Abstract

Mercury (Hg) is a globally widespread and toxic pollutant that bioaccumulates and biomagnifies within terrestrial and aquatic food webs. Numerous adverse effects been documented in wildlife species, such as avian communities, exposed to elevated environmental Hg levels, specifically those inhabiting Hg-sensitive habitats, such as wetland and montane ecosystems. The primary goals of this dissertation were to examine spatial and seasonal patterns of Hg exposure for targeted songbird species occupying *Sphagnum* bog, upland forest and high elevation habitat types in the Adirondack Park of New York State, a biological Hg hotspot. From 2009–2010, *Catharus* thrushes were sampled at 13 study plots along an elevational gradient (450-1400 meters) on Whiteface Mountain. Mercury concentrations were observed to increase along the elevational gradient to 1,075 meters, followed by declining blood concentrations with further increases in elevation. These results are consistent with studies conducted at the same study sites which documented increases in atmospheric Hg deposition and soil Hg along the gradient, with the highest concentrations also occurring within mid- and high elevation forests. A seasonal pattern of increasing, followed by decreasing, blood Hg concentrations was detected across thrush species over the course of the breeding season. During 2008, 2009 and 2011, songbird species were sampled from study sites at *Sphagnum* bog and adjacent upland forests. Songbirds inhabiting *Sphagnum* bogs displayed significantly higher blood Hg concentrations than species within the surrounding forests, and similar patterns of species-level bioaccumulation were evident across each study site. There were no overall seasonal changes in Hg concentrations documented for *Sphagnum* bog songbirds, which remained consistently elevated throughout the breeding season. However, an overall seasonal pattern of increasing, followed by decreasing blood Hg was observed across upland forest songbird species. A comparative analysis was also

conducted utilizing subsets of data from wetland-adjacent upland forests and those sampled on Whiteface Mountain. These results indicated that forest songbirds in proximity to wetland sites had significantly higher Hg concentrations than forest songbirds sampled at Whiteface Mountain, a location well-removed from wetlands. This finding suggests the potential influence of wetland ecosystems on biota within the surrounding landscape. Taken together, these results provide evidence that high-Hg habitat types, such as *Sphagnum* bog ecosystems and montane forests, influence songbird Hg exposure and the associated spatial patterns that were observed as part of this dissertation research. Seasonal fluctuations in blood Hg concentrations were highly variable across study sites and are likely reflective of multiple contributing variables, including dietary selection and molting cycles. Finally, these results contribute to regional wildlife Hg databases and demonstrate the importance of monitoring efforts to further characterize Hg exposure patterns within bioindicator species inhabiting sensitive ecosystems in New York State.

Mercury Exposure within Songbird Communities in the Adirondack Park of New York State

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Dissertation

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Acknowledgements

So many things have brought me to this opening page of text. I've often felt that it's a story that began in 1944 when my grandfather purchased our camp in the Adirondacks, which led to my summers spent in the mountains, and all of the experiences that I was fortunate enough to have while growing up; this is what solidified that I wanted to spend my life in the Adirondacks. It's always been as simple as that. It's a connection to a place that is a part of who I am and that has guided me in my life and throughout my graduate and professional career. From my start with a Master's thesis examining Adirondack plant communities, to my years working on the impacts of mercury contamination in the Common Loon population, to a current focus on mercury exposure in songbird communities within the Park - it's been a progression that has built upon itself along the way. This dissertation is a culmination of those experiences and my effort to continue to give back to the place that gives so much.

Even though I started this endeavor many years ago, I always knew that the day would come that I would complete the task and I'm grateful for the support and encouragement from so many that have allowed this to be possible. For the enduring support from my committee members – Charley Driscoll, Dave Evers, Jamie Lamit, Karen Murray, and Mark Ritchie, your guidance and faith in my abilities is appreciated more than I can express. To the generosity of my funders at New York State Energy Research and Development Authority (NYSERDA) and Northeastern States Research Cooperative (NSRC) that made the research that I conducted possible and provided an opportunity to shine a light on environmental contaminants in Adirondack songbird populations. To the numerous co-workers and friends that assisted with the many facets of this project and provided personal support throughout the process: Melissa Duron, Sue Witmer, Sarah Hendersot, Jennifer Wisinski, Carrie Stallard, Evan Adams, Jason

Townsend, Mario Montesdeoca and so many more. And to my family for everything that they give me each day and without them it would be a different world. And lastly, I would like to dedicate my dissertation to those that started this journey with me and that I have lost along the way: for Remus, who I shared endless adventures with on so many Adirondack lakes and trails, and for my Mother, who was there from the very start of this story and would be so happy to know that I did it. This is for them and the Adirondack mountains that they loved so dearly. Onward.

Der Berg ruft und ich muss ihm folgen.
The mountains are calling and I must go. ~John Muir

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Chapter 1

Introduction

Mercury (Hg) deposition is a global environmental contaminant that requires further study to fully understand and define its impacts across various ecosystems and its associated effects on wildlife populations. As a human health concern, many investigations have been focused on Hg contamination and biomagnification in aquatic habitats (Kamman et al. 2005), but relatively fewer studies have been conducted to establish quantitative baseline information on biotic exposure and the mechanisms of Hg transport and transfer through terrestrial food chains (Cristol et al. 2008; Rimmer et al. 2010). This lack of information greatly limits our understanding of the connectivity and overall impacts of atmospheric Hg deposition across the landscape, particularly within sensitive ecosystems and at-risk wildlife communities. However, many investigations have been conducted within New York State (NYS) to better ascertain the dynamics of Hg cycling for various biotic and abiotic factors, specifically within the Adirondack Park, an area characterized by elevated Hg concentrations (Evers et al. 2007, 2020). Therefore, research studies developed for this dissertation were conducted at study sites in the Adirondack Park to further examine the extent of biotic Hg exposure for songbird species within documented elevated habitat types, and to contribute to a growing regional scientific database for Hg contamination in the northeastern United States.

Atmospheric mercury emissions, transport and deposition

The northeastern United States is a region widely impacted by Hg contamination in part due to the transport and deposition of atmospheric emissions originating from both short- and long-range Hg sources (Fitzgerald et al. 1998; Driscoll et al. 2007; Choi et al. 2008). As a global pollutant, Hg source types include a mix of anthropogenically-generated emissions and releases, natural sources, and re-emissions (Driscoll et al. 2013; UN Environment 2019). Currently, anthropogenic activities account for over 2/3 of the global Hg budget (Mason et al. 1994; Amos et al. 2013), with recent international Hg inventories identifying artisanal and small-scale gold mining (ASGM; 38%) and coal combustion (21%) as leading contributors to global anthropogenic atmospheric Hg emissions (UN Environment 2019). Similarly, in the United States and specifically the northeastern U.S., a primary source of anthropogenic Hg has been attributed to emissions from coal-fired power plants and industrial sources (Lin et al. 2012; Bourtsalas and Themelis 2019; Evers et al. 2020). Mercury emissions can be transported tens to thousands of kilometers and deposition can reflect meteorological characteristics, such as prevailing wind patterns and precipitation rates, as well as elevation, vegetation type, and stochastic seasonal fluctuations (Miller et al. 2005; VanArsdale et al. 2005; Demers et al. 2007; Yu et al. 2013). Therefore, deposition patterns upon the landscape can be influenced by multiple complex and dynamic processes occurring across various spatial and temporal scales.

As historical Hg concentrations have increased approximately three to seven-fold since the Industrial Revolution in the mid-1800s (Drevnick et al. 2012; Amos et al. 2013; Streets et al. 2017), national emissions standards, coupled with international Hg initiatives, have been implemented to actively reduce current environmental Hg loads. The effectiveness of these measures have been subsequently realized through recent studies that have identified regionally declining Hg in air and atmospheric deposition in the United States and continue to be monitored on both global and national scales (Gerson and Driscoll 2016; Zhou et al. 2017; Streets et al. 2019; Olson et al. 2020).

Mercury cycling and wildlife exposure

Following release and deposition, inorganic Hg is converted by anaerobic bacteria into organic methylmercury (MeHg), a known biological toxin that bioaccumulates and biomagnifies within aquatic and terrestrial food webs (Benoit et al. 2003; Podar et al. 2015). It is through the processes of trophic exchange and transfer that Hg biomagnification results in elevated biotic concentrations that have been associated with numerous detrimental impacts on wildlife populations (Scheuhammer et al. 2007; Evers 2018). Therefore, many studies have focused on establishing baseline species exposure profiles and identifying the connections between predator species, positioned at high trophic levels, and lower-level prey species as a means to investigate the transfer pathways and cycling of Hg as an environmental contaminant.

Songbirds as bioindicators of environmental mercury

Population declines in resident and migratory North American bird species are well documented and have been associated with a variety of stressors, including exposure to pollutants (Rosenberg et al. 2019). Species, such as insectivorous songbirds, located at the top of the food chain, are recognized as excellent bioindicators of environmental health and have been widely used in Hg toxicology studies to serve as a reflection of Hg levels within numerous habitat types (Jackson et al. 2015). It is commonly hypothesized that Hg is transferred to songbirds through consumption of invertebrate, prey items located at lower trophic levels (Cristol et al. 2008; Rimmer et al. 2010; Edmonds et al. 2012; Fig. 1). While birds are able to reduce the concentrations of Hg in their bodies through processes such as feather growth and egg deposition (Condon and Cristol 2009; Ackerman et al. 2016a; Whitney and Cristol 2017b), individuals that are exposed to prey species high in Hg content may bioaccumulate Hg at rates greater than their ability to naturally depurate excess body burdens. Considering that songbirds are widespread across the landscape, it is necessary to understand the role that these indicator species represent regarding environmental Hg contamination in New York State.

Numerous studies have been conducted to better assess Hg exposure levels in avian communities across a wide range of species and ecosystems (Ackerman et al. 2016b; Cristol and Evers 2020). As a result, research has identified Hg concentrations within many bird species elevated to levels that exceed established thresholds associated with adverse reproductive, behavioral and physiological effects linked to Hg exposure (Whitney and Cristol 2017a). For example, studies have indicated that songbirds inhabiting wetland ecosystems, which possess oxygen-depleted, acidic conditions that facilitate the formation and bioavailability of MeHg (Ullrich et al. 2001), have elevated blood Hg concentrations and are therefore at greater risk to the deleterious impacts of Hg contamination (Edmonds et al. 2010, 2012; Lane et al. 2011, 2020; Kopec et al. 2018; Adams et al. 2020). Additionally, investigations targeting montane forests, which have been estimated to experience Hg deposition loads from 2-5 times greater than low elevation forests (Lawson et al. 2003; Stankwitz et al. 2012; Blackwell and Driscoll 2015; Gerson et al. 2017), have also documented Hg bioaccumulation within associated songbird communities, which includes the Bicknell's thrush (*Catharus bicknelli*), a high elevation habitat specialist and NYS Species of Special Concern (Rimmer et al. 2005, 2010, 2020; Townsend et al. 2014, 2015). These habitat types are common within the Adirondack Park, a region designated as a biological Hg hotspot due to deposition patterns and landscape characteristics favorable for the efficient conversion and biotic uptake of environmental Hg (Evers et al. 2007; Yu et al. 2011). Therefore, study components for this dissertation targeted avian species within Hg-sensitive Adirondack ecosystems, including *Sphagnum* bog and high elevation forests, to better characterize wildlife

Hg exposure within these habitat types and to further supplement the limited number of studies that have been previously conducted within these sensitive ecosystems.

Research overview & project design

Project sampling to investigate biotic Hg exposure was conducted from 2008-2011 at *Sphagnum* bog, upland forest and montane study sites in the Adirondack Park. Standardized research protocols and field methodologies were based on established avian Hg monitoring projects and were designed to support and inform long-term regional Hg studies on wildlife populations being conducted in the northeastern United States. Samples were collected by field crews comprised of students and staff from: Syracuse University, Biodiversity Research Institute, SUNY College of Environmental Science & Forestry, Northwestern University and Princeton University. All samples were analyzed for total mercury (THg) in the Center for Environmental Systems Engineering (CESE) laboratory at Syracuse University.

Chapter 2: Avian Mercury Exposure along an Elevational Gradient on Whiteface Mountain

This phase of the dissertation was designed to fill current knowledge gaps and to better understand the dynamics of Hg exposure in terrestrial ecosystems, specifically within data-limited, high elevation habitats. Considering that previous studies have demonstrated the effects of elevation on biotic and abiotic Hg concentrations within montane ecosystems (Townsend et al. 2014; Blackwell and Driscoll 2015), an intensive field study was conducted to further investigate patterns of avian Hg concentrations in relation to elevation, as well as seasonal variation.

Project sampling within montane habitats was conducted during the 2009-2010 field seasons along an elevational gradient at 13 established study sites (450-1400 meters) on Whiteface Mountain. To investigate the hypothesis that Hg concentrations increase with a corresponding increase in elevation, samples were collected from forest communities in three zones located along the elevational gradient: deciduous forest, coniferous forest, and alpine forest. At each site, insectivorous songbirds were nonlethally captured, and blood samples were collected. Blood samples in songbirds are reflective of local dietary uptake of Hg; therefore, these tissue samples are representative of Hg concentrations in the associated habitat. Songbirds were sampled over the course of two field seasons and collection efforts took place during periods of peak breeding activity. To examine differences in blood Hg concentrations along the elevational gradient, the following ground-foraging, *Catharus* thrushes were sampled: hermit thrush (*Catharus guttatus*), Swainson's thrush (*Catharus ustulatus*), and Bicknell's thrush. All plots were repeatedly sampled during 2009 and 2010 to better understand seasonal Hg exposure patterns in avian species during the breeding season.

In addition, the red-eyed vireo (*Vireo olivaceus*) and ovenbird (*Seiurus aurocapilla*) were sampled at low elevation sites for a comparative analysis with the *Sphagnum* bog-upland forest research study (Chapter 3).

Chapter 3: Avian Mercury Exposure in Sphagnum Bog and Upland Forest Ecosystems

This phase of the dissertation was designed to compare Hg exposure levels in songbird communities from study sites within *Sphagnum* bogs with adjacent upland forests. Despite assuming similar rates of atmospheric Hg deposition, it was hypothesized that biotic Hg concentrations would be elevated within *Sphagnum* bog ecosystems, due to the enhanced conversion of inorganic Hg to organic MeHg in wetland habitats, when compared to the surrounding upland forests (Jackson et al. 2015; Brasso et al. 2020). Therefore, it was generally anticipated that these two habitat types support different rates of Hg methylation and associated levels of bioavailable MeHg, which would be documented by detectable differences in avian blood Hg concentrations between the *Sphagnum* bog and upland forest ecosystems.

In 2008, 2009 and 2011, sampling efforts were focused within both *Sphagnum* bogs and adjacent upland forests at Massawepie Mire, Spring Pond Bog, Madawaska Flow, and Bloomingdale Bog. In alignment with the capture and tissue sampling protocols utilized in the Whiteface Mountain phase of the dissertation (Chapter 2), songbirds were sampled using nonlethal techniques and blood samples were collected for each individual. To examine patterns of avian Hg exposure, the following species were targeted within each habitat type:

- *Sphagnum* Bog: yellow palm warbler (*Setophaga palmarum*), Lincoln's sparrow (*Melospiza lincolnii*), Nashville warbler (*Leiothlypis ruficapilla*);
- Upland Forest: ovenbird, hermit thrush, and red-eyed vireo.

Similar to the Whiteface Mountain phase, seasonal variation in songbird Hg concentrations was also analyzed for each target species and study sites were sampled multiple times during the field season.

Chapter 4: Project Syntheses and Future Recommendations

In this chapter, a final summary of the major findings from each study is provided, as well as the results from the comparative analysis between the Whiteface Mountain and *Sphagnum* bog-upland forest studies. Overall project results from all phases of the dissertation are further synthesized and presented along with recommendations and guidelines for future research efforts examining Hg contamination within avian communities.

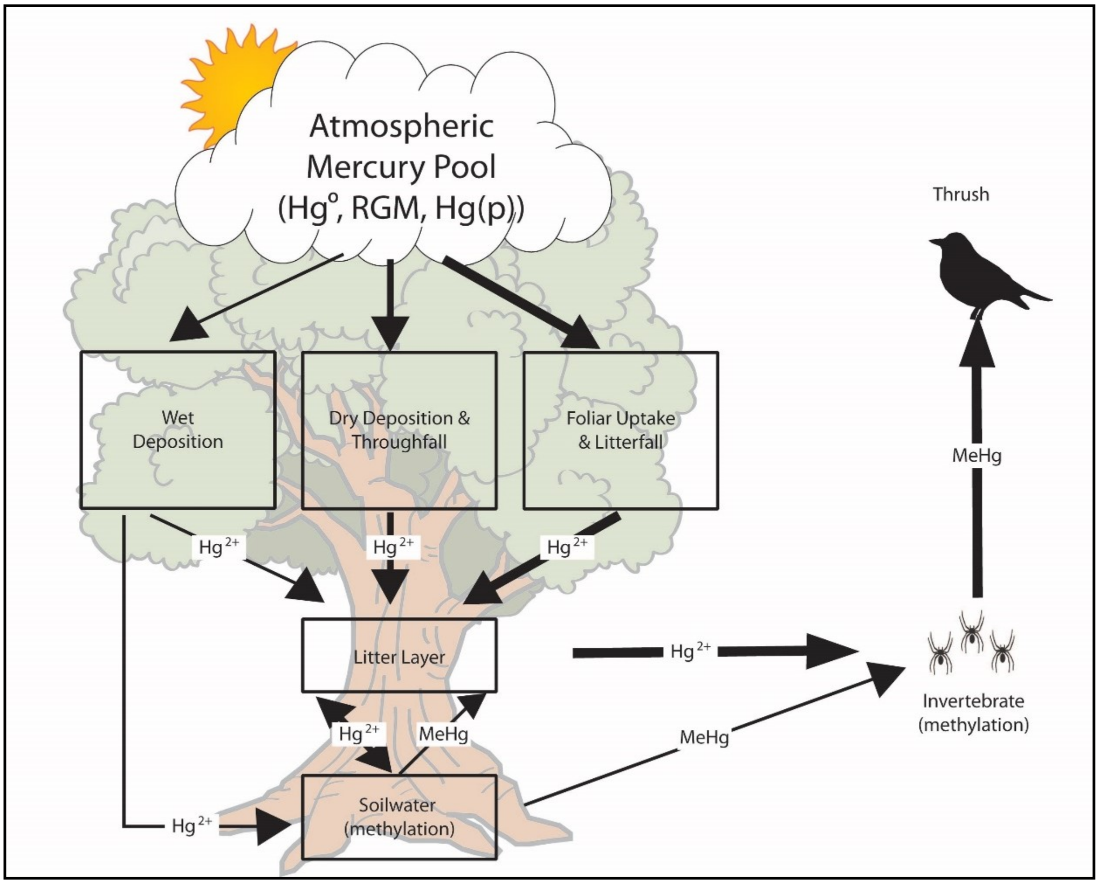

Fig. 1 Hypothesized pathways of mercury bioaccumulation within a terrestrial, insectivore food web. Figure abbreviations are defined as the following: elemental mercury (Hg^0); gaseous oxidized mercury (RGM, Hg^{2+}); particulate mercury (Hg(p)); and methylmercury (MeHg).

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Chapter 2

Mercury Exposure in Songbird Communities along an Elevational Gradient on Whiteface Mountain, Adirondack Park (New York, USA)

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Abstract

Mercury (Hg) is a potent neurotoxin that biomagnifies within food webs. Adverse effects have been documented for avian species related to exposure of elevated Hg levels. High elevation, boreal forests generally receive higher atmospheric Hg deposition and regional studies have subsequently identified elevated blood Hg concentrations in songbird species inhabiting these montane habitats. The overall goal of this study was to investigate spatial and seasonal Hg exposure patterns in songbird species along an elevational gradient on Whiteface Mountain in the Adirondack Park of New York State. Songbird blood samples were collected from June–July in 2009 and 2010 along an elevational gradient at 13 study plots (450–1400 m) with a focus on *Catharus* thrushes, including the hermit thrush, Swainson's thrush, and Bicknell's thrush. The main results of this study documented: (1) an overall linear pattern of increasing blood Hg concentrations with increasing elevation, with additional analysis suggesting a nonlinear elevational pattern of increasing blood Hg concentrations to 1075 m, followed by decreasing concentrations at higher elevations, for all *Catharus* thrush species across the elevational gradient; and (2) an overall nonlinear seasonal pattern of increasing, followed by decreasing blood Hg concentrations across target species. Avian exposure patterns appear driven by elevated atmospheric Hg deposition and increased methylmercury bioavailability within high elevation habitats as compared with low elevation forests. Seasonal patterns are likely influenced by a combination of complex and dynamic variables related to dietary selection and annual molting cycles. Considering that few high elevation analyses have been conducted within the context of regional songbird research, this project complements the results from similar studies and highlights the need for further monitoring efforts to investigate environmental Hg contamination within avian communities.

Keywords: Mercury, Songbird, Elevation, Whiteface Mountain, Adirondack Park

Introduction

Mercury (Hg) is a potent neurotoxin associated with adverse health effects on wildlife populations that have been well-documented in the northeastern United States (Evers and Clair 2005; Bank et al. 2007; Evers et al. 2007). Mercury contamination in the Northeast is largely the result of atmospheric deposition arising from local, regional, and global sources (Fitzgerald et al. 1998; Driscoll et al. 2007). These sources include anthropogenic emissions, such as coal-fired power plants, incinerators, mining and industrial emissions; natural sources, such as soil and mineral weathering and volcanic activity; and secondary emissions (or re-emissions) (Driscoll et al. 2013). Once deposited upon the landscape, sulfate- and iron-reducing bacteria and archaea convert inorganic Hg into methylmercury (MeHg), a biologically available organic form (Benoit et al. 2003; Podar et al. 2015). This toxic form of Hg readily bioaccumulates and biomagnifies within aquatic and terrestrial food webs resulting in elevated concentrations and adverse effects due to environmental exposure (Watras et al. 1998; Scheuhammer et al. 2007; Eagles-Smith et al. 2016). Designated by the U.S. Environmental Protection Agency as a persistent, bioaccumulative, and toxic (PBT) pollutant, Hg has become a globally recognized contaminant in response to its detrimental impacts on wildlife and human health (Vallero 2005). Due to atmospheric sources, Hg is a widespread pollutant across the landscape which has been extensively documented within aquatic ecosystems, including species inhabiting freshwater lakes and streams (Chen et al. 2005; Kamman et al. 2005). By contrast, relatively few investigations have focused on the dynamics of Hg cycling within terrestrial ecosystems, such as upland forest communities (Driscoll et al. 2007).

Research has documented various effects linking elevated Hg exposure to impacts on growth, behavior, development, survivorship, and reproductive success in numerous wildlife species (Wolfe et al. 1998; Whitney and Cristol 2017a; Evers 2018). Many studies of avian communities have focused on high-trophic piscivorous species, such as the common loon (*Gavia immer)*, as MeHg bioaccumulates to high levels within their tissues (Evers et al. 2005; Schoch et al. 2014a, 2020). However, songbirds have also been recognized as ideal indicators of environmental Hg contamination (Jackson et al. 2015; Adams et al. 2020). Through the processes of trophic transfer and uptake of bioavailable MeHg, songbirds are similarly able to bioaccumulate MeHg within various tissue types, thereby reflecting Hg inputs and dynamics within the associated habitat (Cristol et al. 2008; Rimmer et al. 2010; Jackson et al. 2011b). Studies have established that birds are sensitive to the adverse effects of MeHg exposure, including: asymmetrical feather growth (Evers et al. 2008), altered songs (Hallinger et al. 2010), immune and endocrine system disruption (Hawley et al. 2009; Wada et al. 2009; Lewis et al. 2013), skewed sex ratios (Bouland et al. 2012), and reproductive impairment (Brasso and Cristol 2008; Hallinger and Cristol 2011; Jackson et al. 2011a; Varian-Ramos et al. 2014). The results of these studies emphasize the importance of continued research to further quantify exposure levels and the impacts of environmental Hg contamination on avian populations.

The northeastern United States has historically been a region impacted by atmospheric Hg deposition. Numerous studies have been conducted in the Adirondack Park of New York State documenting the extent of Hg contamination on ecosystems and wildlife species (Driscoll et al. 2007; Evers et al. 2020). Based on a synthesis of regional biotic Hg concentrations, portions of the Adirondack Park have been designated as a "biological mercury hotspot" (Evers et al. 2007). These locations are defined as areas that are subject to moderate Hg deposition, but possess landscape characteristics, such as shallow soils, abundant forest and wetlands, and highly acidic habitats, which facilitate the transport of inorganic Hg, its conversion to MeHg, and transfer into aquatic and terrestrial food webs (Driscoll et al. 2007; Evers et al. 2007). Consequently, considerable research has been conducted across various habitat types and wildlife taxa in the Adirondacks, specifically to evaluate biotic and abiotic Hg concentrations and the processes associated with Hg deposition, methylation and transfer pathways (Demers et al. 2007; Yu et al. 2011, 2013; Schoch et al. 2014b; Gerson et al. 2017; Burns and Riva-Murray 2018; Riva-Murray et al. 2020).

Research conducted within montane ecosystems, which are commonly represented in the Adirondack Park, has documented elevated inputs of atmospheric Hg deposition to high elevation forests, due to increased cloud cover and precipitation, when compared with low elevation hardwood forests (Lovett et al. 1982; Miller et al. 2005; Stankwitz et al. 2012). Coniferous forests, which are the dominant cover type at high elevations, are able to efficiently remove atmospheric Hg via throughfall relative to deciduous forests (Miller et al. 2005; Sheehan et al. 2006). These results are consistent with montane Hg studies conducted on Whiteface Mountain, located in the High Peaks of the Adirondack mountains, which similarly indicated increases in abiotic Hg concentrations as a function of elevation (Blackwell and Driscoll 2015; Gerson et al. 2017). Further, regional studies targeting songbirds inhabiting montane forests documented elevated MeHg blood concentrations, specifically within high elevation boreal specialists, such as the Bicknell's thrush (*Catharus bicknelli*; Rimmer et al. 2005, 2010; Townsend et al. 2014). Considering the limited number of observations documenting Hg concentrations for avian species inhabiting montane habitats, additional research is needed to further establish baseline Hg exposure levels and evaluate the risk this contaminant poses to songbird communities. Recent studies in the Northeast have shown patterns of declining atmospheric Hg concentrations and deposition due to reductions in Hg emissions from regional point sources (Gerson and Driscoll 2016; Zhou et al. 2017; Mao et al. 2017; Olson et al. 2020), likely resulting from air quality management including the Mercury and Air Toxics Standards (MATS) rule. Ideally, these continued declines should promote the recovery of Adirondack ecosystems, such as high elevation forests, and subsequently limit the biotic Hg uptake of at-risk wildlife populations.

The primary objectives of this study were to document spatial and seasonal patterns of blood Hg concentrations along an elevational gradient for avian communities within montane forests in the Adirondack Park of New York State. To achieve these objectives, songbird species, with a focus on *Catharus* thrushes, were sampled on Whiteface Mountain from 450–1400 m over the course of two complete breeding seasons. This study documented Hg exposure patterns for all targeted and opportunistically sampled species, and specifically examined elevational and seasonal patterns in blood Hg concentrations for *Catharus* thrushes. Additionally, both within- and between-year variations in Hg concentrations were documented for a limited number of individuals that were opportunistically recaptured during sampling efforts. Results from this study complement similar songbird research and provides valuable quantitative data to improve understanding of Hg cycling and bioavailability for avian communities within sensitive montane ecosystems in the Adirondack Park.

Methods

Study site description

Project sampling was conducted at study plots on Whiteface Mountain (44.36°N, 73.90°W) in the Adirondack Park of New York State (Fig. 1). Located in the Wilmington Wild Forest and McKenzie Mountain Wilderness of the Adirondack High Peaks Region, Whiteface Mountain is the fifth highest peak (1483 m) in New York State. Whiteface Mountain is also the site of the State University of New York–Albany Atmospheric Sciences Research Center (ASRC), which coordinates and administers long-term research of cloud-water chemistry and atmospheric monitoring stations at both low elevation (604 m) and summit locations. A National Atmospheric Deposition Program (NADP) station, at which precipitation chemistry and atmospheric deposition are monitored, is also located on-site. Whiteface Mountain is intensively utilized as a year-round recreational area, which includes extensive hiking trails, ski resort, and seasonal vehicle access to the summit via the Veterans' Memorial Highway. Undeveloped portions of Whiteface are currently classified under the Adirondack Park State Land Master Plan as Wilderness and Wild Forest and all areas are managed under the jurisdiction of the New York State Department of Environmental Conservation (NYSDEC).

Forest communities on Whiteface Mountain are comprised of three primary zones, which include the deciduous forest, coniferous forest, and the alpine forest (Blackwell and Driscoll 2015). The low elevation deciduous forest (400–900 m) is dominated by American beech (*Fagus grandifolia)*, yellow birch (*Betula alleghaniensis)*, red maple (*Acer rubrum)*, and sugar maple (*Acer saccharum)*. The mid-elevation coniferous forest (1000–1300 m) is composed primarily of balsam fir (*Abies balsamea)* and red spruce (*Picea rubens)*. The high elevation alpine forest (1350–1483 m) is a krummholz mixed community of balsam fir, paper birch (*Betula papyrifera)*, red spruce, and mountain ash (*Sorbus americana)*.

Research approach and study design

To investigate spatial and seasonal patterns of Hg concentrations in terrestrial biota, songbird blood samples were collected from June–July in 2009 and 2010 along an elevational gradient at 13 study plots (450–1400 m) on Whiteface Mountain. Sampling efforts were timed to correspond with periods of peak breeding activity for songbird species in the northeastern United States. Study plots were established along both the eastern and western transects of Whiteface Mountain and were located across the elevational gradient within each of the three major forest communities described (deciduous, coniferous and alpine habitat). 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 on these songbirds is included in Supporting Information (SI Table 1).

To document overall Hg exposure patterns within the avian community on Whiteface Mountain, results are presented for all songbird species sampled, which include species of interest that were targeted for capture, as well as those that were sampled opportunistically. However, the primary target species selected to document elevational and seasonal patterns in blood Hg concentrations were three migratory *Catharus* thrushes: hermit thrush (*Catharus guttatus*), Swainson's thrush (*Catharus ustulatus*) and Bicknell's thrush. Similar in both their ecology and foraging strategies (De Graaf et al. 1985), these species are distributed along the entire elevational gradient on Whiteface Mountain. The hermit thrush occurs across a wide range of elevations in the eastern United States and has been documented up to 1380 m, but has a mean elevation of 200 m (Dellinger et al. 2012). For this study, hermit thrushes were sampled between 450–900 m. Swainson's thrush generally occurs in the highest densities between approximately

800–1200 m in the northeastern United States (Mack and Yong 2000) and were found to span a majority of the elevational gradient from 600–1400 m. The Bicknell's thrush is a high elevation specialist whose breeding range is primarily restricted to elevations above 1100 m (Townsend et al. 2015). All Bicknell's thrushes sampled during this study were located between 1200–1400 m.

To further investigate spatial and seasonal Hg patterns for songbirds within sensitive habitats, a contemporaneous multi-year field study was conducted in 2008, 2009, and 2011 at several *Sphagnum* bog wetland complexes and adjacent upland forests in the Adirondack Park. To supplement the wetland research, a subset of data from low elevation plots on Whiteface Mountain, which included hermit thrushes, red-eyed vireos (*Vireo olivaceus)*, and ovenbirds (*Seiurus aurocapilla)*, were used for comparative analysis with the same target species at upland forest sites (Sauer et al. 2020). All songbird capture and tissue sampling methodologies were the same between research projects.

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, 6- and 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. A total of 30–50 µl 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 (NYSDEC TRP #5472-1502, NYSDEC License to Collect or Possess #394), federal (Permit #22636) and IACUC (Permit #09-009) 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. EPA 1998). Quality assurance for each analytical run of ten 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 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 ± 0.9% (n = 20) for SRM 1515, 95 ± 0.6% (n = 29) for SRM 2976, 98 ± 1.1% (n = 18) for SRM 955c and 97 ± 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 methylmercury (Rimmer et al. 2005; Edmonds et al. 2010). All blood Hg concentrations are expressed as µg/g, wet weight (ww).

Statistical analysis

Two general linear models were specified to test for differences in blood Hg concentrations in *Catharus* thrushes along an elevational gradient on Whiteface Mountain. Blood Hg data were $\log_e$-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. The first model assessed the effect of elevation, date (ordinal day), year (2009, 2010), aspect (east vs. west transect) and sex on Hg concentrations in bird blood. This approach assumes that *Catharus* thrushes are similar indicators of ecosystem MeHg across all sampling locations. The second model further evaluated the importance of elevation in a species-specific manner by including the effect of species (hermit thrush, Swainson's thrush, Bicknell's thrush), community type (an elevation-correlated categorical variable for forest type: deciduous forest, coniferous forest, alpine forest), date (ordinal day), year (2009, 2010), aspect (east vs. west transect) and sex on Hg concentrations in bird blood. Differences among species were accounted for by nesting species within community type to determine how elevation-related habitats affected blood Hg concentrations for each species. Significance was determined using a *t*-test for individual model parameters and an *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.

Trends in songbird Hg concentrations with elevation and ordinal day were further examined with piecewise regression to determine if nonlinear trends were present and to identify a breakpoint between two models with different slopes. Piecewise regression was estimated using the NLIN function (Ryan and Porth 2007).

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 2009–2010, a total 207 adult songbirds, representing 15 species, were sampled and analyzed ($n = 220$) for blood Hg concentrations to characterize exposure along an elevational gradient on Whiteface Mountain (Fig. 2; Table 1). For all species sampled, individual blood Hg concentrations levels ranged from a low of 0.018 µg/g in an ovenbird to a high of 0.266 µg/g for a red-eyed vireo.

Mercury exposure in thrush species along an elevational gradient

The overall r^2 was 0.24 for the model that estimated the effect of elevation on blood Hg concentrations across all thrush species. Across groups, elevation ($F_{1,8} = 9.21$, $p = 0.003$), year ($F_{1,87} = 9.37$, $p = 0.003$), and aspect ($F_{1,87} = 7.49$, $p = 0.008$) were strong predictors of Hg concentrations in bird blood. Thrush blood Hg concentrations increased significantly with elevation ($\beta = 0.0002 \pm 0.00005$, $p = 0.003$). Overall, blood Hg concentrations in *Catharus* thrushes were found to increase along the elevational gradient, were highest on the western vs. eastern elevational transect ($\beta = 0.05 \pm 0.02$, $p = 0.008$; difference = 0.09 ± 0.04), and 2009 had higher Hg concentrations than 2010 ($\beta = 0.06 \pm 0.02$, $p = 0.003$; difference = 0.11 ± 0.04).

The model assessing blood Hg concentrations in *Catharus* species nested within forest community types, also had sufficient fit ($r^2 = 0.35$). Across groups, community type ($F_{2,86} = 4.81$, $p = 0.01$), year ($F_{1,87} = 12.28$, $p < 0.001$) and aspect ($F_{1,87} = 7.76$, $p = 0.007$) were strong predictors of Hg concentrations in bird blood. Similar to the first model, blood Hg concentrations were higher along the western transect compared to the eastern transect (difference = 0.10 ± 0.04, $p = 0.007$) and were elevated in 2009 as compared to 2010 (difference = 0.12 ± 0.04, $p < 0.001$). Additionally, blood Hg concentrations were highest within mid-elevation, coniferous forests, which were significantly different from low elevation, deciduous forests (difference = 0.19 ± 0.06, $p = 0.008$). *Post hoc* comparisons using the Tukey–Kramer HSD test further indicated that hermit thrushes in deciduous forests had significantly lower blood Hg concentrations than both Swainson's and Bicknell's thrush inhabiting coniferous forests (difference = 0.17 ± 0.04, $p = 0.004$; difference = 0.16 ± 0.05, $p = 0.03$, respectively). Within-species, only Swainson's thrush showed differences among forest community types, as those individuals inhabiting deciduous forests were marginally lower than those within coniferous forest (difference = 0.16 ± 0.05, $p = 0.06$).

Using piecewise regression to further examine spatial patterns across the elevational gradient, overall Hg concentrations in thrushes increased from an elevation of 450 to 1075 m (slope = 0.0005 ± 0.0002 on log scale; $p = 0.01$; +13% per 100 m), and significantly decreased from 1075 to 1400 m (slope = −0.0006 ± 0.0002; $p = 0.02$; −11% per 100 m; Fig. 3a). Sampled along the elevational gradient, Swainson's thrush exhibited a weak increase from an elevation of

600 to 983 m (slope = 0.0010 ± 0.0006; p = 0.09; +25% per 100 m), and significantly decreased from 983 to 1400 m (slope = −0.0007 ± 0.0003; p = 0.02; −15% per 100 m; Fig. 3c). No elevational changes in blood Hg concentrations were found for hermit (p = 0.73; Fig. 3b) or Bicknell's thrush (p = 0.58; Fig. 3d) using linear regression.

Mercury concentrations and seasonal effects

Across both general linear models, ordinal date ($F_{1,87}$ = 0.47, p = 0.49; $F_{1,87}$ = 0.99, p = 0.32, respectively) did not affect blood Hg concentrations. However, using piecewise regression, overall Hg concentrations in thrushes increased from the beginning of the season (ordinal day 155, June 4) to ordinal day 178 (June 27; slope = 0.0117 ± 0.0027; p = 0.001; +3.6% per day) and decreased from ordinal day 178 to ordinal day 209 (July 28; slope = −0.0121 ± 0.0034; p = 0.003; −1.8% per day; Fig. 4a). When examined separately, seasonal patterns of blood Hg concentrations differed among species. Mercury concentrations in hermit thrushes increased from the beginning of the season to ordinal day 188 (July 7; slope = 0.0096 ± 0.0030; p = 0.01, +2.9% per day; Fig. 4b), but data were not sufficient to describe the seasonal pattern after ordinal day 188 (n = 3). Mercury concentrations in Swainson's thrushes increased from ordinal day 158 (June 7) to ordinal day 178 (slope = 0.0152 ± 0.0047; p = 0.01, +4.4% per day), and decreased from ordinal day 178 to ordinal day 209 (slope = −0.0154 ± 0.0056; p = 0.02, −2.1% per day; Fig. 4c). No seasonal changes in blood Hg concentrations were evident for Bicknell's thrush using linear (p = 0.71; Fig. 4d) or piecewise regression.

Discussion

This study was designed to provide an assessment of Hg exposure patterns for avian communities within montane forests in the Adirondack Park, New York State. The main results of this study documented: (1) an overall linear pattern of increasing blood Hg concentrations with increasing elevation, with additional analysis suggesting a nonlinear elevational pattern of increasing blood Hg concentrations to 1075 m, followed by decreasing concentrations thereafter, for all *Catharus* thrush species across the elevational gradient; and (2) an overall nonlinear seasonal pattern of increasing, followed by decreasing blood Hg concentrations across thrush species on Whiteface Mountain.

Avian mercury bioaccumulation and elevational patterns in montane ecosystems

Across the suite of 15 songbird species sampled on Whiteface Mountain, *Catharus* thrushes were found to exhibit some of the highest mean Hg concentrations relative to other species sampled within the avian community (Fig. 2). Mercury exposure levels for thrushes documented in this study are comparable with those described through similar research efforts in both New York and Vermont that also utilized *Catharus* thrushes as an indicator of blood Hg concentrations in high elevation forests (Rimmer et al. 2005, 2010; Townsend et al. 2014). Specifically, Bicknell's thrush mean blood Hg values (0.093 µg/g, ww) were similar to those in the Catskill Mountains of New York (0.107 µg/g, ww; Townsend et al. 2014), an earlier study on Whiteface Mountain (0.080 µg/g, ww; Rimmer et al. 2005) and two studies on Stratton Mountain in Vermont (range of 0.088–0.120 µg/g, ww; Rimmer et al. 2005, 2010), suggesting similar regional Hg exposure levels in the northeastern United States.

Linear and nonlinear patterns between blood Hg concentrations and elevation were documented across all *Catharus* thrushes (Figs 3a, 5e) and one individual thrush species (Fig.

3c). Swainson's thrush, which was sampled along a majority of the elevational gradient, displayed an increase in blood Hg concentrations up to 983 m, followed by a decrease thereafter (Fig. 3c). No elevational changes were found for either hermit (Fig. 3b) or Bicknell's thrush (Fig. 3d), which is likely due to the limited elevational range occupied by each individual species along the gradient. The overall pattern of increasing blood Hg concentrations in *Catharus* thrushes with increasing elevation was also detected by Townsend et al. (2014) through a similar investigation examining Hg exposure in terrestrial food web compartments along an elevational gradient at Slide Mountain in the Catskill region. The results of Townsend et al. (2014) further documented corresponding patterns of elevational increases in Hg concentrations for biotic (salamanders) and abiotic (leaf litter, organic soil horizons) samples. A study of nestling bald eagles in New York State also indicated elevated Hg concentrations in breast feathers at higher elevation sites as compared to low elevation sites (De Sorbo et al. 2020).

Previous research has demonstrated that high elevation boreal forests are subjected to elevated atmospheric Hg deposition resulting from increased precipitation rates and enhanced cloud cover relative to lower elevation hardwood forests (Lovett et al. 1982; Miller et al. 2005; Stankwitz et al. 2012). Further, coniferous forest cover types are characterized by year-round leaf cover and a high leaf area index, that promotes the efficient removal of atmospheric Hg compared to deciduous forest types (Miller et al. 2005; Sheehan et al. 2006). Data collected as part of a concurrent study conducted at the same research plots in 2009–2010 on Whiteface Mountain, to assess Hg concentrations in live foliage, litterfall, organic soil horizons, throughfall and cloud water, indicated that both atmospheric Hg deposition and organic soil Hg concentrations increased along the elevational gradient (Blackwell and Driscoll 2015; Fig. 5a). Moreover, the pathways of atmospheric Hg inputs varied among elevation zones, with litterfall

Hg dominating inputs to the lower elevation deciduous zone, throughfall supplying the largest fraction of Hg in the coniferous zone, and cloud deposition providing the greatest Hg in the high elevation alpine zone.

A repeated sampling of the study plots established by Blackwell and Driscoll (2015) in 2009–2010, was conducted in 2015 (Gerson et al. 2017) to examine spatial and seasonal patterns of MeHg inputs and concentrations within various abiotic compartments across the elevational gradient. These findings similarly indicated patterns of increasing Hg with elevation, with the highest MeHg concentrations for litterfall and organic soil horizons detected within mid-elevation coniferous forests (Fig. 5d). Despite these patterns of atmospheric MeHg deposition, MeHg supply was dominated by production within soils. The results of Gerson et al. (2017) also documented that the percent of total Hg as MeHg in soils was highest in low elevation deciduous forests and decreased with elevation, likely influenced by variation in temperature, as warmer temperatures enhance the production of MeHg (Ullrich et al. 2001; Fig. 5c). While Hg losses by evasion have not been measured on Whiteface Mountain, it is hypothesized that losses are lowest in the coniferous forest due to a dense closed canopy limiting photoreduction, highest in the alpine forest due to high Hg inputs and an open terrain, and intermediate in the deciduous forest due to the seasonally open and closed canopy structure (Fig. 5b). Other regional studies have also shown this pattern of increasing deposition and soil Hg with elevation, with Hg deposition similarly being highest within coniferous forest types (Witt et al. 2009; Stankwitz et al. 2012).

Taken together, the results of these studies suggest that MeHg bioavailability and subsequent avian biotic uptake are reflective of atmospheric Hg deposition and conversion of this input to MeHg concentrations within the associated environment, as particularly demonstrated by the connections between patterns of songbird blood Hg concentrations (Fig. 5e) and associated soil MeHg on Whiteface Mountain (Fig. 5d; Gerson et al. 2017). Considering that *Catharus* thrushes are ground-foraging species (De Graff et al. 1985), which consume invertebrate prey items inhabiting within or near surface soils, this link provides further insight to better understand the environmental pathways for biotic Hg exposure in terrestrial species. Although information for biological Hg exposure levels along an elevation gradient is limited, the combination of corroborating research results, particularly for those site-specific studies conducted on Whiteface Mountain, suggest that processes related to atmospheric Hg deposition and methylation pathways in boreal forests likely control MeHg bioavailability and influence exposure levels documented in songbird species inhabiting these sensitive, montane habitats.

Sample collection across both the eastern and western transects allowed for the examination of additional within-site observations related to potential spatial patterns. For thrush species sampled, overall blood Hg was significantly higher on the western slope of the mountain as compared to the eastern slope. These observations describe the spatial variation documented within the dataset and may reflect a possible effect of slope orientation on songbird blood Hg concentrations, however additional sampling efforts would be required to more definitively assess this potential spatial pattern.

Seasonal patterns in avian mercury exposure

There was a significant overall seasonal increase in blood Hg concentrations until ordinal day 178 (June 27), followed by a decline for the combined thrush species during the course of the field season (Fig. 4a). When analyzed separately both the hermit (Fig. 4b) and Swainson's thrush (Fig. 4c) demonstrated similar seasonal patterns, however samples for the hermit thrush were not sufficient to determine the seasonal pattern after ordinal day 188 (July 7). The

Bicknell's thrush showed no significant seasonal effects (Fig. 4d). This overall pattern of seasonal increase followed by a decrease is similar to results documented within other upland forest Adirondack study sites (Sauer et al. 2020), but considerable variation exists across studies that have examined seasonal patterns of Hg exposure within avian communities. Seasonal patterns reported from studies that have examined Bicknell's thrush (Rimmer et al. 2005, 2010; Townsend et al. 2014) found generally declining blood Hg concentrations during the course of the breeding season. However, Rimmer et al. (2010) also noted an increase in blood Hg concentrations until approximately early to mid-June, followed by a decline for the remainder of the season, which is similar to the overall pattern observed across thrush species on Whiteface Mountain. This decline in Bicknell's thrush blood Hg was attributed to a seasonal shift in dietary selection based on prey availability, which suggests that songbirds rely primarily on a high-Hg invertebrate foraging base in the early season, followed by lower Hg food items, such as Lepidoptera larvae (Cristol et al. 2008; Edmonds et al. 2012) and fruit, which are more available later in the breeding season. While this seasonal pattern was not observed specifically for Bicknell's thrush on Whiteface, possibly due to limited sample size, the overall pattern of increasing, followed by decreasing Hg concentrations, may indicate that similar processes linking seasonal phenology, shifts in prey availability, and biotic dietary uptake of Hg are common at montane systems in the Northeast. Studies of other avian species within the Northeast have also documented seasonal fluctuations in blood Hg concentrations while on their breeding grounds. A long-term study of saltmarsh sparrows (*Ammospiza caudacuta)* at several sites in New England (Lane et al. 2020) documented a pattern of increasing blood Hg concentrations through mid-July followed by a corresponding decline. Another study of marsh birds in Maine (Kopec et al. 2018) similarly found an increase in Hg blood concentrations from arrival on the breeding grounds until approximately mid-July. While the patterns of Hg bioaccumulation across studies are similar, differences related to the timing of seasonal Hg declines are likely linked to associated differences in habitat type and natural history of species sampled.

As shifts in dietary selection likely contribute to seasonal changes in blood Hg concentrations, reductions in concentrations are also affected by annual molting cycles through the depuration of Hg into growing feathers (Furness et al. 1986; Condon and Cristol 2009; Whitney and Cristol 2017b). The pre-basic molt for Bicknell's, Swainson's and hermit thrushes begins during July (Mack and Yong 2000; Dellinger et al. 2012; Townsend et al. 2015), which also corresponds with the general timing of declining Hg concentrations observed on Whiteface Mountain. Additionally, seasonal patterns in soil MeHg concentrations have been observed on Whiteface Mountain (Gerson et al. 2017) with the highest values in July. This peak was attributed to an increase in microbial methylation activity due to warmer temperatures and increased precipitation rates resulting in wetter, anoxic soil conditions. This pattern further suggests the link between abiotic soil Hg concentrations and biological uptake within associated avian communities.

Finally, blood Hg concentrations from a limited number of target and non-target species were examined for within and between-year recaptures (SI Table 1). Fluctuations in blood Hg concentrations were highly variable within the dataset, however, a greater proportion of individuals were documented to exhibit decreases in blood Hg concentrations (82% of captures within-season; 62% of captures between seasons) as compared to increases in concentrations. Blood Hg concentrations for all resampled *Catharus* thrushes were found to decline both within and between seasons, with the exception of one hermit thrush that displayed a within-season

82% increase, followed by a 17% decline. A limited number of observations for repeated blood Hg sampling of avian species have been reported (Rimmer et al. 2005; Kopec et al. 2018; Schoch et al. 2020) and all studies have similarly documented highly variable results. Data from these observations reflect the dynamics associated with individual Hg exposure and provides an indication of within-site and age-related patterns of bioaccumulation.

Taken together, the observed seasonal patterns for *Catharus* thrushes on Whiteface Mountain are likely influenced by a combination of variables including dietary selection, prey availability, and molting cycles. While the dynamics and mechanisms related to seasonal patterns of Hg exposure are still uncertain, additional capture efforts as part of future monitoring studies would allow for a better understanding of the complexities associated with blood Hg concentrations in songbird communities during the breeding season.

Adverse effects thresholds in Whiteface Mountain avian communities

There were no individuals captured along the elevational gradient on Whiteface Mountain that approached established blood Hg thresholds associated with adverse reproductive impacts (<0.7 µg/g, low risk; 0.7–1.2 µg/g, moderate risk; 1.2–1.7 µg/g, high risk; and >1.7 µg/g, very high risk; Jackson et al. 2011a). The highest Hg concentrations for all songbirds sampled were for a low elevation red-eyed vireo (0.266 µg/g) and a mid-elevation Swainson's thrush (0.233 µg/g). Therefore, songbirds sampled at study sites on Whiteface Mountain are considered to be generally low risk to the documented effects of Hg exposure (Jackson et al. 2011a). However, the Bicknell's thrush is widely regarded as a species of conservation concern due to declining population levels, along with habitat degradation and loss at both its wintering and breeding grounds (Townsend et al. 2015). Currently listed under the International Union for

Conservation of Nature (IUCN) Red List as a vulnerable species and classified by the NYSDEC as a Species of Special Concern, the Bicknell's thrush is a long-distance, migratory species, whose limited breeding habitat is restricted to montane spruce-fir forests. Documented breeding locations for this high elevation specialist in New York State are limited to the Catskill and Adirondack Mountains, which has designated Bicknell's thrush breeding habitat on Whiteface Mountain as a Sub-Alpine Forest Bird Conservation Area. While Hg concentrations for this species on Whiteface Mountain do not approach established threshold levels associated with adverse reproductive effects, blood Hg concentrations have been documented at twice the level on wintering grounds in the Dominican Republic, as compared to breeding habitat in the northeastern United States (Townsend et al. 2013), indicating chronic year-round exposure. Considering that Hg sensitivity and toxicity thresholds for individual species are largely unknown, the Bicknell's thrush, as well as its associated congeners, may be vulnerable to the documented physiological impacts due to exposure on both the wintering grounds and breeding habitat on Whiteface Mountain.

Conclusions

This study provides the first observations to examine spatial and seasonal patterns of songbird blood Hg concentrations along an elevational gradient in the Adirondack Park in New York State. In summary, overall thrush exposure patterns appear likely driven by elevated atmospheric Hg deposition and increased MeHg bioavailability within coniferous and alpine habitats as compared to deciduous forests. While results are highly variable, data suggests that seasonal patterns are influenced by a number of complex and dynamic variables, such as individual foraging strategies, prey availability, and depuration patterns related to annual molting cycles. Finally, while *Catharus* thrush species were not documented to exhibit Hg concentrations that approached established threshold levels for impacts on reproductive success, monitoring studies to more accurately define the extent of Hg as a biological stressor within data-limited alpine forests would contribute valuable quantitative data regarding the ecological health of breeding habitat for these migratory songbird species occupying sensitive montane habitats. Considering that few high elevation analyses have been conducted within the context of regional songbird research, this project complements the results from similar studies and contributes to the knowledge base relating to environmental Hg contamination and bioaccumulation within regional avian communities. Ultimately, regulations promoting reductions in Hg emissions, such as the Mercury and Air Toxics Standards (MATS) rule at the national level and the Minamata Convention, supported through the United Nations Environmental Programme at the international level, will work to limit both wildlife exposure levels and minimize the associated impacts in sensitive montane habitats, such as the Adirondack Park.

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Tables

Table 1. Arithmetic mean blood mercury concentrations (µg/g, ww ± SE), sample size (*n*), and Hg range for songbirds sampled on Whiteface Mountain, New York, 2009–2010.

Species	Mean Hg (µg/g) ± SE (n)	Hg Range (µg/g)	Foraging Guild	Foraging Layer
Target Species				
Bicknell's Thrush	0.093 ± 0.007 (22)	0.051 - 0.180	Omnivore	Ground/Lower Canopy
Hermit Thrush	0.067 ± 0.005 (25)	0.035 - 0.119	Insectivore	Ground
Swainson's Thrush	0.095 ± 0.006 (42)	0.019 - 0.233	Omnivore	Ground/Lower Canopy
Non-target Species				
American Robin	0.053 (1)		Vermivore	Ground
Black and White Warbler	0.065 ± 0.008 (3)	0.053 - 0.080	Insectivore	Bark
Blackpoll Warbler	0.059 ± 0.009 (3)	0.044 - 0.074	Insectivore	Upper Canopy
Black-throated Blue Warbler	0.033 (1)		Insectivore	Lower Canopy
Black-throated Green Warbler	0.043 (1)		Insectivore	Lower Canopy
Blue-headed Vireo	0.135 ± 0.022 (2)	0.112 - 0.157	Insectivore	Lower Canopy
Nashville Warbler	0.040 ± 0.016 (2)	0.024 - 0.056	Insectivore	Lower Canopy
Ovenbird	0.054 ± 0.003 (32)	0.018 - 0.096	Insectivore/Molluscovore	Ground
Red-eyed Vireo	0.116 ± 0.012 (19)	0.062 - 0.266	Insectivore	Upper Canopy
Slate-colored Junco	0.052 ± 0.004 (35)	0.027 - 0.151	Omnivore	Ground
White-throated Sparrow	0.044 ± 0.004 (30)	0.023 - 0.153	Omnivore	Ground
Yellow-rumped Warbler	0.088 ± 0.006 (2)	0.081 - 0.094	Insectivore	Lower Canopy

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

Figures

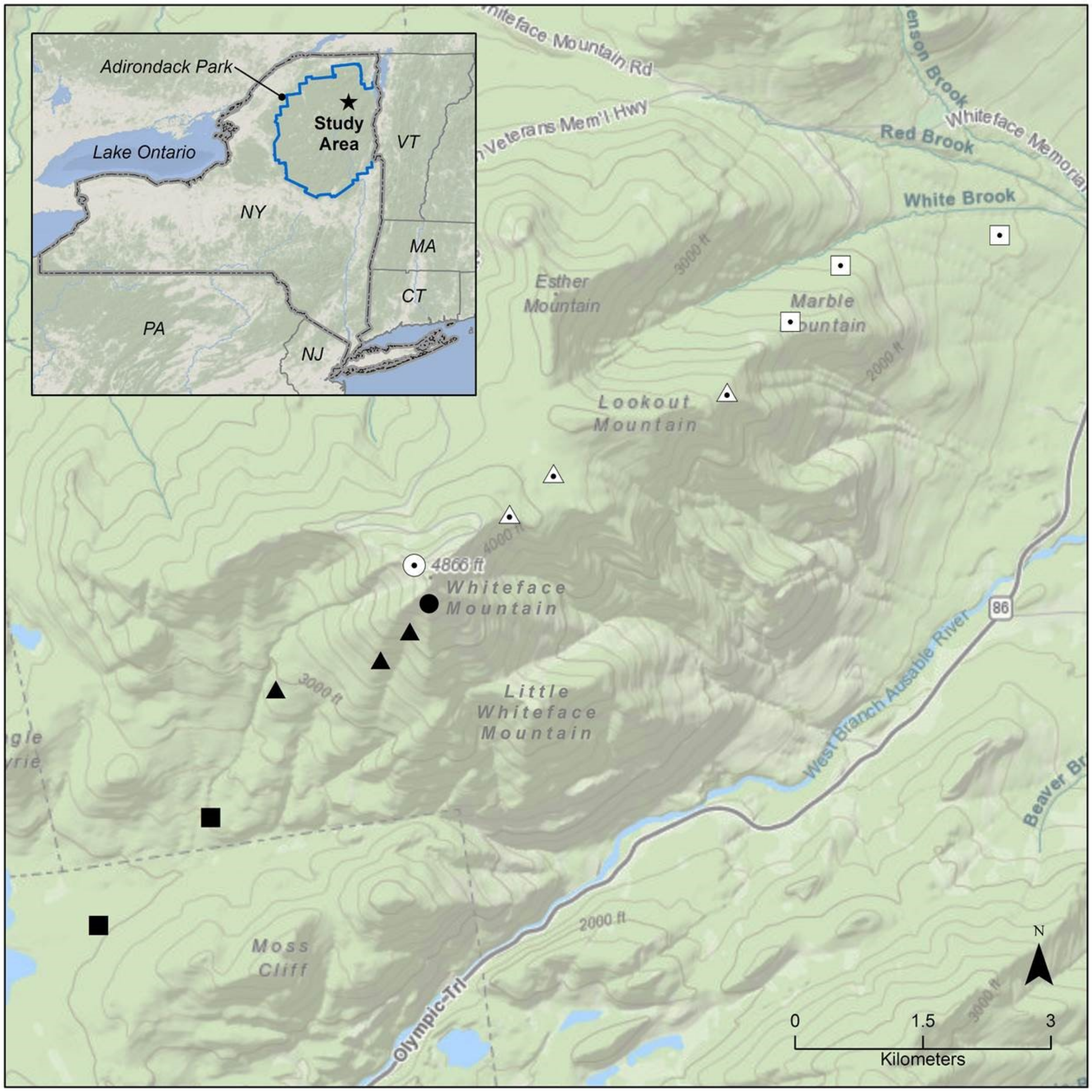

Fig. 1 Songbird sampling locations on Whiteface Mountain, Adirondack Park, New York, 2009–2010. Study sites are located on the western (black symbols) and eastern (white dot symbols) transects. Square symbols represent deciduous forests, triangles are coniferous forests, and circles are alpine zones.

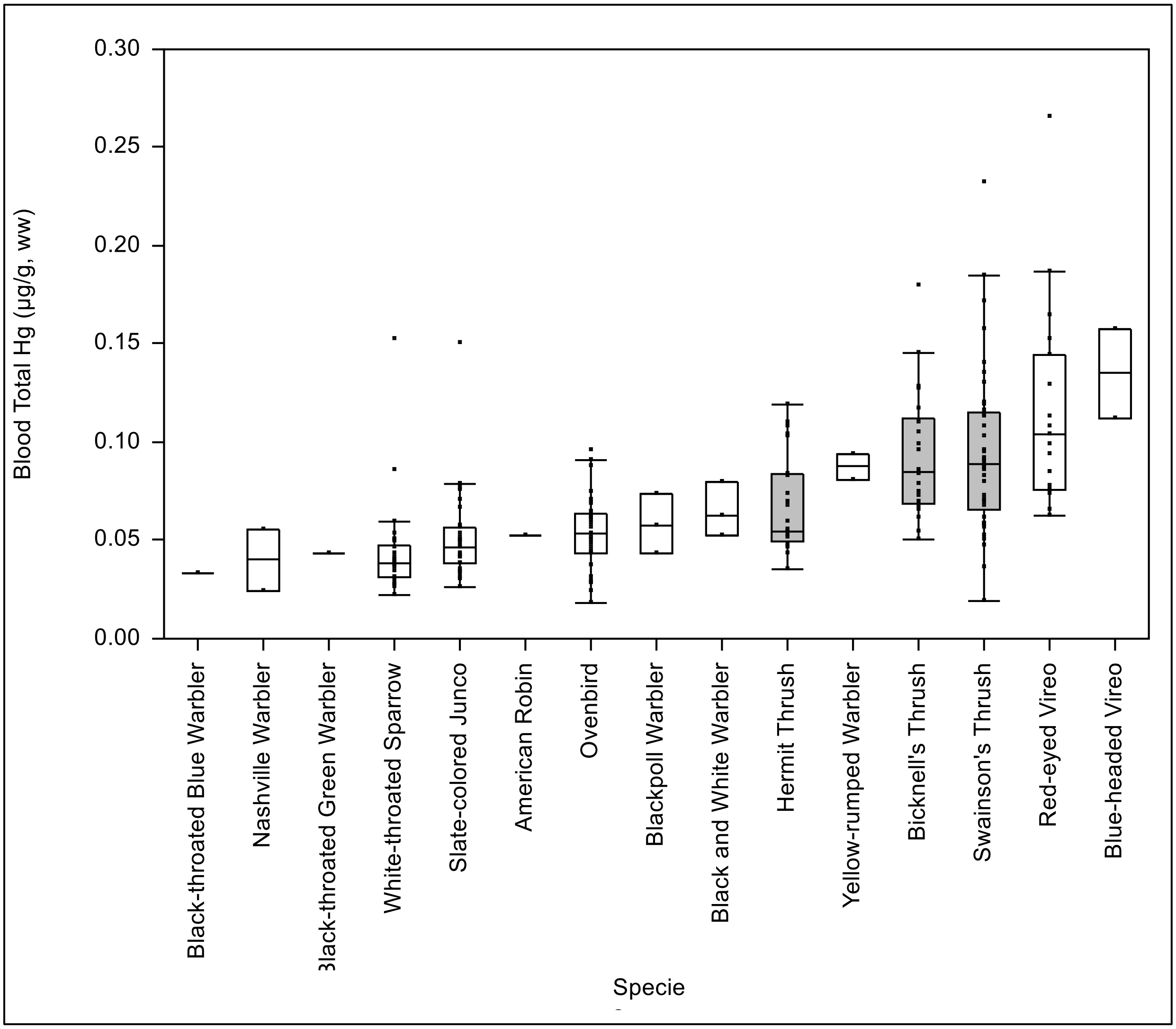

Fig. 2 Blood mercury concentrations (µg/g, ww) for songbird species on Whiteface Mountain, New York, 2009–2010. Box plots denote the median (horizontal line within the box) and the 25th and 75th quantiles (lower and upper edges of the box). Target species are shown in gray shading. Table 1 includes sample size (n) for songbirds sampled on Whiteface Mountain.

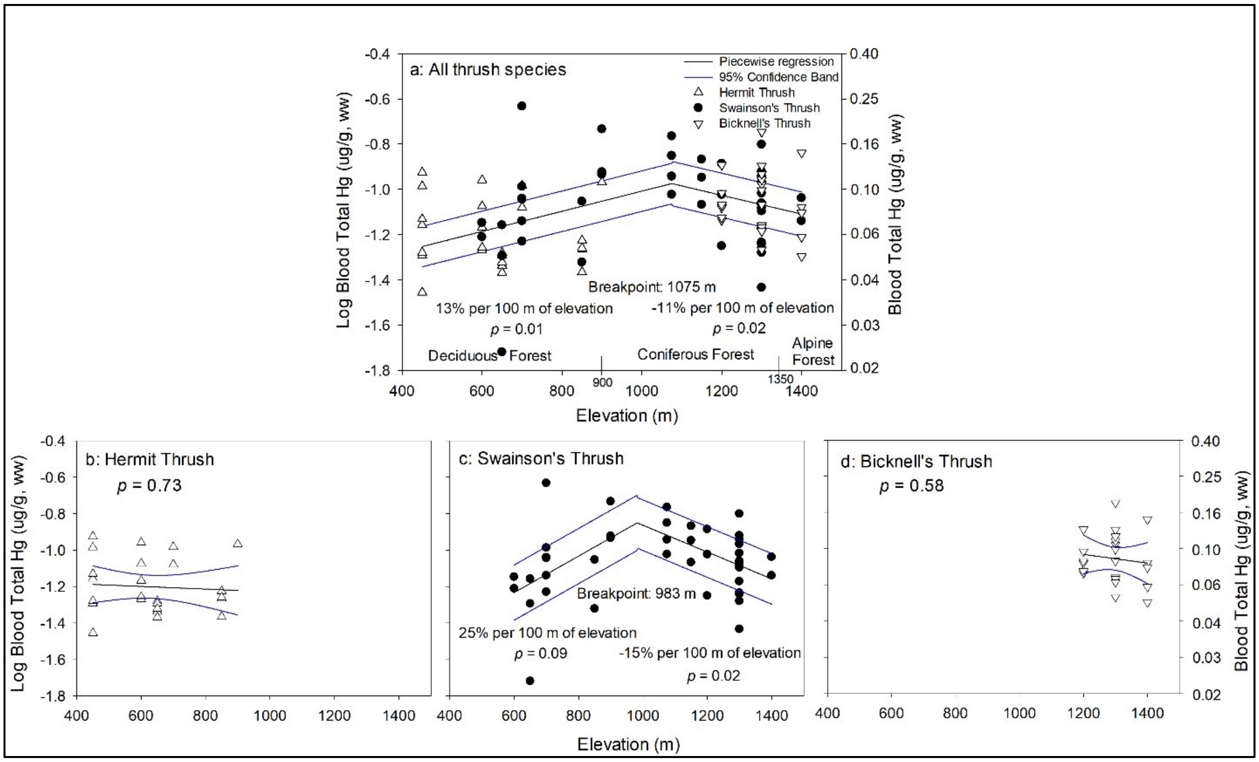

Fig. 3 Elevational patterns in blood mercury concentrations (µg/g, ww) on Whiteface Mountain, New York, 2009–2010 for: **a** all thrush species, **b** Hermit Thrush, **c** Swainson's Thrush, and **d** Bicknell's Thrush. Breakpoint was estimated using piecewise regression with NLIN function in SAS. If no breakpoint was detected, single linear trend is shown based on linear regressions.

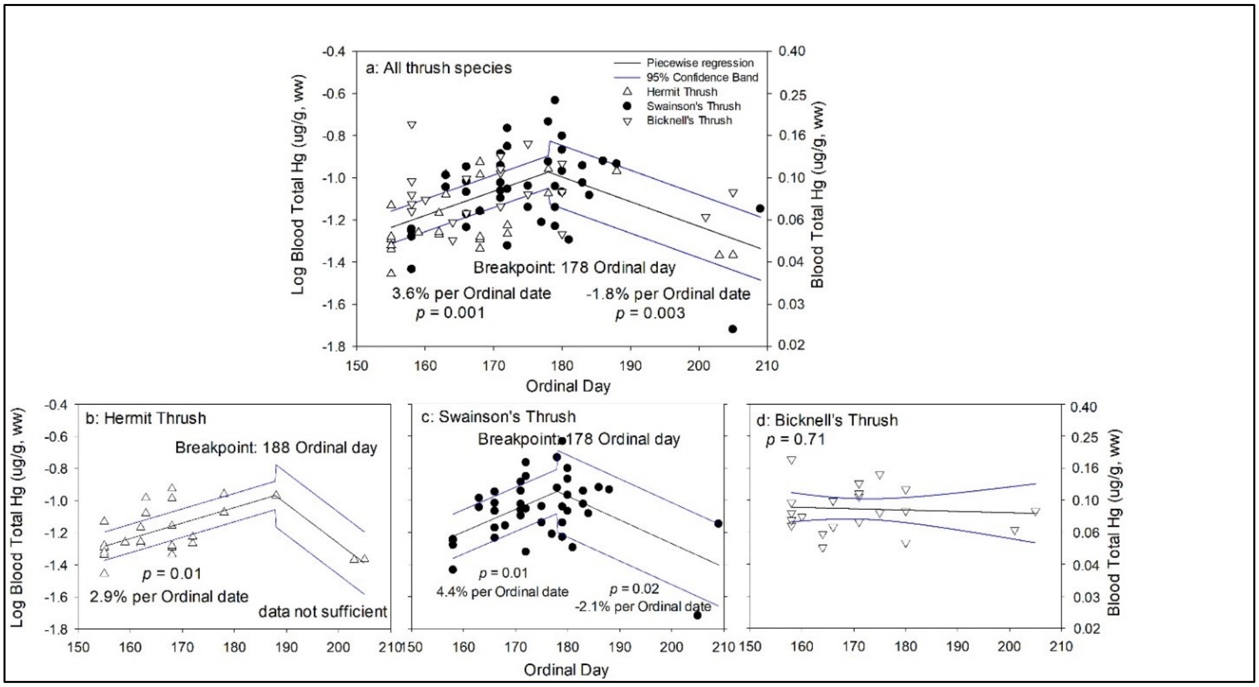

Fig. 4 Seasonal patterns in blood mercury concentrations (μg/g, ww) on Whiteface Mountain, New York, 2009–2010 for: **a** all thrush species, **b** Hermit Thrush, **c** Swainson's Thrush, and **d** Bicknell's Thrush. Data points are representative of each individual at the time of first capture during the breeding season. Breakpoint was estimated using piecewise regression with NLIN function in SAS. If no breakpoint was detected, single linear trend is shown based on linear regressions.

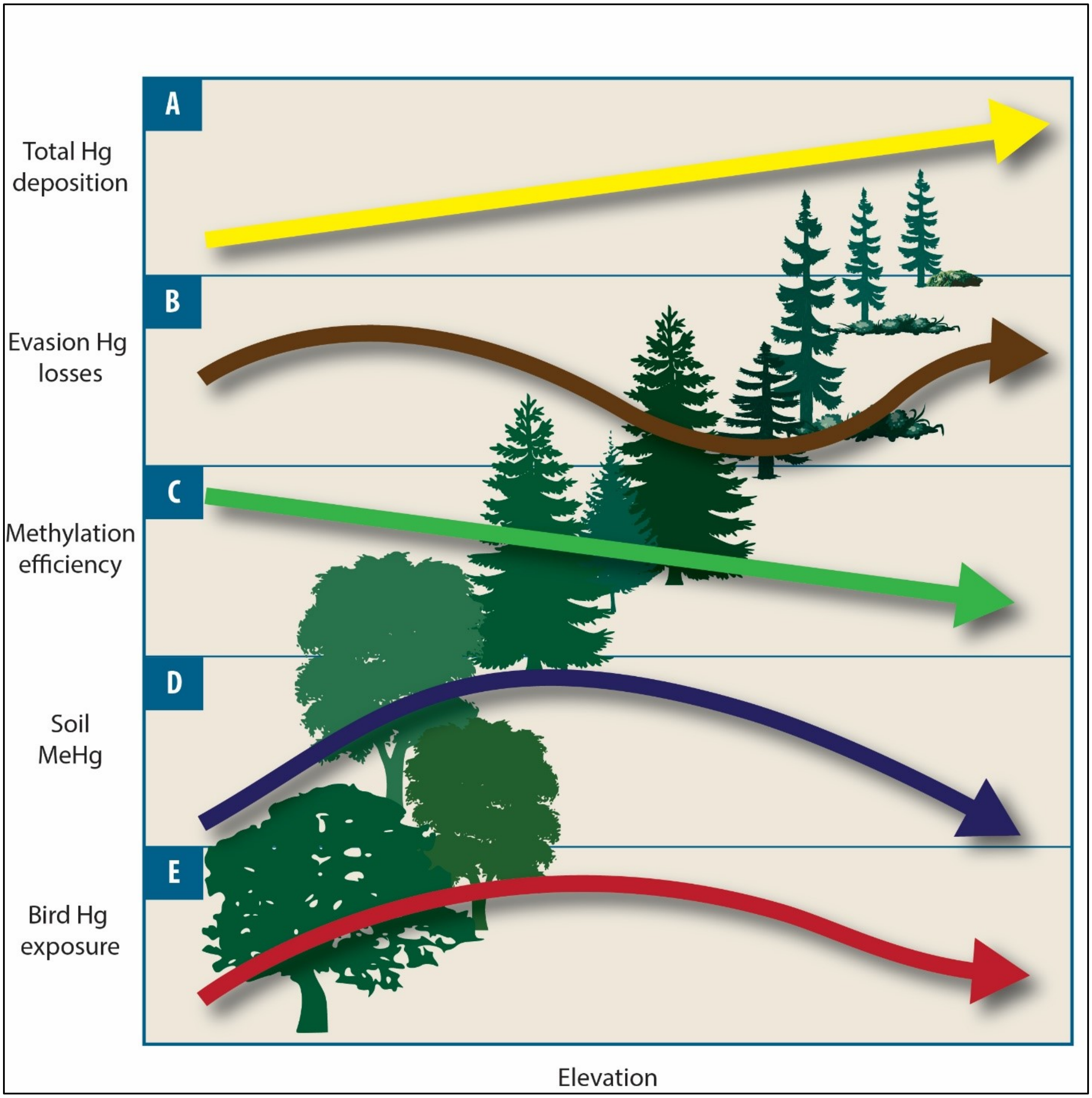

Fig. 5 Conceptual diagram showing elevational patterns for **a** total Hg deposition, **b** hypothesized evasion Hg losses, **c** methylation efficiency, **d** soil MeHg concentrations, and **e** *Catharus* thrush Hg exposure along an elevational gradient on Whiteface Mountain, New York.

Supporting Information

Blood Mercury Concentrations for Resampled Whiteface Mountain Songbirds

To examine within-season changes in blood Hg exposure, a total of 11 individuals were resampled within the same breeding season and species composition included both target (n = 6) and non-target (n = 5) species (SI Table 1). All resampled songbirds were adults and all individuals were male. Across all individuals, eight (73%) were found to decrease (-2% to -76%), one was found to increase (+103%), and two (18%) birds that were sampled three times during the season were found to increase, followed by a decrease (+82%, – 17%; +4%, -22%). All *Catharus* thrushes that were recaptured within the same breeding season were found to decrease in blood Hg concentrations, with the exception of one hermit thrush (*Catharus guttatus)* that exhibited an increase, followed by a decrease. A red-eyed vireo (*Vireo olivaceus*) exhibited the highest seasonal increase in Hg concentrations (+103%), while the steepest within-season decline was documented in a hermit thrush (-76%).

To assess between-year fluctuations in blood Hg exposure, a total of 13 songbirds were recaptured in both the 2009 and 2010 breeding seasons. Of this sample, eight (62%) birds were found to decrease (-2 to -35%) between years and five (38%) individuals increased (+13 to +155%). A slate-colored junco (*Junco hyemalis*) exhibited the greatest increase of +155%, while all between-year declines in Hg were found to be less than -35%. Additionally, one ovenbird (*Seiurus aurocapilla*) sampled during three recaptures both within and between the 2009 and 2010 field seasons was found to exhibit a consistent decline in blood Hg concentrations over time (-2 to -17%).

SI Table 1. Within and between-year changes in blood Hg concentrations (µg/g, ww) for target and non-target adult songbirds sampled on Whiteface Mountain, New York, 2009-2010. Values designated with an asterisk (*) represent within-year recaptures that were excluded from statistical analysis. Values in bold represent between-year recaptures.

Species	Sex	Date Sampled (Ordinal Day)	Blood Hg (µg/g, ww)	Δ Hg (µg/g)	% Δ Hg	Community Type
Target Species						
Bicknell's Thrush	M	6/7/2010 (158)	0.096	-0.020	-21%	Coniferous
		7/4/2010 (185)	*0.076			
Hermit Thrush	M	6/17/2009 (168)	0.103	-0.078	-76%	Deciduous
		7/23/2009 (204)	*0.025			
Hermit Thrush	M	6/17/2009 (168)	0.070	-0.033	-47%	Deciduous
		7/23/2009 (204)	*0.037			
Hermit Thrush	**M**	**6/17/2009 (168)**	**0.051**	**-0.016**	**-31%**	**Deciduous**
		6/4/2010 (155)	**0.035**			
Hermit Thrush	**M**	**6/17/2009 (168)**	**0.052**	**-0.001**	**-2%**	**Deciduous**
		6/4/2010 (155)	**0.051**			
Hermit Thrush	M	6/4/2010 (155)	0.046	-0.002	-4%	Deciduous
		6/30/2010 (181)	*0.044			
Hermit Thrush	M	6/4/2010 (155)	0.048	-0.013	-27%	Deciduous
		6/30/2010 (181)	*0.035			
Hermit Thrush	M	6/11/2010 (162)	0.055	+0.045	+82%	Deciduous
		7/6/2010 (187)	*0.100	-0.017	-17%	
		7/28/2010 (209)	*0.083			
Swainson's Thrush	**M**	**6/20/2009 (171)**	**0.080**	**-0.028**	**-35%**	**Coniferous**
		6/7/2010 (158)	**0.052**			
Non-target Species						
Ovenbird	**M**	**6/17/2009 (168)**	**0.045**	+**0.006**	+**13%**	**Deciduous**
		6/4/2010 (155)	**0.051**			
Ovenbird	**M**	**6/17/2009 (168)**	**0.054**	**-0.009**	**-17%**	**Deciduous**
		6/4/2010 (155)	**0.045**	**-0.001**	**-2%**	
		6/29/2010 (180)	***0.044**			
Ovenbird	**M**	**6/17/2009 (168)**	**0.057**	**-0.006**	**-11%**	**Deciduous**
		6/29/2010 (180)	**0.051**			
Ovenbird	**M**	**6/21/2009 (172)**	**0.038**	+**0.009**	+**24%**	**Deciduous**
		7/2/2010 (183)	**0.047**			
Ovenbird	M	6/11/2010 (162)	0.091	-0.002	-2%	Deciduous
		7/6/2010 (187)	*0.089			
Red-eyed Vireo	M	6/11/2010 (162)	0.104	+0.004	+4%	Deciduous
		7/6/2010 (187)	*0.108	-0.024	-22%	
		7/28/2010 (209)	*0.084			
Red-eyed Vireo	M	6/11/2010 (162)	0.065	+0.067	+103%	Deciduous
		7/6/2010 (187)	*0.132			

Species	Sex	Date Sampled (Ordinal Day)	Blood Hg (µg/g, ww)	Δ Hg (µg/g)	% Δ Hg	Community Type
Slate-colored Junco	**M**	**6/20/2009 (171)**	**0.058**	**-0.008**	**-14%**	**Coniferous**
		6/7/2010 (158)	**0.050**			
Slate-colored Junco	**M**	**6/21/2009 (172)**	**0.031**	**+0.048**	**+155%**	**Deciduous**
		7/2/2010 (183)	**0.079**			
Slate-colored Junco	**M**	**6/24/2009 (175)**	**0.042**	**-0.003**	**-7%**	**Alpine**
		6/13/2010 (164)	**0.039**			
Slate-colored Junco	**M**	**6/29/2009 (180)**	**0.056**	**-0.015**	**-27%**	**Coniferous**
		6/15/2010 (166)	**0.041**			
White-throated Sparrow	**M**	**6/21/2009 (172)**	**0.035**	**+0.007**	**+20%**	**Coniferous**
		6/8/2010 (159)	**0.042**			
White-throated Sparrow	**M**	**6/21/2009 (172)**	**0.035**	**+0.015**	**+43%**	**Coniferous**
		6/8/2010 (159)	**0.050**			
White-throated Sparrow	M	6/24/2009 (175)	0.039	-0.008	-21%	Alpine
		7/29/2009 (210)	*0.031			

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Chapter 3

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 species-level 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 found 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

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. 1998; Scheuhammer et al. 2007; Eagles-Smith et al. 2016, 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, 2020). However, it is also critical to establish the extent of Hg contamination within terrestrial ecosystems (Driscoll et al. 2007). Numerous studies have identified sub-lethal 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. 2020). 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. 2020) 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, 2020; Jackson et al. 2015; Adams et al. 2020). 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 among 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. 2020). Whiteface Mountain (44.36˚N, 73.90˚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, 6- and 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 µl 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 ± 1.1% (n = 35) for SRM 1515, 102 ± 0.9% (n = 35) for SRM 2976, 99 ± 1.6% (n = 15) for SRM 966, 106 ± 1.2% (n = 22) for SRM 955c, and 109 ± 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 ± 0.9% (n = 20) for SRM 1515, 95 ± 0.6% (n = 29) for SRM 2976, 98 ± 1.1% (n = 18) for SRM 955c and 97 ± 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 wetland-adjacent 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 determined 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 ± 0.035 µg/g, n = 106) as compared to the adjacent surrounding forests (0.182 ± 0.016 µg/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 ± 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 ± 0.015 µg/g), followed by Lincoln's sparrow (0.245 ± 0.021 µg/g), and yellow palm warbler had the highest blood Hg levels across all sites (0.581 ± 0.091 µg/g; $p < 0.0001$ for all comparisons; Fig. 3; Table 1). *Post hoc* comparisons for upland forest birds indicated that ovenbirds (0.078 ± 0.005 µg/g) and hermit thrushes (0.143 ± 0.013 µg/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 ± 0.037 µg/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 ± 0.005 µg/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 ± 0.003 µg/g), followed by hermit thrushes (0.067 ± 0.005 µg/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 ± 0.012 μg/g), which were significantly different than both ovenbirds and hermit thrushes (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 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 ± 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 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 too infrequent past ordinal day 188 ($n = 3$) 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 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, 2020; Winder and Emslie 2011; Adams et al. 2020). 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. 2020). 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-eyed 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 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, which is a lower canopy gleaner, and the red-eyed vireo, an upper canopy feeder (De Graaf et al. 1985). Given that dragonflies, damselflies and diptera (flies) are known prey items for the red-eyed 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 low-elevation 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 yellow 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. 2020).

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 red-eyed 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. 2020). 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. 2020). 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 low-elevation 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 µg/g, high risk; and >1.7 µg/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 red-eyed vireo and four yellow palm warblers. One yellow palm warbler and one red-eyed 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 µg/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 yellow 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 well-documented physiological effects of Hg exposure and the potential impacts on reproductive success, this 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 species-specific 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; Olson et al. 2020). 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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Environmental Conservation (NYSDEC), Adirondack Chapter of The Nature Conservancy & Adirondack Land Trust, and Massawepie Scout Camps for providing access to study sites at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog. We would like to thank Mario Montesdeoca for laboratory support and assistance. And finally, we greatly appreciate the tireless efforts of several project interns, fellow graduate students, colleagues and family members that provided invaluable field assistance during the course of this research: Julia Braunmueller, Chelsea Baldino, Kendra Nash, Brad Blackwell, Melissa Duron, Lyneé Sauer, Mary Sauer and Bob Sauer.

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Tables

Table 1. Arithmetic mean blood mercury concentrations (µg/g, ww ± SE), sample size (n), 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 (µg/g) ± SE (n)	Hg Range (µg/g)	Foraging Guild	Foraging Layer
***Sphagnum* Bog Target Species**					
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		

Species	Site	Mean Hg (µg/g) ± SE (n)	Hg Range (µg/g)	Foraging Guild	Foraging Layer
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	Madawaska Flow	0.018 (1)		Frugivore/Insectivore	Upper Canopy/Air
Common Yellowthroat	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 Canopy
Scarlet Tanager	Massawepie Mire	0.061 (1)		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

Species	Site	Mean Hg (µg/g) ± SE (n)	Hg Range (µg/g)	Foraging Guild	Foraging Layer
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		

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

[a]Overall mean Hg values do not include species listed for Whiteface Mountain.

Figures

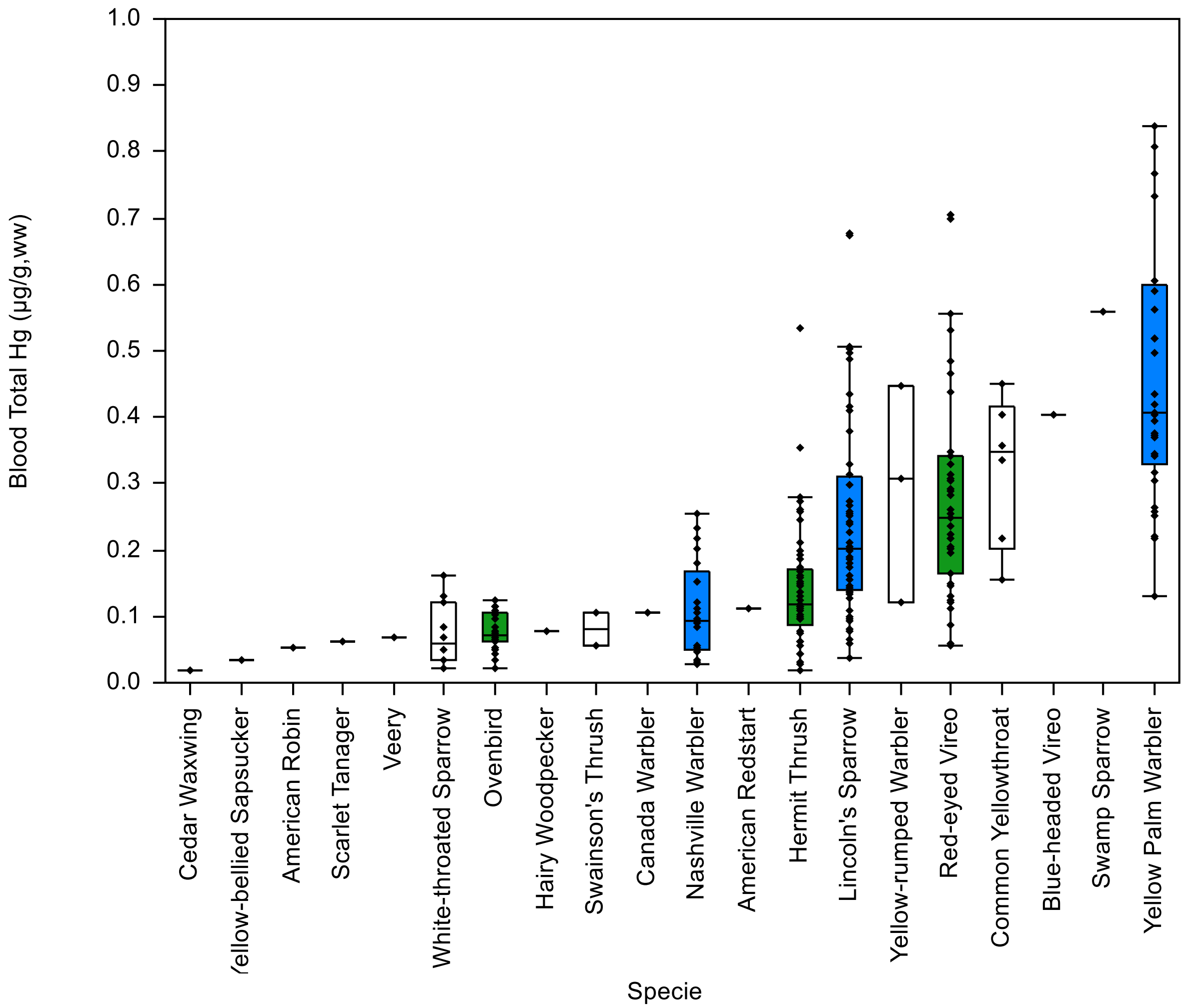


Fig. 1 Blood mercury concentrations (µg/g, ww) for songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011. Box plots denote the median (horizontal line within the box) and the 25th and 75th quantiles (lower and upper edges of the box). Four 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. Table 1 includes sample size (n) for songbirds sampled at all study sites.

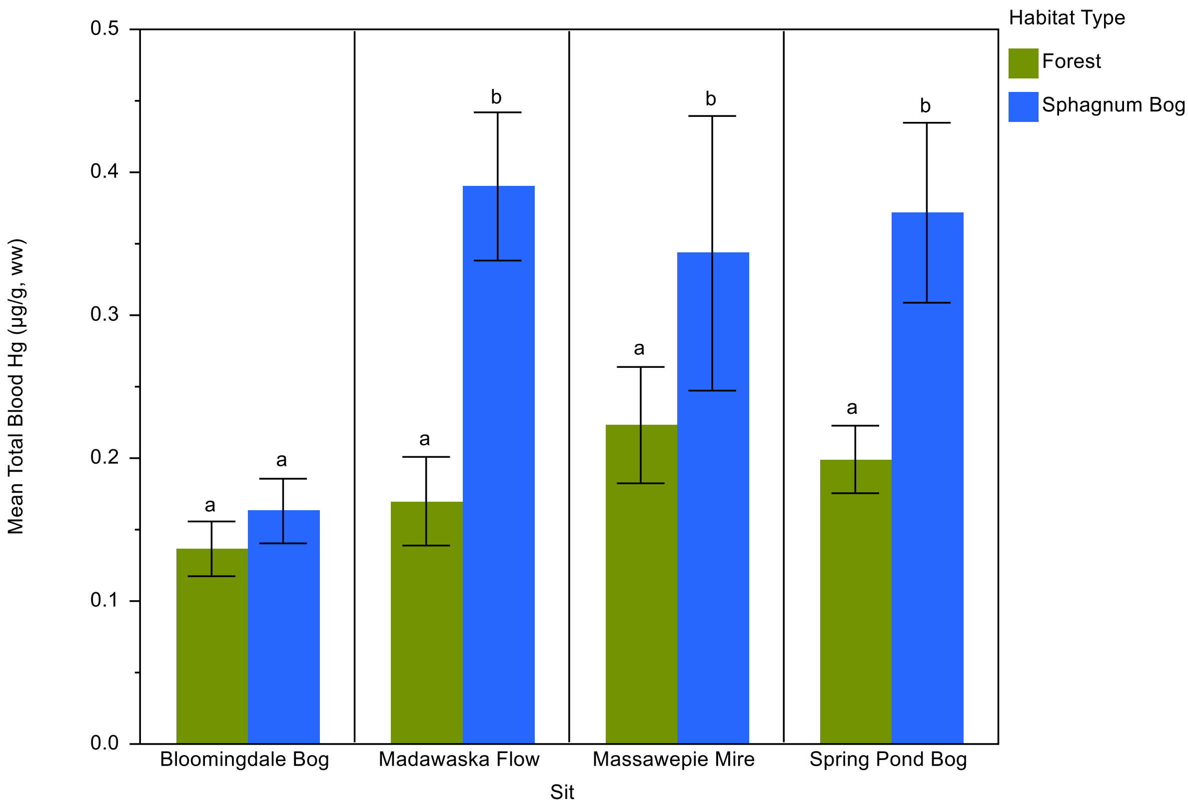


Fig. 2 Arithmetic mean blood mercury concentrations (µg/g, ww ±SE) for songbird species in *Sphagnum* bog and upland forest habitats at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008, 2009, 2011. Different letters denote significant differences between habitat types within each site. Table 1 includes sample size (n) for songbirds sampled at all study sites.

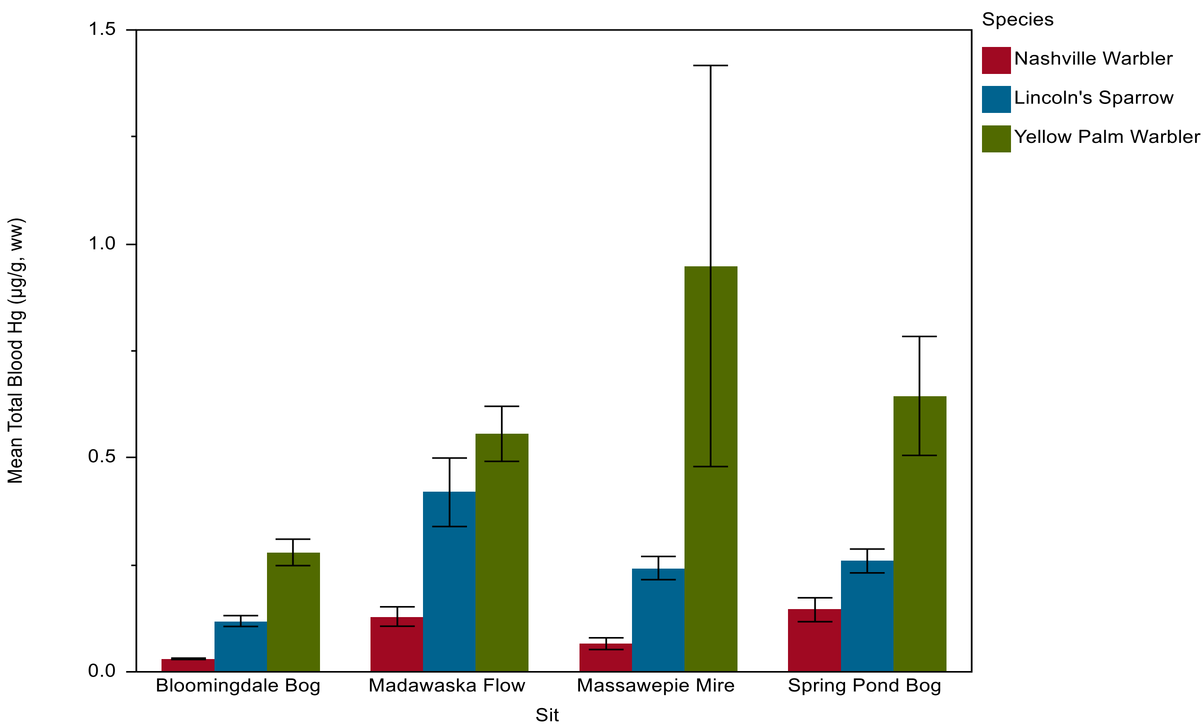


Fig. 3 Species-level exposure patterns using arithmetic mean blood mercury concentrations (µg/g, ww ± SE) for *Sphagnum* bog songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011. Table 1 includes sample size (n) for songbirds sampled at all study sites.

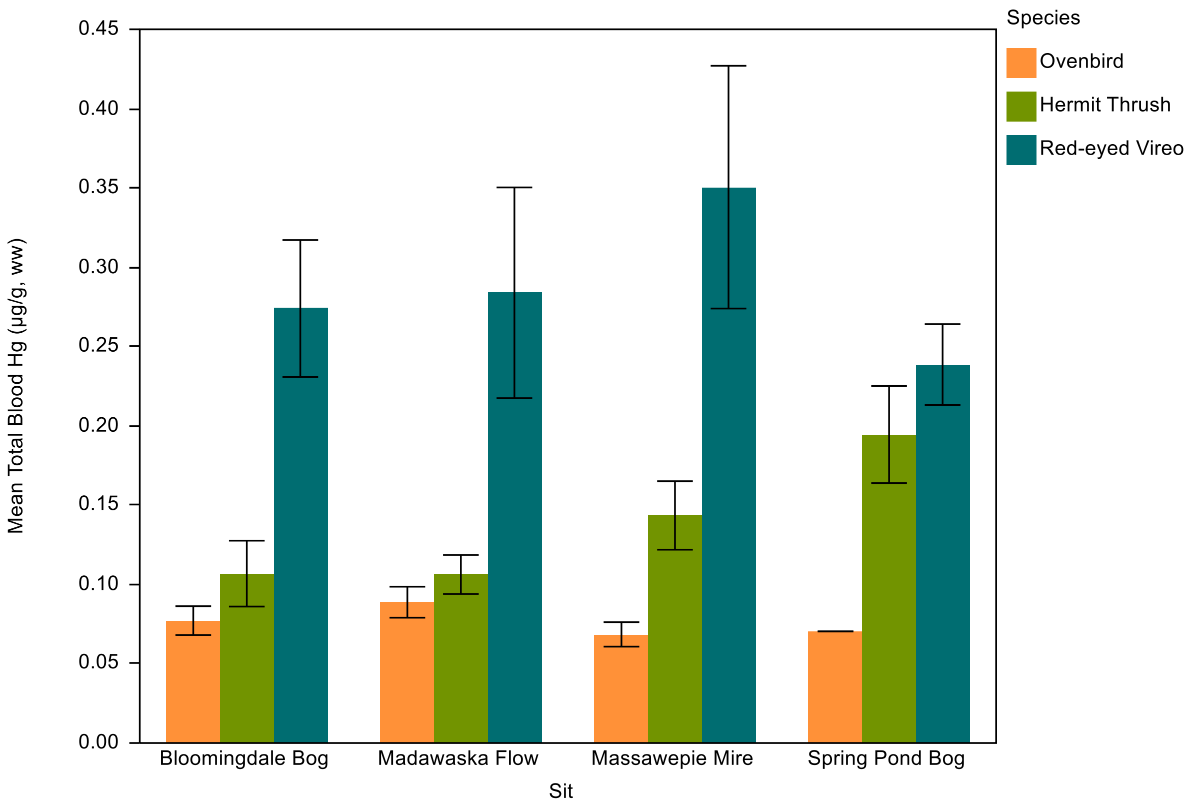


Fig. 4 Species-level exposure patterns using arithmetic mean blood mercury concentrations (µg/g, ww ± SE) for upland forest songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, and Spring Pond Bog, New York, 2008, 2009, 2011. Table 1 includes sample size (n) for songbirds sampled at all study sites.

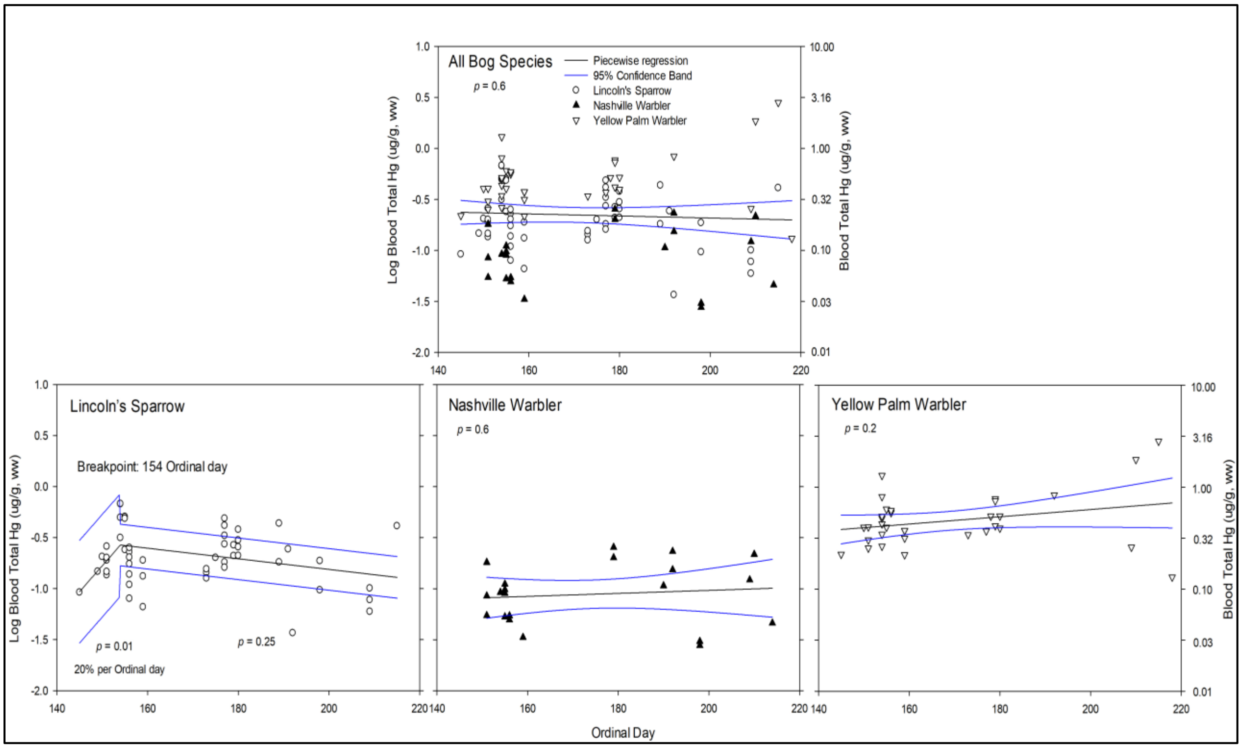


Fig. 5 Seasonal patterns in blood mercury concentrations (µg/g, ww) for *Sphagnum* bog songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008, 2009, 2011. Single linear trend is shown based on linear regressions if no breakpoint was detected by piecewise regression.

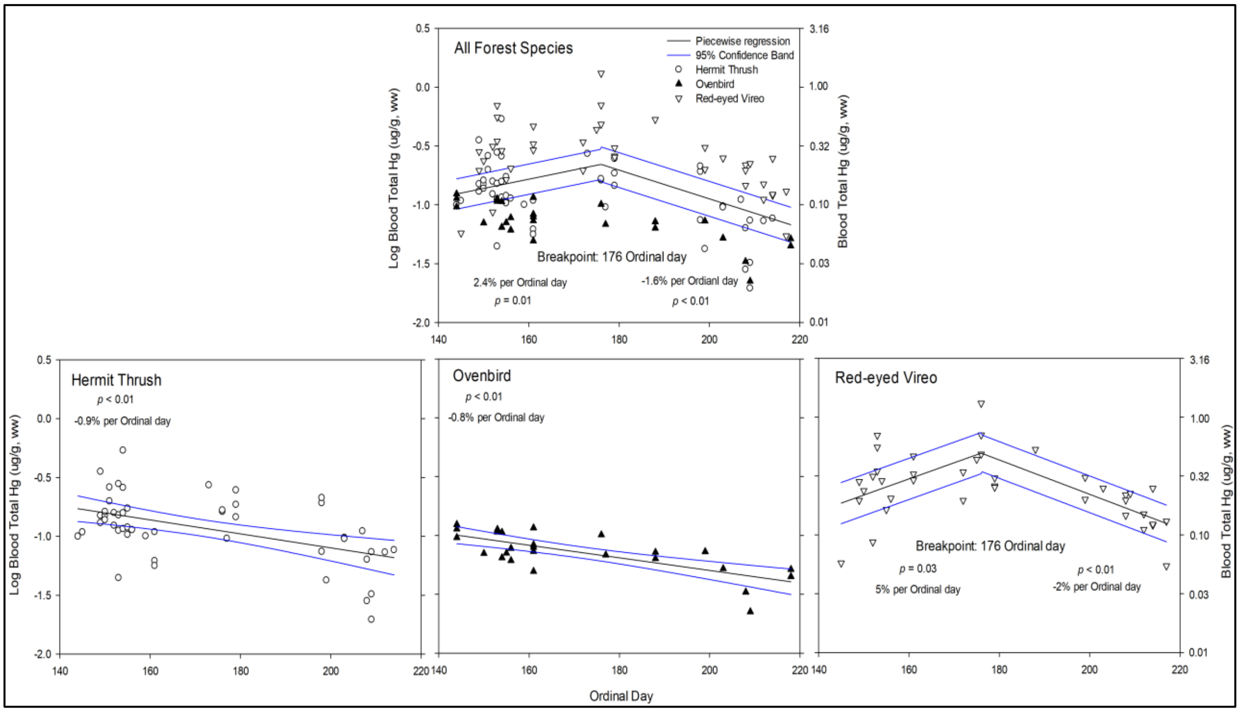
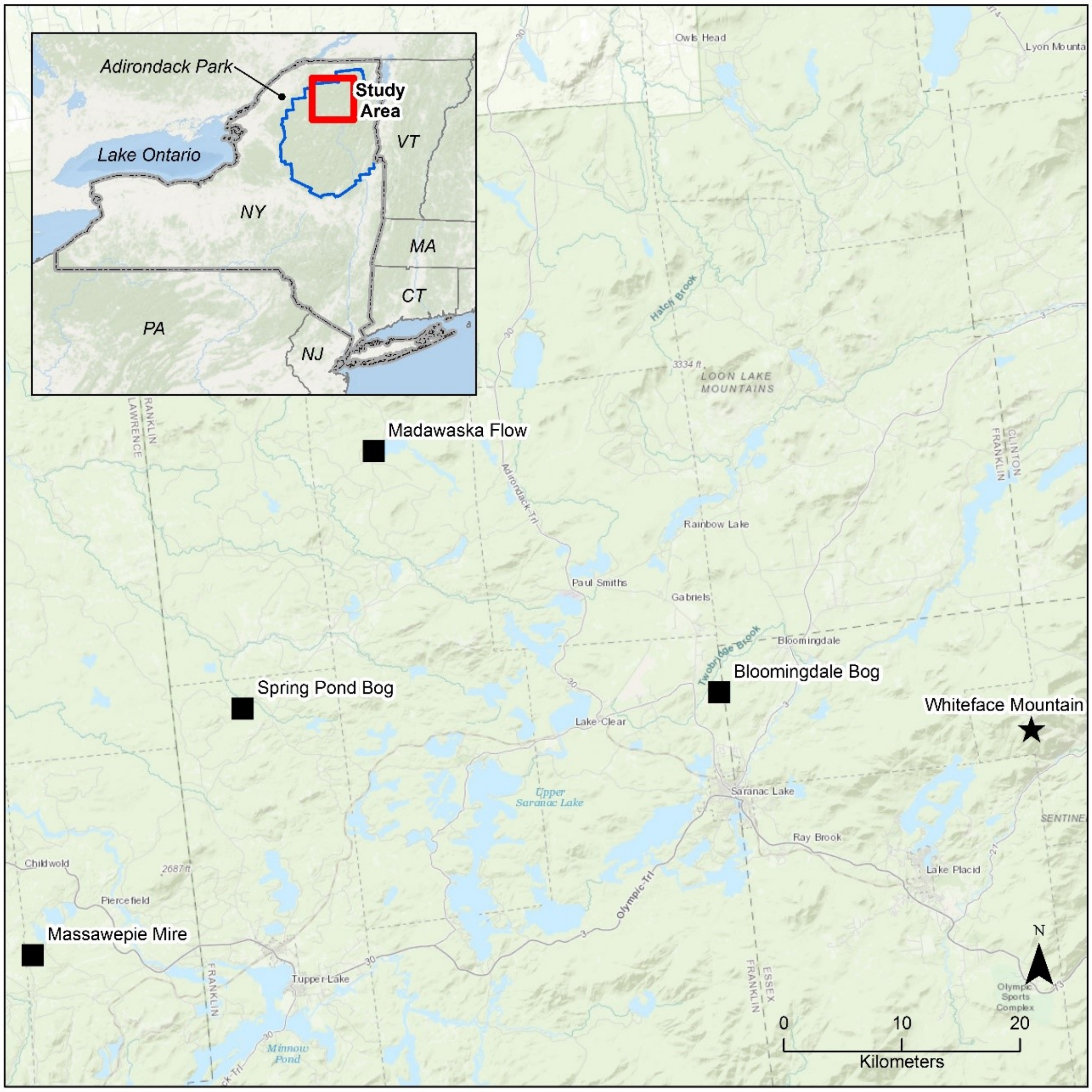


Fig. 6 Seasonal patterns in blood mercury concentrations (µg/g, ww) for upland forest songbird species at Bloomingdale Bog, Madawaska Flow, Massawepie Mire and Spring Pond Bog, New York, 2008, 2009, 2011. Single linear trend is shown based on linear regressions if no breakpoint was detected by piecewise regression.

Supporting Information



SI Fig 1 Location of *Sphagnum* bog and adjacent upland forest songbird sampling sites at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, Spring Pond Bog, and upland forest site not in proximity to a wetland at Whiteface Mountain, Adirondack Park, New York.

Blood Mercury Concentrations for Resampled *Sphagnum* Bog and Upland Forest Songbirds

Sphagnum Bog

To examine within-season changes in blood Hg exposure, a total of 18 individuals were resampled within the same breeding season (SI Table 1). All resampled songbirds were adults and were comprised of both males and females. Of these birds, six (33%) individuals were found to decrease (-11 to -78%), 11 (61%) were found to increase (+7 to +311%), and one bird was found to maintain the same blood Hg concentrations. Of this total, two Lincoln's sparrows (*Melospiza lincolnii;* +131; +311%) and two yellow palm warblers (*Setophaga palmarum;* +158%; +98%) exhibited the highest within-season blood Hg increases, while a Lincoln's sparrow was documented to decline by -78%.

Additionally, five songbirds were recaptured during different years. Mercury concentrations were found to decrease in three birds (-9 to -31%) and increase in two individuals (+8%, +30%) between years. Within this total, a yellow palm warbler sampled four times both within and between years was documented to have within-season Hg increases (2009, +9% and 2011, +7%) and a between year Hg decrease (-31%).

Upland Forests

A total of 16 individuals were resampled within the same breeding season (SI Table 1). All resampled songbirds were adults, with the exception of one juvenile hermit thrush (*Catharus guttatus*) that was sampled in 2009 and recaptured as an adult in 2011. Blood Hg concentrations were found to decrease in 11 (69%) individuals (-1 to -71%), increase in two (13%) red-eyed vireos (*Vireo olivaceus;* +51%; +101%), and three (19%) hermit thrushes that were sampled three times within the field season exhibited an increase in Hg (+2 to +9%), followed by a decrease (-55 to -76%).

Additionally, six songbirds were recaptured during subsequent field seasons. Blood Hg decreased in one hermit thrush (-74%) between years and increased in the five remaining birds (+44 to +483%). The greatest changes in Hg concentrations included an increase of +376% (2009-2011) for the juvenile hermit thrush that was recaptured as an adult and a +483% increase for a red-eyed vireo (2009-2011).

SI Table 1. Within and between-year changes in blood Hg concentrations (μg/g, ww) for target and non-target songbirds sampled in Adirondack study sites, New York. Values designated with an asterisk (*) represent within-year recaptures that were excluded from statistical analysis. Values in bold represent between-year recaptures. All re-sampled individuals were adults, with the exception of one juvenile capture designated by italics.

Species	Sex	Date Sampled	Blood Hg (μg/g, ww)	Δ Hg (μg/g)	% Δ Hg	Site
***Sphagnum* Bog Species**						
Lincoln's Sparrow	M	6/25/2008	0.415	-0.164	-40%	Massawepie Mire
		7/25/2008	*0.251			
Lincoln's Sparrow	**M**	**6/3/2009**	**0.678**	**-0.193**	**-28%**	**Madawaska Flow**
		6/4/2011	**0.485**			
Lincoln's Sparrow	M	6/8/2009	0.189	-0.065	-34%	Bloomingdale Bog
		7/17/2009	*0.124			
Lincoln's Sparrow	M	6/8/2009	0.066	-0.024	-36%	Bloomingdale Bog
		8/6/2009	*0.042			
Lincoln's Sparrow	**M**	**6/8/2009**	**0.132**	**+0.011**	**+8%**	**Bloomingdale Bog**
		6/22/2011	**0.143**			
Lincoln's Sparrow	**M**	**7/17/2009**	**0.097**	**+0.029**	**+30%**	**Bloomingdale Bog**
		6/22/2011	**0.126**			
Lincoln's Sparrow	M	5/25/2011	0.092	-0.072	-78%	Bloomingdale Bog
		7/28/2011	*0.020			
Lincoln's Sparrow	F	5/31/2011	0.258	+0.338	+131%	Spring Pond Bog
		7/7/2011	*0.596			
Lincoln's Sparrow	M	5/31/2011	0.200	+0.621	+311%	Spring Pond Bog
		7/7/2011	*0.821			
Lincoln's Sparrow	M	6/4/2011	0.240	+0.139	+58%	Madawaska Flow
		6/27/2011	*0.379			
Lincoln's Sparrow	M	6/5/2011	0.251	0.000	0%	Massawepie Mire
		7/8/2011	*0.251			
Lincoln's Sparrow	M	6/5/2011	0.109	-0.024	-22%	Massawepie Mire
		7/9/2011	*0.085			
Nashville Warbler	M	6/3/2009	0.092	+0.013	+14%	Madawaska Flow
		7/11/2009	*0.105			
Nashville Warbler	M	6/8/2009	0.033	+0.015	+45%	Bloomingdale Bog
		7/17/2009	*0.048			
Yellow Palm Warbler	M	6/27/2008	0.732	+0.252	+34%	Spring Pond Bog
		7/27/2008	*0.984			

Species	Sex	Date Sampled	Blood Hg (µg/g, ww)	Δ Hg (µg/g)	% Δ Hg	Site
Yellow Palm Warbler	M	6/3/2009	0.435	+0.106	+24%	Madawaska Flow
		7/10/2009	*0.541			
Yellow Palm Warbler	**M**	**6/3/2009**	**0.807**	**+0.071**	**+9%**	**Madawaska Flow**
		7/11/2009	***0.878**	**-0.271**	**-31%**	
		6/4/2011	**0.607**	**+0.044**	**+7%**	
		6/27/2011	***0.651**			
Yellow Palm Warbler	**M**	**6/8/2009**	**0.374**	**-0.032**	**-9%**	**Bloomingdale Bog**
		6/22/2011	**0.342**			
Yellow Palm Warbler	F	6/8/2009	0.376	-0.043	-11%	Bloomingdale Bog
		7/17/2009	*0.333			
Yellow Palm Warbler	M	5/31/2011	0.303	+0.478	+158%	Spring Pond Bog
		7/6/2011	*0.781			
Yellow Palm Warbler	M	6/4/2011	0.404	+0.235	+58%	Madawaska Flow
		6/27/2011	*0.639			
Yellow Palm Warbler	M	6/5/2011	0.562	+0.548	+98%	Massawepie Mire
		7/8/2011	*1.110			
Forest Species						
Hermit Thrush	M	6/1/2009	0.123	-0.056	-46%	Madawaska Flow
		7/21/2009	*0.067			
Hermit Thrush	M	6/1/2009	0.158	-0.101	-64%	Madawaska Flow
		7/21/2009	*0.057			
Hermit Thrush	M	6/2/2009	0.112	-0.044	-39%	Madawaska Flow
		7/22/2009	*0.068			
Hermit Thrush	**M**	**6/10/2009**	**0.109**	**-0.081**	**-74%**	**Bloomingdale Bog**
		7/27/2011	**0.028**			
Hermit Thrush	M	7/17/2009	0.212	-0.118	-56%	Bloomingdale Bog
		8/6/2009	*0.094			
Hermit Thrush	***M***	***8/5/2009***	***0.033***	***+0.124***	***+376%***	***Madawaska Flow***
		6/3/2011	**0.157**			
Hermit Thrush	M	5/28/2008	0.150	+0.012	+8%	Massawepie Mire
		6/24/2008	*0.162	-0.111	-69%	
		7/26/2008	*0.051			
Hermit Thrush	M	6/2/2008	0.258	-0.065	-25%	Spring Pond Bog
		6/27/2008	*0.193			
Hermit Thrush	M	6/27/2008	0.185	-0.131	-71%	Spring Pond Bog
		7/27/2008	*0.054			
Hermit Thrush	M	6/24/2008	0.166	-0.072	-43%	Massawepie Mire
		7/25/2008	*0.094			
Hermit Thrush	M	5/30/2011	0.149	+0.003	+2%	Spring Pond Bog
		6/28/2011	*0.152	-0.116	-76%	
		7/31/2011	*0.036			

Species	**Sex**	**Date Sampled**	**Blood Hg (µg/g, ww)**	**Δ Hg (µg/g)**	**% Δ Hg**	**Site**
Hermit Thrush	M	5/30/2011	0.138	+0.012	+9%	Spring Pond Bog
		6/28/2011	*0.150	-0.082	-55%	
		7/31/2011	*0.068			
Hermit Thrush	M	6/5/2011	0.113	-0.040	-35%	Massawepie Mire
		7/9/2011	*0.073			
Ovenbird	**M**	**6/10/2009**	**0.049**	**+0.047**	**+96%**	**Bloomingdale Bog**
		5/24/2011	**0.096**			
Ovenbird	**M**	**7/18/2009**	**0.073**	**+0.040**	**+55%**	**Bloomingdale Bog**
		5/24/2011	**0.113**			
Ovenbird	M	5/30/2011	0.070	-0.004	-6%	Spring Pond Bog
		6/28/2011	*0.066			
Ovenbird	M	6/4/2011	0.071	-0.001	-1%	Massawepie Mire
		7/9/2011	*0.070			
Red-eyed Vireo	M	6/2/2009	0.349	-0.105	-30%	Madawaska Flow
		7/22/2009	*0.244			
Red-eyed Vireo	**M**	**8/5/2009**	**0.054**	**+0.261**	**+483%**	**Madawaska Flow**
		6/1/2011	**0.315**	**+0.160**	**+51%**	
		6/26/2011	***0.475**			
Red-eyed Vireo	M	6/3/2011	0.288	+0.292	+101%	Madawaska Flow
		6/26/2011	*0.580			
Yellow-rumped Warbler	**F**	**7/10/2009**	**0.309**	**+0.137**	**+44%**	**Madawaska Flow**
		6/27/2011	**0.446**			

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Chapter 4

Synthesis and Future Recommendations

The results of the studies from this dissertation provide valuable quantitative data relating to Hg exposure levels within regional songbird communities and contribute much needed information to better define the connections between Hg as an environmental stressor and its impact on *Sphagnum* bog, upland forests and montane ecosystems. Further, the analysis of data from these projects was one of the first to examine avian blood Hg concentrations within various habitat types in the Adirondack Park of New York State. The following provides a synthesis of the study-specific results, an overall research summary related to songbird Hg bioaccumulation within sensitive, Adirondack ecosystems, and recommendations for future research efforts.

Avian mercury exposure in Adirondack montane ecosystems

The primary objectives of this research component were to investigate spatial and seasonal Hg exposure patterns in *Catharus* thrushes (hermit, Swainson's and Bicknell's) along an elevational gradient on Whiteface Mountain. None of the individuals that were captured on Whiteface Mountain exceeded established blood Hg thresholds that are associated with adverse reproductive effects (Jackson et al. 2011), therefore sampled songbirds were generally considered to be at low risk to the impacts of Hg (Chapter 2, Table 1, Figure 2). However, the Bicknell's thrush would serve as an ideal candidate for future Hg monitoring studies, as a neotropical species of conservation concern that is chronically exposed to Hg contamination on both the wintering and breeding grounds.

Across thrush species, both linear and non-linear analyses documented spatial patterns of increasing blood Hg concentrations along the elevational gradient. Specifically, overall blood Hg concentrations were observed to increase to an elevation of 1,075 m, followed by a subsequent decline with higher elevation (Chapter 2, Figure 3a, 5e), and songbird species within mid-elevation, coniferous forests were found to be significantly higher than those within low elevation, deciduous forest types. The effect of elevation on both biotic (Townsend et al. 2014) and abiotic (Stankwitz et al. 2012) Hg concentrations has been supported in other regional contaminant studies, as mid- and high elevation forests are generally subjected to elevated atmospheric Hg deposition and possess characteristics that promote the removal of Hg relative to low elevation deciduous forests (Lovett et al. 1982; Miller et al. 2005). Further, investigations examining abiotic Hg elevational patterns, conducted at the same study plots on Whiteface Mountain, documented similar increases in atmospheric Hg deposition and soil concentrations along the elevational gradient (Blackwell and Driscoll 2015; Chapter 2, Figure 5a), with the highest MeHg concentrations in organic soils also occurring within mid-elevation coniferous forests (Gerson et al. 2017; Chapter 2, Figure 5d). Therefore, based on the results of this research and similar investigations, the observed effect of elevation on songbird Hg exposure patterns is likely driven by mechanisms related to elevated atmospheric Hg deposition, conversion into bioavailable MeHg, and subsequent uptake by *Catharus* thrushes within coniferous and alpine habitats.

Overall seasonal patterns displayed a non-linear increase in blood Hg concentrations until June 27th, which was followed by a decline for the remainder of the field season (Chapter 2, Figure 4a), while species-specific seasonal patterns were found to vary among thrushes (Chapter 2, Figure 4b, 4c, 4d). The overall seasonal pattern was similar to that documented in upland forest songbirds at study sites in proximity to Adirondack *Sphagnum* bog ecosystems (Chapter 3, Figure 6), as well as research examining marsh birds at various locations in New England (Kopec et al. 2018; Lane et al. 2020). Additionally, other studies examining the Bicknell's thrush

(Rimmer et al. 2005, 2010; Townsend et al. 2014) identified generally declining blood Hg concentrations during the course of the field season, which was linked to a dietary shift from predominantly high-Hg to low-Hg prey items based on the seasonal emergence and timing of prey availability. Annual molting cycles also contribute to seasonal reductions in blood Hg concentrations (Condon and Cristol 2009), which begin in early July for *Catharus* species and correspond with the observed general timing of declining Hg body burdens. Finally, Gerson et al. (2017) detected a seasonal pattern in soil MeHg concentrations on Whiteface Mountain with the highest values occurring in July, which works to further establish the transfer pathways between abiotic soil Hg and associated biotic uptake, particularly within ground-foraging *Catharus* thrushes.

Avian mercury exposure in Adirondack Sphagnum bog and upland forest ecosystems

The overall objectives for this phase of the dissertation were to examine and compare spatial and seasonal avian Hg exposure patterns in *Sphagnum* bog ecosystems and adjacent upland forests (Chapter 3, Table 1, Figure 1). Across habitat types, the majority of individuals exhibited blood Hg concentrations that were categorized as low risk to the reproductive impacts associated with Hg exposure (Jackson et al. 2011), however a limited number of yellow palm warblers and red-eyed vireos were classified within moderate, high and very high risk categories.

Overall, blood Hg concentrations for songbird species inhabiting *Sphagnum* bogs were significantly higher than those occupying adjacent upland forests, and the within-site magnitude for this effect of habitat type varied across study site locations (Chapter 3, Figure 2). Among *Sphagnum* bogs, avian Hg concentrations at Bloomingdale Bog, an anecdotally drier study site with presumably reduced MeHg conversion and bioavailability, were found to be significantly lower than songbirds at other *Sphagnum* bog locations exhibiting more saturated habitat characteristics. No significant differences in songbird blood Hg concentrations were observed among sampled upland forest sites. Generally, research has identified elevated blood Hg concentrations in songbird species inhabiting wetland ecosystems, resulting from associated anoxic and acidic conditions that promote the methylation of Hg and subsequent uptake into biotic food webs (Ullrich et al. 2001). Further, these results are consistent with a regional avian Hg synthesis which specifically documented blood Hg concentrations in wetland songbirds that were elevated over those species inhabiting upland forests (Jackson et al. 2015).

Consistent species-level patterns of Hg bioaccumulation were evident at each study site within *Sphagnum* bogs (Nashville warbler<Lincoln’s sparrow<yellow palm warbler) and upland forests (ovenbird<hermit thrush<red-eyed vireo; Figure 1; Chapter 3, Figure 3, 4). All target species were designated as insectivores, with the exception of the omnivorous Lincoln’s sparrow (De Graaf et al. 1985), and individual dietary accounts indicated significant overlap in potential prey items among target species. Foraging guild is generally considered an important predictor of avian blood Hg concentrations due to MeHg biomagnification within food webs (Jackson et al. 2015), as individuals selecting invertebrate prey items from higher trophic levels will subsequently be exposed to elevated Hg concentrations (Cristol et al. 2008; Edmonds et al. 2012). Therefore, species-specific prey selection and foraging strategies likely influence the patterns documented at each study site and account for the elevated Hg concentrations observed in the yellow palm warbler and red-eyed vireo.

Additionally, all target species were classified as ground-foragers, except for the Nashville warbler and red-eyed vireo, which are lower and upper level canopy feeders, respectively. In upland forest species, documented high-Hg prey items for the red-eyed vireo, such as dragonflies, may serve as a subsidy from the nearby *Sphagnum* bog and thereby influence the observed species patterns when compared to the hermit thrush and ovenbird (Figure 1). Finally, considering the ability of *Sphagnum* bog systems to efficiently methylate Hg, ground-foraging species sourcing prey items from this substrate, such as the yellow palm warbler and Lincoln's sparrow, may be actively selecting prey items with higher Hg concentrations than those invertebrates consumed by the Nashville warbler as a lower canopy gleaner, thereby driving the bioaccumulations patterns documented in *Sphagnum* bog habitats (Figure 1).

There were no overall seasonal changes in blood Hg concentrations detected across *Sphagnum* bog songbirds, however blood Hg concentrations for Lincoln's sparrow increased through June 3rd and remained steady throughout the field season (Chapter 3, Figure 5). The lack of a seasonal pattern for *Sphagnum* bog songbirds suggest that individuals tended to have consistently elevated blood Hg concentrations throughout the breeding season, while the rapid increase for Lincoln's sparrow is likely reflective of a high-Hg foraging prey base upon arrival at the breeding grounds with an uptake of similarly elevated invertebrates for the remainder of the field season. In contrast, overall blood Hg concentrations in upland forest songbirds exhibited a non-linear increase until June 25th followed by a decline for the duration of the sampling period, which was similarly demonstrated by the red-eyed vireo (Chapter 3, Figure 6). Both the hermit thrush and ovenbird experienced linear declines in blood Hg during the course of the field season. As previously stated, the effect of ordinal day on blood Hg concentrations is limited in observations, but is similar to seasonal patterns observed in regional songbird Hg studies that have been attributed to factors such as shifts in dietary selection and depuration of Hg in feathers during annual molting cycles (Rimmer et al. 2010; Kopec et al. 2018; Lane et al. 2020).

Comparison of avian mercury exposure in Adirondack upland forests from wetland-adjacent & Whiteface Mountain sites

A comparative analysis was further conducted between research studies to examine songbird Hg patterns related to habitat, species bioaccumulation and seasonal trends, utilizing the same target species from upland forests in proximity to wetlands (Chapter 3) and a subset of data from low elevation sites on Whiteface Mountain (Chapter 2). Blood Hg concentrations from forested songbirds on Whiteface Mountain were observed to be significantly lower than species in wetland-adjacent upland forests, which suggests that *Sphagnum* bogs may be contributing to elevated songbird Hg levels in nearby forests due to the transfer of aquatic subsidies (Chapter 3, Table 1). Additionally, species patterns of bioaccumulation (ovenbird<hermit thrush<red-eyed vireo) were found to be similar between study site locations, which suggests that similar processes contributing to this relative pattern are potentially applicable across a larger landscape spatial scale (Figure 1). Finally, an overall seasonal pattern of increasing blood Hg concentrations was observed until July 7 for Whiteface Mountain species, however Hg samples were too infrequent after this date to describe the pattern for the remainder of the field season. This overall pattern in songbird blood Hg with a mid-season peak is similar to that observed for wetland-adjacent forest species, however a lack of data following this peak on Whiteface Mountain prevents further comparison between study site locations.

Research Summary & Future Recommendations

While each study was independently designed as an intensive, multi-year research project to address patterns of avian Hg exposure within various habitat types, the project methodologies were also intended to complement each other for a broader understanding of the health of songbird communities across the Adirondack Park. The following provides a final synthesis of the overall findings compiled from this dissertation, along with related recommendations for future research efforts:

- **While the majority of songbirds sampled across all study sites were considered low risk to the impacts of Hg exposure, a limited number of songbirds were documented to exceed established threshold levels associated with adverse impacts on reproductive success.** These at-risk species were comprised of the yellow palm warbler, a wetland-obligate species, and the red-eyed vireo, a common forest songbird. Considering the potential impacts on reproductive impairment and subsequent implications on long-term population dynamics for these at-risk species, the results of these studies provide evidence regarding the need to incorporate these focal songbird species into regional Hg monitoring initiatives.
- **Songbirds occupying mid- and high elevation habitats on Whiteface Mountain were found to have higher blood Hg concentrations than songbird species inhabiting lower elevations.** These exposure patterns are likely driven by elevated atmospheric Hg deposition and increased Hg bioavailability within high elevation forests as compared to low elevation forests. Although the Bicknell's thrush, a long-distance migrant and high elevation habitat specialist experiencing population declines, did not approach Hg concentrations associated with impacts on reproductive success, future monitoring efforts to better identify and characterize Hg concentrations within alpine forests would provide valuable scientific data regarding critical breeding habitat for songbird species occupying these sensitive montane forests.
- **Habitat type was demonstrated to influence biotic Hg exposure levels, as songbird species occupying *Sphagnum* bog habitats exhibited significantly higher Hg levels than**

those inhabiting adjacent upland forest ecosystems. Songbird blood Hg concentrations are reflective of variables such as habitat bioavailability, which was comparatively elevated within wetland systems. At each study site, the yellow palm warbler and red-eyed vireo exhibited elevated Hg levels, as well as additional non-target species, including the common yellowthroat, swamp sparrow, blue-headed vireo and yellow-rumped warbler. Therefore, these species, which may be vulnerable to the multi-systemic impacts of Hg exposure, should be prioritized as avian species of concern and included as part of sampling protocols for future Hg research studies. Further, research efforts targeting study sites within high-Hg habitat types, such as wetland ecosystems, would be beneficial to improve knowledge of site-specific Hg exposure levels, identification of regional biological hotspots, and the spatial influence of these locations on the surrounding Adirondack landscape.

- **Seasonal patterns in songbird Hg concentrations varied between project locations and habitat type, and repeated captures of individuals both within and between sampling years indicated highly variable fluctuations in blood Hg levels.** These varying results suggest that seasonal patterns are influenced by a combination of multiple contributing factors, such as foraging strategies, seasonal dietary shifts, and annual molting patterns. Considering that few field investigations have been conducted to examine seasonal Hg fluctuations in avian species, additional studies would be necessary to more definitively assess these patterns in regional songbird communities.

Finally, as scientists, conservation organizations and wildlife managers build upon existing information to design effective Hg monitoring plans, the following general guidelines may be beneficial to direct the development of future studies relating to the assessment of songbird Hg levels across the Adirondack Park and greater Northeastern landscape:

- Conduct multi-year studies incorporating annual sampling regimes for both targeted and generalized capture of songbird species, across a wide variety of ecosystems and at established long-term ecological research sites, to further identify and monitor exposure patterns within at-risk songbirds and sensitive habitat types.
- Additional collection of biotic food web samples, including multi-trophic invertebrate prey items, for MeHg and stable isotope analysis to better characterize the mechanisms and complexities associated with Hg cycling and transfer through terrestrial food webs.
- Coordinated regional collaborations to develop standardized collection protocols and monitoring networks to improve understanding of the relationships between Hg deposition, biotic exposure levels, and patterns of Hg contamination across the Northeastern landscape.

The results of these studies provide evidence of the varying extent and magnitude of Hg contamination within several ecologically distinct habitat types located in the Adirondack Park. All habitats are geographically well-removed from regional emissions sources, but all are also categorized as a biological Hg hotspot. Therefore, these data illustrate the ability of atmospherically deposited Hg to be transferred and biomagnify from the base of the food web to elevated levels within songbird communities and reinforce the need to promote legislation designed to improve regional air quality emissions standards. Considering that songbirds face population declines due to a myriad of interconnected direct and indirect stressors (Rosenberg et al. 2019), regulations directly targeting Hg emissions and releases, such as the Mercury and Air Toxics Standards (MATS) and the Minamata Convention, will effectively contribute to reducing environmental Hg loads and associated wildlife exposure levels. Ultimately, it is intended that the results from this dissertation can serve to supplement and inform future research efforts, be utilized by policymakers to support legislation related to critical issues of air quality and wildlife health, and advance understanding of the ecological links between Hg deposition and avian communities in the Adirondack Park of New York State.

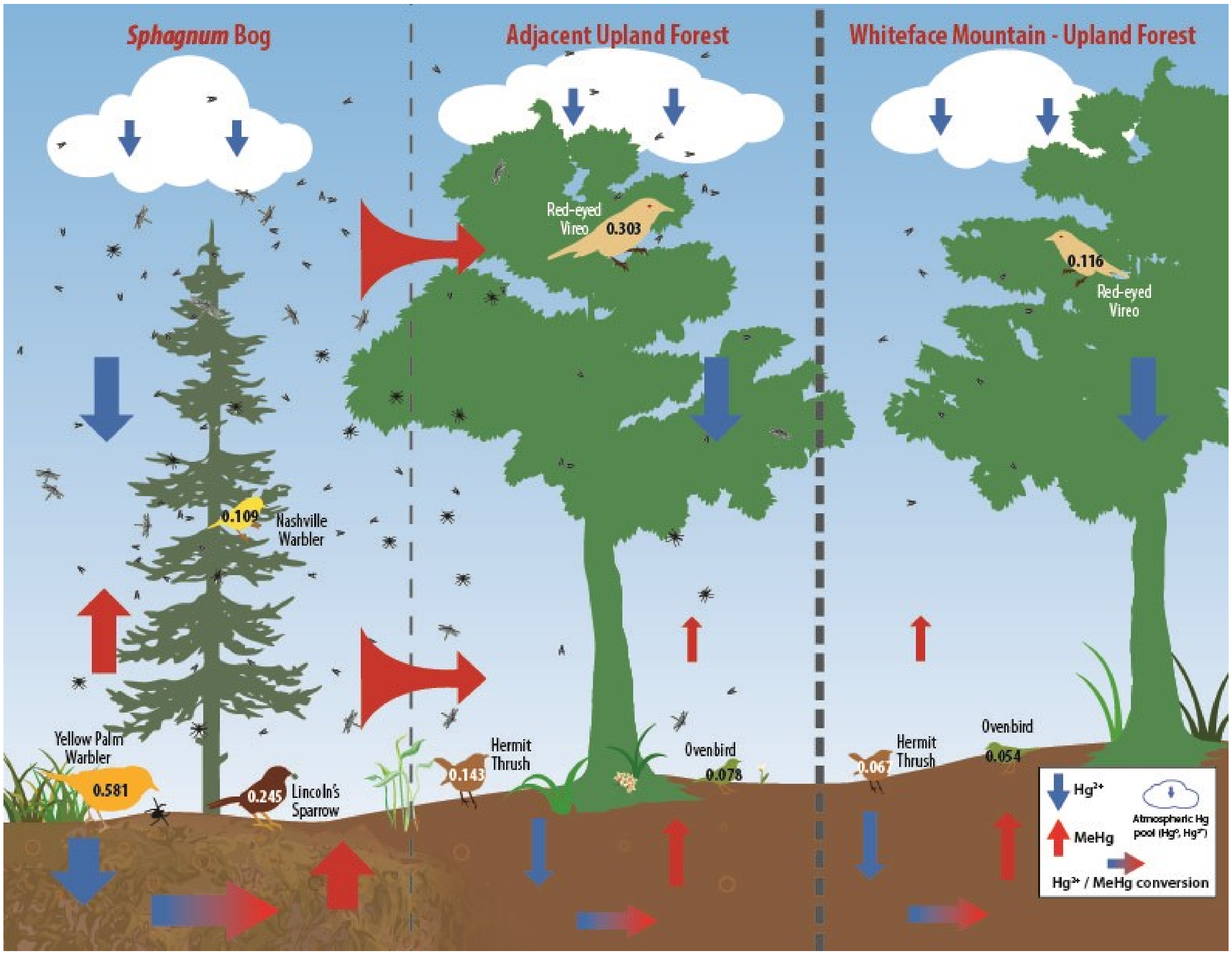

Fig 1 Conceptual diagram comparing inputs and transfers of inorganic and methylmercury in wetlands, and adjacent and distant upland forest ecosystems. Mean blood Hg concentrations (µg/g, ww), atmospheric Hg inputs (blue arrows), and hypothesized MeHg transfer pathways (red arrows) within foraging strata for songbird species in *Sphagnum* bog and upland forests at Bloomingdale Bog, Madawaska Flow, Massawepie Mire, Spring Pond Bog, and Whiteface Mountain, New York, 2008-2011.

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