frozen and transported to Syracuse University for total Hg analysis. Project results are reported for adult songbird Hg concentrations. All banding and sampling efforts were conducted under the required state, federal and IACUC permits.

Laboratory analysis

All songbird blood samples were analyzed in the Center for Environmental Systems Engineering laboratory (CESE) at Syracuse University. Blood samples were analyzed for total Hg concentrations using a Direct Mercury Analyzer (Milestone DMA-80), according to U.S. Environmental Protection Agency method 7473 (U.S. E.P.A. 1998). Quality assurance for each analytical run of 10 samples was conducted with a method blank, instrument blank, duplicate sample, and verification with National Institute of Standards and Technology (NIST) certified standard reference materials (SRM) for continuing calibration verification and quality control samples. Certified standard reference materials for Sphagnum bog and upland forest samples included apple leaves (NIST SRM 1515), mussel tissue (NIST SRM 2976), bovine blood (NIST SRM 966), caprine blood (NIST SRM 955c), and Seronorm-whole blood L-2. Mean percent recoveries (±SE) of total Hg were $100 \pm 1.1\%$ (*n* = 35) for SRM 1515, $102 \pm 0.9\%$ (*n* = 35) for SRM 2976, $99 \pm 1.6\%$ (n = 15) for SRM 966, $106 \pm$ 1.2% (n = 22) for SRM 955c, and $109 \pm 1.5\%$ (n = 21) for Seronorm. Certified standard reference materials for Whiteface Mountain samples included apple leaves (SRM 1515), mussel tissue (SRM 2976), caprine blood (SRM 955c), and Seronorm-whole blood L-2. Mean percent recoveries (±SE) of total Hg were $100 \pm 0.9\%$ (n = 20) for SRM 1515, $95 \pm 0.6\%$ (n = 29) for SRM 2976, $98 \pm 1.1\%$ (*n* = 18) for SRM 955c and $97 \pm 0.8\%$ (n = 26) for Seronorm. All analyzed blood samples were above the method detection limit (0.12 ng). Methylmercury analyses were not conducted for songbird blood, as previous research has documented that approximately 95% of total Hg is in the form of MeHg (Rimmer et al. 2005; Edmonds et al. 2010). All blood Hg concentrations are expressed as µg/g, wet weight (ww).

Statistical analysis

Blood Hg data were log-transformed prior to analysis. Data were assessed for normality and homogeneity of variance using a visual examination of the residuals and overall model fit was assessed based on r^2 . A small number of individuals were resampled during repeated sampling efforts within the same year. To ensure sample independence, only blood Hg from the first sample obtained for each individual within each year was analyzed. Blood samples from individuals that were recaptured between years were treated as independent and included in the analysis. Two general linear models were specified to test for differences in blood Hg concentrations between Sphagnum bog and forest habitats, along with wetlandadjacent upland forests and upland forests on Whiteface Mountain. The first model assessed the effect of habitat (forest, bog), site (Bloomingdale Bog, Madawaska Flow, Massawepie Mire, Spring Pond Bog), species (yellow palm warbler, Lincoln's sparrow, Nashville warbler, hermit thrush, ovenbird, red-eyed vireo), date (ordinal day), year (2008, 2009, 2011) and sex on Hg concentrations in bird blood. In addition to each of these covariates, differences among sites were accounted for by nesting species and site within habitat type and including an interaction between date and habitat type. The second model evaluated differences between forest species in upland forests adjacent to wetlands and low-elevation Whiteface Mountain forest sites using site (Whiteface Mountain, Bloomingdale Bog, Madawaska Flow, Massawepie Mire, Spring Pond Bog), species (hermit thrush, ovenbird, red-eyed vireo), date (ordinal day), year (2008, 2009, 2010, 2011) and sex on Hg concentrations in bird blood. Differences among sites were accounted for by nesting species within site and including an interaction between date and site. Significance was determined using a t-test for individual model parameters and F test for covariates. For general linear models that indicated a significant categorical effect, t-tests or Tukey's HSD *post hoc* tests were conducted to evaluate differences among groups. Data for blood Hg concentrations are reported as raw data or arithmetic means and standard error (SE).

Linear trends in songbird Hg concentrations with ordinal date were further examined with piecewise regression to determine any changes in slope and to identify a breakpoint between two models with different slopes. Piecewise regression was estimated using the NLIN function. Statistical tests were conducted using JMP 9.0 (SAS Institute Inc. 2010) and SAS 9.4 (SAS Institute Inc. 2013) and were considered significant at $\alpha < 0.05$.

Results

Avian mercury exposure - all species

During 2008, 2009, and 2011, a total of 242 adult songbirds, representing 20 species, were sampled and analyzed (n = 252) for blood Hg concentrations to characterize exposure from *Sphagnum* bog and upland forest habitats at Bloomingdale Bog, Massawepie Mire, Madawaska Flow, and Spring Pond Bog (Fig. 1; Table 1). Across all *Sphagnum* bog habitats (n = 114), blood Hg concentrations ranged from a low of 0.018 µg/g in a cedar waxwing at Madawaska Flow to a high of 2.815 µg/g for a yellow palm warbler at Massawepie Mire. Within the forested study sites adjacent to wetlands (n = 138), blood Hg concentrations ranged from 0.020 µg/g for a hermit thrush at Spring Pond Bog to a high of 1.313 µg/g for a red-eyed vireo at Massawepie Mire.

Mercury concentrations in *Sphagnum* bog and upland forest habitats

Model fit for the comparison between *Sphagnum* bog and adjacent upland forest sites was sufficient. The overall r^2 was 0.65 and there was no evidence of violation of assumptions. Across groups, habitat (F_{1,219} = 31.34, p < 0.0001), site (F_{6,214} = 7.88, p < 0.0001), species (F_{4,216} = 55.65, p < 0.0001) and the interaction between ordinal day and site (F_{1,219} = 24.32, p < 0.0001) were strong predictors of Hg concentrations in bird blood.

Across study sites, overall mean songbird blood Hg was significantly higher in *Sphagnum* bog habitat $(0.323 \pm 0.035 \,\mu\text{g/g}, n = 106)$ as compared to the adjacent surrounding

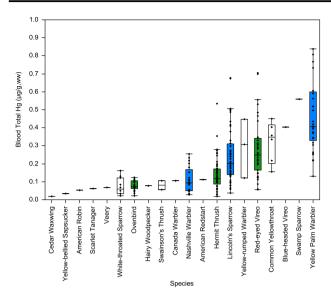


Fig. 1 Blood mercury concentrations ($\mu g/g$, ww) for songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011. Box plots denote the median (horizontal line within the box) and the 25th and 75th quantiles (lower and upper edges of the box). Four observations of high blood mercury concentrations are not depicted within the given bounds, including three yellow palm warblers (1.299 ppm, 1.861 ppm, 2.815 ppm) and one red-eyed vireo (1.313 ppm) in order to focus on the range of observations for the majority of samples collected. Target species are shown in blue (*Sphagnum* bog) and green (upland forest) shading

forests $(0.182 \pm 0.016 \mu g/g)$, n = 115). This effect varied among sites and blood Hg concentrations ranged from 2.29 times higher at Madawaska Flow (difference = 0.39 ± 0.07 , p < 0.0001), 1.87 times higher at Spring Pond Bog (difference = 0.22 ± 0.07 , p = 0.03), 1.54 times higher at Massawepie Mire (difference = 0.19 ± 0.06 , p = 0.03), to a non-significant relationship at Bloomingdale Bog (Fig. 2). The effect of habitat was significant overall, and this pattern was driven by differences in blood Hg concentrations at three of the four sites.

Mean blood Hg concentrations were found to vary significantly among the *Sphagnum* bog sites, but not among the adjacent upland forest sites. *Post hoc* comparisons using the Tukey's HSD method indicated that *Sphagnum* bog songbirds at Bloomingdale Bog had significantly lower blood Hg concentrations than songbirds at Madawaska Flow (difference = -0.45 ± 0.07 , p < 0.0001; 2.39 times higher), Spring Pond Bog (difference = -0.39 ± 0.07 , p < 0.0001; 2.28 times higher) and Massawepie Mire (difference = $-0.33 \pm$ 0.07, p = 0.0002; 2.10 times higher; Fig. 2). However, *post hoc* comparisons among adjacent upland forest sites did not indicate any statistically significant pairwise differences.

Across all sites, mean blood Hg concentrations varied significantly among *Sphagnum* bog species and upland forest species. Results of *post hoc* comparisons for *Sphagnum* bog songbirds indicated that Nashville warbler exhibited the lowest blood Hg concentrations $(0.109 \pm 0.015 \,\mu\text{g/g})$, followed by Lincoln's sparrow $(0.245 \pm 0.021 \,\mu\text{g/g})$, and yellow palm warbler had the highest blood Hg levels across all sites $(0.581 \pm 0.091 \,\mu\text{g/g}; p < 0.0001$ for all comparisons; Fig. 3; Table 1). *Post hoc* comparisons for upland forest birds indicated that ovenbirds $(0.078 \pm 0.005 \,\mu\text{g/g})$ and hermit thrushes $(0.143 \pm 0.013 \,\mu\text{g/g})$ were marginally different from each other (difference = 0.16 ± 0.06 , p = 0.06), while red-eyed vireos were significantly higher than both $(0.303 \pm 0.037 \,\mu\text{g/g})$; difference from ovenbirds = 0.53 ± 0.06 , difference from hermit thrushes = 0.36 ± 0.05 , p < 0.0001 for both; Fig. 4; Table 1).

Proximity to wetlands influencing avian mercury concentrations in upland forests

The model comparing blood Hg concentrations among wetland-adjacent upland forest sites with upland forest sites at Whiteface Mountain also had sufficient fit ($r^2 = 0.67$) and no evidence of assumption violation. Across groups, site ($F_{4,186} = 7.87$, p < 0.0001), species ($F_{10,180} = 15.64$, p < 0.0001) and the interaction between ordinal day and site ($F_{4,186} = 3.78$, p = 0.01) were strong predictors of Hg concentrations in bird blood.

Mean blood Hg concentrations of songbirds at Whiteface Mountain study sites were significantly lower $(0.074 \pm 0.005 \,\mu\text{g/g})$ than songbirds in upland forests adjacent to wetlands at Madawaska Flow (difference = 0.28 ± 0.06 , p < 00001; 2.28 times higher), Spring Pond Bog (difference = 0.29 ± 0.11 , p = 0.05; 2.69 times higher), Massawepie Mire (difference = 0.34 ± 0.08 , p = 0.0003; 3.01 times higher) and Bloomingdale Bog (difference = 0.27 ± 0.06 , p < 0.0001; 1.84 times higher).

A consistent pattern of Hg bioaccumulation among forest species was observed for Whiteface Mountain forest species with songbirds at each upland forest study site adjacent to wetlands (Fig. 4). *Post hoc* comparisons indicated that ovenbirds had the lowest blood Hg concentrations $(0.054 \pm 0.003 \,\mu g/g)$, followed by hermit thrushes $(0.067 \pm 0.005 \,\mu g/g)$, which did not significantly differ from each other (difference = 0.10 ± 0.05 , p = 0.88). The highest blood Hg concentrations were found in red-eyed vireos $(0.116 \pm 0.012 \,\mu g/g)$, which were significantly difference = 0.34 ± 0.06 , p < 0.0001; difference = 0.24 ± 0.07 , p < 0.03, respectively; Table 1).

Seasonal changes in avian mercury concentrations

In each of the previous models, significant differences were found in the influence of ordinal day on blood Hg concentrations. Using the general linear model, no seasonal changes were observed with ordinal day in *Sphagnum* bog

Table 1 Arithmetic mean blood mercury concentrations ($\mu g/g$, ww ± SE), sample size (<i>n</i>), and Hg range for songbirds sampled at Bloomingdale
Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008, 2009, 2011

Species	Site	Mean Hg $(\mu g/g) \pm SE$ (<i>n</i>)	Hg range (µg/g)	Foraging guild	Foraging layer
Sphagnum bog target spe	ecies				
Lincoln's Sparrow	All	0.245 ± 0.021 (52)	0.037-0.678	Omnivore	Ground
	Bloomingdale Bog	0.119 ± 0.013 (12)	0.059-0.189		
	Madawaska Flow	0.420 ± 0.080 (8)	0.037-0.678		
	Massawepie Mire	0.243 ± 0.027 (19)	0.080-0.486		
	Spring Pond Bog	0.259 ± 0.028 (13)	0.136-0.506		
Nashville Warbler	All	0.109 ± 0.015 (21)	0.028-0.254	Insectivore	Lower Canopy
	Bloomingdale Bog	0.030 ± 0.002 (3)	0.028-0.033		
	Madawaska Flow	0.129 ± 0.023 (6)	0.090-0.232		
	Massawepie Mire	0.066 ± 0.014 (4)	0.049-0.107		
	Spring Pond Bog	0.145 ± 0.028 (8)	0.046-0.254		
Yellow Palm Warbler	All	0.581 ± 0.091 (33)	0.131-2.815	Insectivore	Ground
	Bloomingdale Bog	0.279 ± 0.031 (8)	0.131-0.376		
	Madawaska Flow	0.556 ± 0.064 (8)	0.345-0.838		
	Massawepie Mire	0.948 ± 0.469 (5)	0.371-2.815		
	Spring Pond Bog	0.645 ± 0.139 (12)	0.253-1.862		
Forest target species					
Hermit Thrush	All	0.143 ± 0.013 (49)	0.020-0.536	Insectivore	Ground
	Bloomingdale Bog	0.107 ± 0.021 (13)	0.028-0.272		
	Madawaska Flow	0.106 ± 0.012 (9)	0.044-0.158		
	Massawepie Mire	0.143 ± 0.022 (12)	0.063-0.354		
	Spring Pond Bog	0.195 ± 0.031 (15)	0.020-0.536		
	^a Whiteface Mountain	0.067 ± 0.005 (25)	0.035-0.119		
Ovenbird	All	0.078 ± 0.005 (27)	0.022-0.124	Insectivore/ Molluscovore	Ground
	Bloomingdale Bog	0.077 ± 0.009 (12)	0.022-0.124		
	Madawaska Flow	0.089 ± 0.010 (7)	0.052-0.113		
	Massawepie Mire	0.068 ± 0.008 (7)	0.033-0.101		
	Spring Pond Bog	0.070 (1)			
	^a Whiteface Mountain	0.054 ± 0.003 (32)	0.018-0.096		
Red-eyed Vireo	All	0.303 ± 0.037 (39)	0.054-1.313	Insectivore	Upper Canopy
	Bloomingdale Bog	0.274 ± 0.043 (8)	0.057-0.466		
	Madawaska Flow	0.284 ± 0.066 (10)	0.054-0.699		
	Massawepie Mire	0.350 ± 0.077 (16)	0.121-1.313		
	Spring Pond Bog	0.239 ± 0.026 (5)	0.150-0.305		
	^a Whiteface Mountain	0.116 ± 0.012 (19)	0.062-0.266		
Non-target species					
American Redstart	Spring Pond Bog	0.112 (1)		Insectivore	Lower Canopy/Air
American Robin	Bloomingdale Bog	0.053 (1)		Vermivore	Ground
Blue-headed Vireo	Madawaska Flow	0.404 (1)		Insectivore	Lower Canopy
Canada Warbler	Spring Pond Bog	0.106 (1)		Insectivore	Lower Canopy
Cedar Waxwing Common Yellowthroat	Madawaska Flow	0.018 (1)		Frugivore/Insectivore	Upper Canopy/Air
	All	0.320 ± 0.046 (6)	0.157–0.450	Insectivore	Lower Canopy
	Madawaska Flow	0.312 ± 0.055 (5)	0.157–0.450		
	Massawepie Mire	0.359 (1)			
Hairy Woodpecker	Massawepie Mire	0.079 (1)		Insectivore/Frugivore	Bark/Lower Canop

Species	Site	Mean Hg $(\mu g/g) \pm SE$ (<i>n</i>)	Hg range (µg/g)	Foraging guild	Foraging layer
Scarlet Tanager	Massawepie Mire	0.061 (1)	0.061-0.061	Insectivore	Upper Canopy
Swainson's Thrush	All	0.080 ± 0.025 (2)	0.055-0.105	Omnivore	Ground/ Lower Canopy
	Bloomingdale Bog	0.105 (1)			
	Spring Pond Bog	0.055 (1)			
Swamp Sparrow	Madawaska Flow	0.560 (1)		Omnivore	Ground
Veery	Bloomingdale Bog	0.069 (1)		Omnivore	Ground/ Lower Canopy
White-Throated Sparrow	All	0.074 ± 0.015 (10)	0.023-0.161	Omnivore	Ground
	Bloomingdale Bog	0.036 ± 0.008 (3)	0.023-0.051		
	Madawaska Flow	0.055 ± 0.012 (4)	0.034-0.084		
	Massawepie Mire	0.161 (1)			
	Spring Pond Bog	0.126 ± 0.006 (2)	0.120-0.131		
Yellow-bellied Sapsucker	Bloomingdale Bog	0.034 (1)		Omnivore	Bark
Yellow-rumped Warbler	All	0.292 ± 0.094 (3)	0.122-0.446	Insectivore	Lower Canopy
	Bloomingdale Bog	0.122 (1)			
	Madawaska Flow	0.377 ± 0.069 (2)	0.309-0.446		

Table 1 (continued)

Foraging guild and foraging layer classifications are based on De Graaf et al. (1985)

^aOverall mean Hg values do not include species listed for Whiteface Mountain

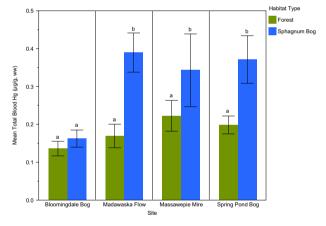


Fig. 2 Arithmetic mean blood mercury concentrations ($\mu g/g$, ww \pm SE) for songbird species in *Sphagnum* bog and upland forest habitats at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008, 2009, 2011. Different letters denote significant differences between habitat types within each site

songbirds ($\beta = -0.001 \pm 0.0008$, t = -1.36, p = 0.18), while a linear decrease was evident in upland forest species ($\beta = -0.003 \pm 0.0007$, t = -4.93, p < 0.0001). Using piecewise regression to further investigate these patterns, *Sphagnum* bog songbirds were found to have no seasonal patterns from ordinal day 145 (May 25) to ordinal day 218 (August 6; Fig. 5). At the species scale, there was evidence that Lincoln's sparrow blood Hg concentrations increased from ordinal day 145 to ordinal day 154 (June 3; slope = $0.0916 \pm 0.0173 \log$ blood Hg; p = 0.01; +20% per day), but showed no change through ordinal day 215 (August 3; p = 0.25). No seasonal patterns in blood Hg concentrations were found for other bog species.

In forest species at wetland-adjacent upland sites, overall Hg blood concentrations in songbirds increased from the beginning of the season, ordinal day 144 (May 24) to ordinal day 176 (June 25; slope = 0.0109 ± 0.0041 ; p = 0.01; +2.4% per day) and decreased from ordinal day 176 to ordinal day 218 (August 6; slope = -0.0128 ± 0.0032 ; p < 0.01; -1.6% per day; Fig. 6). When examined separately, seasonal patterns of blood Hg concentrations differed among species. Mercury concentrations in red-eyed vireos increased from the beginning of the season to ordinal day 176 (slope = 0.0164 ± 0.0055 ; p = 0.03; +5.0% per day) and decreased from ordinal day 176 to ordinal day 217 (August 5; slope = -0.0156 ± 0.0027 ; p < 0.01; -2.0%per day). Seasonal blood Hg concentrations were found to decline in both hermit thrushes (slope = -0.0059 ± 0.0015 ; p < 0.01; -0.9% per day) and ovenbirds (slope = -0.0054 ± 0.0010 ; p < 0.01; -0.8% per day).

Similar overall seasonal patterns were found at the Whiteface Mountain upland forest sites, as blood Hg concentrations significantly increased from the beginning of the season (ordinal day 155, June 4) to ordinal day 188 (July 7; slope = 0.0071 ± 0.0019 ; p = 0.01; +2.0% per day), but samples were infrequent past ordinal day 188 (n = 14) and

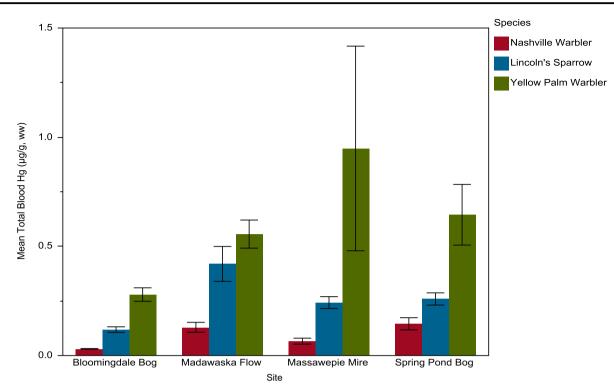


Fig. 3 Species-level exposure patterns using arithmetic mean blood mercury concentrations ($\mu g/g$, ww ± SE) for *Sphagnum* bog songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011

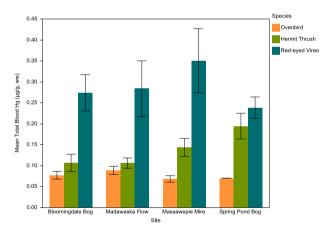


Fig. 4 Species-level exposure patterns using arithmetic mean blood mercury concentrations (μ g/g, ww ± SE) for upland forest songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011

seasonal patterns beyond that date were unclear. At the species level, Hg concentrations in hermit thrushes increased from the beginning of the season (slope = 0.0096 ± 0.0030 ; p = 0.01, +2.9% per day), but samples were infrequent past ordinal day 188 (n = 3) and we lack data to describe the seasonal pattern after that date. Similarly, blood Hg concentrations significantly increased in ovenbirds from ordinal day 155 to ordinal day 192 (July 11; slope = 0.0058 ± 0.0025 ; p = 0.03; +1.5% per day), but

samples (n = 5) were not sufficient to determine the seasonal pattern after ordinal day 192. No seasonal changes in blood Hg concentrations were found for red-eyed vireos. In both analyses of overall seasonal patterns in blood Hg concentrations, *Sphagnum* bog species tended to have consistently high blood Hg concentrations, while upland forest species (wetland-adjacent and Whiteface Mountain) tended to have lower concentrations that initially increased, peaking mid-season, and followed by a decrease in blood Hg concentrations for the remainder of the season.

Discussion

This research was designed to document and compare patterns of Hg exposure for songbird communities in *Sphagnum* bog complexes with upland forest habitats in the Adirondack Park of New York State. The overall results showed that: (1) blood Hg concentrations were elevated in songbird species inhabiting *Sphagnum* bog habitats as compared to nearby upland forest species; (2) target species within each habitat type exhibited consistent species-level patterns of Hg concentrations at each study site; and (3) seasonal measurements documented no change in blood Hg concentrations for songbirds within *Sphagnum* bog habitats, however this pattern contrasted with upland forest species, which showed an overall

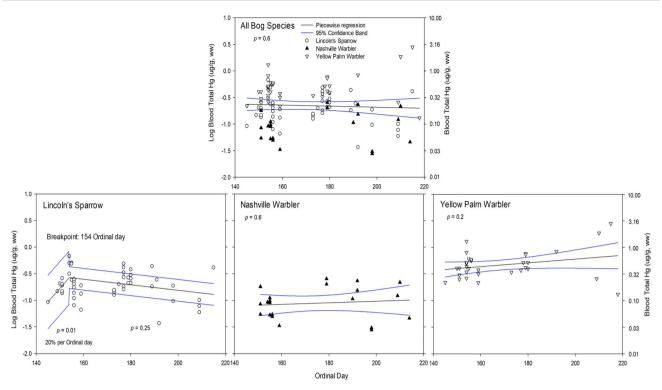


Fig. 5 Seasonal patterns in blood mercury concentrations ($\mu g/g$, ww) for *Sphagnum* bog songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008,

2009, 2011. Single linear trend is shown based on linear regressions if no breakpoint was detected by piecewise regression

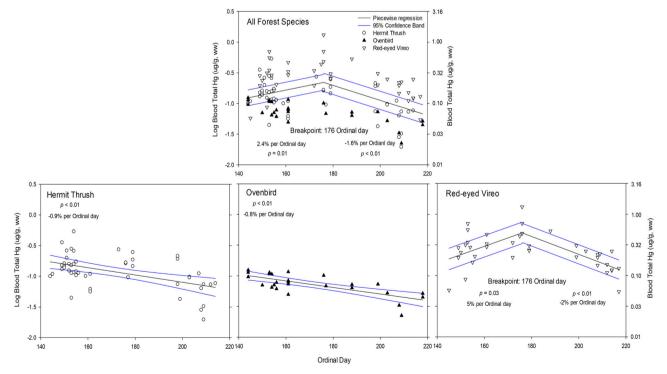


Fig. 6 Seasonal patterns in blood mercury concentrations (μ g/g, ww) for upland forest songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008,

2009, 2011. Single linear trend is shown based on linear regressions if no breakpoint was detected by piecewise regression

seasonal pattern of increasing, followed by decreasing blood Hg concentrations.

Mercury concentrations in *Sphagnum* bog and upland forest habitats

Across all study sites, overall blood Hg concentrations in Sphagnum bog songbirds was 1.78 times higher than species sampled within adjacent forested sites (Fig. 2). These results are consistent with a regional synthesis of Northeastern songbirds, which also documented elevated blood Hg concentrations in freshwater wetland species when compared to upland forest species (Jackson et al. 2015). Wetlands have been widely associated with elevated blood Hg concentrations in songbird species due to microbial processes associated with reducing conditions which enhance methylation rates (Ullrich et al. 2001), resulting in increased MeHg availability and biotic uptake (Edmonds et al. 2010, 2012; Lane et al. 2011, 2019; Winder and Emslie 2011; Adams et al. 2019). Blood Hg concentrations were found to differ between habitat types within each study site, with Sphagnum bog species having approximately twice the Hg concentrations of forested species at both Madawaska Flow and Spring Pond Bog. While songbird blood Hg concentrations were found to be similar across each of the forested study sites, differences were observed among the Sphagnum bog sites, with songbirds at Bloomingdale Bog being significantly lower than those species sampled at Madawaska Flow, Spring Pond Bog and Massawepie Mire (Fig. 2). No quantitative investigation was conducted to determine differences in biophysical characteristics among study locations that might contribute to this pattern. However, anecdotally Bloomingdale Bog, which had the lowest blood Hg concentrations for both forest and bog species, appeared to have much a lower water stage relative to the ground surface compared to the other study sites. This result documenting relatively low blood Hg concentrations for species within a relatively drier site might be expected given that anoxic, saturated and acidic conditions associated with wetland habitats are known to promote the formation and transport of MeHg, which subsequently influence biotic uptake and exposure levels (Ullrich et al. 2001; Selvendiran et al. 2008; Wang et al. 2019). Finally, blood Hg concentrations in songbirds from low-elevation upland forest sites at Whiteface Mountain were significantly lower than upland forest songbirds located in proximity to *Sphagnum* bog complexes (Table 1). Considering that forested songbirds on Whiteface Mountain are relatively distant from any wetland systems, this result suggests the possibility that Sphagnum bog systems at the sampled study sites are influencing blood Hg concentrations of adjacent forest species through the transfer of nearby aquatic subsidies (Cristol et al. 2008; Tsui et al. 2018). Taken together, the results of the current study along with observations documented from regional studies, suggest the importance of further monitoring efforts to investigate the effect of habitat type on blood Hg concentrations, as well as the influence of wetland ecosystems on surrounding avian communities.

Species-level patterns of mercury concentrations

Across all study sites, similar species-level patterns of Hg concentrations were consistently documented within each habitat type (Figs 3 and 4). At Sphagnum bog sites, overall blood Hg concentrations increased from Nashville warbler to Lincoln's sparrow (2.25 times higher) to yellow palm warbler (5.33 and 2.37 times higher, respectively; Table 1). At all upland forest sites, overall blood Hg concentrations increased from ovenbird to hermit thrush (1.83 times higher) to red-eved vireo (3.88 and 2.12 times higher, respectively; Table 1). Research has indicated that foraging guild is an important predictor of blood Hg concentrations, with insectivore species demonstrating higher blood Hg concentrations than omnivorous species (Jackson et al. 2015). All of the target species for this study are classified as insectivores, with the exception of the omnivorous Lincoln's sparrow, for which plant material accounts for approximately 10% of the total diet (De Graaf et al. 1985). As MeHg is transferred and biomagnifies within food webs, individuals that are selecting prey items from higher trophic levels will subsequently be exposed to higher Hg levels (Cristol et al. 2008; Rimmer et al. 2010; Edmonds et al. 2012). Therefore, dietary patterns and prey selection are likely contributing to these observed patterns of species bioaccumulation across sites.

For Sphagnum bog species, yellow palm warblers are known to feed on a mix of insects including beetles, grasshoppers, spiders, flies and caterpillar larvae (Wilson 2013); Lincoln's sparrow are known to forage on a variety of arthropods and insect larvae, including beetles, spiders, flies and caterpillars (Ammon 1995); and Nashville warblers consume a variety of insects in both the adult and larval stages, including flies, grasshoppers and caterpillars (Lowther and Williams 2011). For upland forest species, major food items for red-eyed vireos include a variety of flies, beetles, spiders, dragonflies, damselflies, grasshoppers and caterpillars (Cimprich et al. 2018); hermit thrushes will forage on a mix of insects as well as fruit (Dellinger et al. 2012); and ovenbirds are known to consume a mix of forest invertebrates, which include beetles, ants, weevils, flies and caterpillars (Porneluzi et al. 2011). Based on the available data describing major food items for each target species, there is a clear overlap of prey items consumed among target species. MeHg concentrations are known to vary widely among invertebrate species, with high trophic invertebrates, like spiders and

dragonflies, having higher MeHg concentrations as compared to lower trophic insects, such as caterpillars (Cristol et al. 2008; Rimmer et al. 2010). Therefore, it is possible that foraging strategies may predispose certain species to select higher MeHg prey items while on their breeding grounds, specifically the red-eyed vireo and yellow palm warbler. However, detailed dietary analyses would be required to better estimate the contribution of species-specific prey selection as it relates to the observed species patterns of Hg concentrations across study sites.

Additionally, all species are classified as ground foragers, with the exception of the Nashville warbler, as a lower canopy gleaner, and the red-eyed vireo, as an upper canopy feeder (De Graaf et al. 1985). Given that dragonflies, damselflies and diptera (flies) are known prey items for the redeved vireo, these invertebrates may be influencing the elevated blood Hg concentrations as a subsidy from the nearby Sphagnum bog. Further, as an upper canopy feeder, these prey items would likely not be as prevalent in the forest understory or selected by ground-foraging hermit thrushes and ovenbirds. Sphagnum bogs are known to retain and methylate stores of atmospherically-derived Hg (Grigal 2003; Yu et al. 2010), potentially resulting in elevated MeHg concentrations for invertebrate communities inhabiting this habitat as compared to those in upland forests. Sphagnum bog ground foragers that are sourcing prey items from this substrate, such as the yellow palm warbler and Lincoln's sparrow, are likely exposed to higher MeHg concentrations which are reflected in the elevated blood Hg concentrations observed within these species, particularly when compared to the Nashville warbler that forages within the lower canopy. Finally, this pattern of increasing Hg concentrations from ovenbird to red-eyed vireo was also detected for lowelevation species sampled on Whiteface Mountain, which suggests that processes driving similar patterns of species bioaccumulation may be operating at a broad spatial scale. Overall, the specific processes related to these consistent species-level patterns of blood Hg concentrations at each study site remain unclear, but are likely linked to dietary differences in prey selection and foraging strata. However, additional research would be required to better understand these relative patterns of Hg exposure among species.

Seasonal patterns in avian mercury exposure

Seasonal patterns for blood Hg concentrations were found to vary between the *Sphagnum* bog and upland forest habitat sites. For target songbirds within the *Sphagnum* bog, there was no overall seasonal change in blood Hg concentrations (Fig. 5), which suggests that exposure levels remain chronically elevated in *Sphagnum* bog species for the duration of the breeding season. When analyzed separately, there was no change for both the Nashville and vellow palm warblers, however the Lincoln's sparrow exhibited a significant increase in blood Hg until ordinal Day 154 (June 3) and then remained stable during the course of the field season. Studies of the Bicknell's thrush (Catharus bicknelli), a high-elevation specialist, have documented a similar rapid increase in bioaccumulation until approximately early-mid June, followed by a steady decline for the remainder of the breeding season (Rimmer et al. 2010). This pattern is attributed to a dietary shift based on prey availability, from consumption of high-Hg items upon arrival on the breeding grounds, followed by a transition to lower Hg food items, such as Lepidoptera larvae and fruit later in the field season (Cristol et al. 2008; Rimmer et al. 2010). The seasonal pattern for Lincoln's sparrow may indicate a rapid increase in blood Hg concentrations due to consumption of high Hg prey items after arrival on Sphagnum bog breeding sites, with consistent uptake of similarly elevated food items for the remainder of the season. Blood Hg concentrations were also examined for a small number of individuals from both within and between year captures (Supplementary information Table 1). Fluctuations within the dataset were highly variable, however a greater proportion of Sphagnum bog songbirds exhibited increases in Hg concentrations for individuals resampled within and between years than those experiencing declining blood Hg concentrations. A limited number of observations for repeated blood Hg sampling of individuals have been reported within various studies also documenting variable results (Rimmer et al. 2005; Kopec et al. 2018; Schoch et al. 2019).

In upland forest songbirds, overall blood Hg concentrations increased until ordinal day 176 (June 25) and then declined for the remainder of the breeding season (Fig. 6). When assessed separately, blood Hg concentrations in redeved vireos followed the same overall pattern, while concentrations in the hermit thrush and ovenbird were found to consistently decline through the breeding season. Research related to general seasonal patterns in songbird blood Hg concentrations are both limited and highly variable. The overall seasonal pattern of increasing, followed by decreasing blood Hg is similar to seasonal trends documented for Catharus thrushes sampled along an elevational gradient on Whiteface Mountain (Sauer et al. 2019). In addition to the Bicknell's thrush research previously noted, regional studies of Catharus thrushes have also documented generally declining Hg concentrations during the course of the breeding season (Rimmer et al. 2005; Townsend et al. 2014). A study of marsh birds in Maine (Kopec et al. 2018) found a seasonal pattern of increasing blood Hg levels until approximately mid-July, which was similar to seasonal patterns for a long-term study of saltmarsh sparrows (Ammospiza caudacuta) documenting an increase in exposure levels until approximately mid-July, followed by

declining concentrations (Lane et al. 2019). Seasonal decreases in Hg concentrations are also attributed to depuration of Hg through feather growth during annual molting cycles (Furness et al. 1986; Condon and Cristol 2009; Whitney and Cristol 2017b). The onset of pre-basic molt begins in late-June for ovenbirds (Porneluzi et al. 2011) and July for hermit thrushes (Dellinger et al. 2012) and red-eyed vireos (Cimprich et al. 2018), which would contribute to declining blood Hg concentrations as the breeding season progresses. Further, evaluation of lowelevation songbirds from Whiteface Mountain documented an overall seasonal pattern of increasing blood Hg concentrations until ordinal day 188 (July 7), however data were not sufficient to determine the seasonal trend after this date. This pattern was similarly followed by both the hermit thrush and ovenbird, but no seasonal changes were detected for red-eyed vireos. This seasonal trend for low-elevation songbirds on Whiteface Mountain corresponds with seasonal changes observed as part of the current research in upland forest sites adjacent to bog wetlands as well those from regional studies, however additional data would be needed to better assess patterns in songbird blood Hg across the breeding season. A limited number of upland forest individuals were also sampled within and between breeding seasons and examined for fluctuations in blood Hg concentrations. Of the total, 11 of the 16 individuals resampled exhibited declining Hg concentrations within the breeding seasons, while 5 of the 6 individuals sampled between years were found to have increases in blood Hg concentrations (Supplementary information Table 1). Taken together, observations from the current research and evidence from previous studies, suggest that seasonal patterns of blood Hg concentrations for songbirds within Sphagnum bog habitats and upland forests are likely linked to a combination of variables including habitat-driven Hg concentrations in food resources, seasonal dietary shifts, and annual molting cycles. Considering the limited amount of field research that has been conducted to specifically examine seasonal changes in songbird Hg concentrations, research would be necessary to further identify and better assess patterns of seasonal blood Hg fluctuations in regional songbird communities.

Adverse effects thresholds in *Sphagnum* bog-upland forest avian communities

Across the 20 species sampled, yellow palm warblers and red-eyed vireos exhibited some of the highest blood Hg concentrations within their respective habitats, as compared to associated *Sphagnum* bog and upland forest songbirds (Fig. 1). Current estimates for blood Hg concentrations associated with adverse effects levels in songbirds were developed as part of a study examining the impact of Hg on the reproductive success in a wild population of Carolina

wrens (Thryothorus ludovicianus, Jackson et al. 2011a). The following values were used as benchmarks to represent the risk of adverse effects associated with blood Hg concentrations: <0.7 µg/g, low risk; 0.7–1.2 µg/g, moderate risk; $1.2-1.7 \mu g/g$, high risk; and >1.7 $\mu g/g$, very high. Of the total birds sampled, five individuals (1.9%) were found to exceed blood Hg concentrations that placed them within the moderate risk level associated with 10% reductions to the probability of nesting success, which include one redeyed vireo and four yellow palm warblers. One yellow palm warbler and one red-eved vireo (0.8%) were categorized as being at high risk (20% reductions to the probability of nesting success), and two yellow palm warblers (0.8%) at Massawepie Mire (2.82 µg/g) and Spring Pond Bog $(1.86 \,\mu\text{g/g})$ were classified as being at very high risk (>30%) reduction to the probability of nesting success) to the impacts of Hg on reproductive success. While most songbird blood samples were categorized as being at a generally low risk, it is important to consider that species identified as exhibiting elevated Hg levels, like the red-eyed vireo and vellow palm warbler, may be potentially vulnerable to the documented multi-systemic effects of Hg exposure and would serve as valuable focal species for future songbird monitoring and research efforts.

Conclusions

This study provides the first observations to examine spatial and seasonal patterns of Hg exposure for songbird blood Hg concentrations within Sphagnum bog and adjacent upland forest habitats in the Adirondack Park. The compilation of information from this dataset allows for examination of species-level patterns of Hg concentrations, among and within-site comparisons, and assessment with established threshold levels associated with adverse effects. In summary, habitat type was demonstrated to influence biotic Hg exposure levels, as songbird species occupying Sphagnum bog habitats exhibited significantly higher blood Hg concentrations than those inhabiting adjacent forest systems. A comparison between study sites with forest songbirds from Whiteface Mountain, a study site well-removed from wetlands, further suggests that aquatic subsidies from Sphagnum bog systems may be contributing to elevated Hg concentrations within biota in adjacent upland forest ecosystems. At each study site, the yellow palm warbler and red-eyed vireo exhibited elevated blood Hg concentrations and were the only species documented to exceed established effects thresholds relating to blood Hg concentrations and impacts on reproductive success. Considering the welldocumented physiological effects of Hg exposure and the potential impacts on reproductive success, our study reinforces the need to incorporate and monitor these avian

species of concern as part of future Hg research initiatives. Seasonal patterns for blood Hg concentrations were found to vary between habitat type as songbirds within *Sphagnum* bog habitats remained consistently high during the field season and upland forest species demonstrated increasing followed by decreasing exposure patterns, which were consistent with other regional studies. Considering the variability within seasonal observations and the potential factors that influence individual concentrations, additional research would be needed to further characterize seasonal patterns of Hg exposure within avian communities.

Given the limited base of scientific data related to songbird exposure levels across the Adirondack Park, future research should emphasize habitat types with a propensity for MeHg formation, specifically wetland systems. Such efforts would improve understanding of site and speciesspecific Hg exposure levels, the spatial extent of wetland systems and their influence on the surrounding landscape, and the location and extent of biological hotspots across the Adirondacks and other mercury-sensitive regions. Recent studies have documented declining atmospheric Hg concentrations and deposition in the northeastern United States (Gerson and Driscoll 2016; Zhou et al. 2017; Mao et al. 2017). As a result, research is also needed to document the effectiveness of environmental initiatives designed to reduce Hg emissions and releases, such the U.S. Environmental Protection Agency Mercury Air and Toxics Standards (MATS) rule and the United Nations Environmental Programme Minamata Convention, in mitigating Hg exposure in wildlife communities within sensitive habitats, such as the Adirondack Park.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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