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# Songbirds as sentinels of mercury in terrestrial habitats of eastern North America

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**Abstract** Mercury (Hg) is a globally distributed environmental contaminant with a variety of deleterious effects in fish, wildlife, and humans. Breeding songbirds may be useful sentinels for Hg across diverse habitats because they can be effectively sampled, have well-defined and small territories, and can integrate pollutant exposure over time and space. We analyzed blood total Hg concentrations from 8,446 individuals of 102 species of songbirds, sampled on their breeding territories across 161 sites in eastern North America [geometric mean Hg concentration = 0.25 µg/g wet weight (ww), range <0.01–14.60 µg/g ww]. Our records span an important time period—the decade leading up to implementation of the USEPA Mercury and Air Toxics Standards, which will reduce Hg emissions from coal-fired power plants by over 90 %. Mixed-effects modeling indicated that habitat, foraging guild, and age were important predictors of blood Hg concentrations across species and sites. Blood Hg concentrations in adult invertebrate-eating songbirds were consistently higher in wetland habitats (freshwater or estuarine) than upland forests. Generally, adults exhibited higher blood Hg concentrations than juveniles within each habitat type. We used model results to examine species-specific differences in blood Hg concentrations during this time period, identifying potential Hg sentinels in each region and habitat type. Our results present the most comprehensive assessment of blood Hg concentrations in eastern songbirds to date, and thereby provide a valuable framework for designing and evaluating risk assessment schemes using sentinel songbird species in the time after implementation of the new atmospheric Hg standards.

**Keywords** Bioaccumulation · Mercury · Passeriformes · Sentinel · Songbird

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## Introduction

Sentinel species historically used to assess contaminant risk to ecosystem and human health have ranged from terrestrial and aquatic invertebrates (Brown and Luoma 1995; Bundy et al. 2007) to marine megafauna (Bossart 2006). A suitable sentinel species has at least the following characteristics: (1) utilizes a restricted home range that overlaps the area of interest, (2) integrates contaminant exposure across a defined period of time and space, (3) is widespread and abundant, permitting extensive sampling and (4) is reflective of contaminant availability or risk to an endpoint of interest (Beeby 2001; Basu et al. 2007; Burger and Gochfeld 2004, National Research Council 1991). Additionally, we should have a well-developed understanding of the basic biology of a sentinel species and how the contaminant of interest impacts their physiology (van der Schalie et al. 1999; Basu et al. 2007). The definition of "sentinel species" and efficacy of their use has been debated (Stahl 2008), but for our purposes, we define a sentinel in the simplest terms: a species that has the ability to accumulate a contaminant and can provide a baseline for understanding contaminant risk in a community or ecosystem (Beeby 2001).

Mercury (Hg) is a persistent environmental contaminant with global implications for human, wildlife, and ecosystem health (Driscoll et al. 2013; Wiener 2013). Despite the global ubiquity of Hg, wildlife exposure and risk is often determined at the local scale because Hg must be methylated by microbes before it can become readily available to wildlife (Wren et al. 1995; Scheuhammer et al. 2007, 2012) and Hg methylation is a local-scale process. The higher methylation potential of aquatic ecosystems, and the human health focus on fish consumption, have resulted in most Hg sentinel species being fish or fish-eating wildlife, especially fish-eating birds (Burger and Gochfeld 2004; Evers 2006; Grove et al. 2009).

Informed by a recent appreciation for the porosity of terrestrial-aquatic ecotones, terrestrial species with indirect ties to aquatic food webs, such as snakes, spiders, songbirds, and bats, are increasingly being sampled for Hg bioaccumulation (Cristol et al. 2008; Drewett et al. 2013; Yates et al. 2014). These invertebrate-eating species (hereafter "invertivores") appear to bioaccumulate and biomagnify MeHg through the terrestrial food web in a manner similar to aquatic species (Cristol et al. 2008; Newman et al. 2011). They also are sensitive to the impacts of this Hg exposure, with adverse impacts to invertivore songbird species including endocrine, immunological and neurological disruption (Wada et al. 2009; Lewis et al. 2013; Scoville and Lane 2013), altered song quality (Hallinger et al. 2010; McKay and Maher 2012), decreased flight performance (Carlson et al. 2014) and reduced reproductive success (Brasso and Cristol 2008; Jackson et al. 2011a; Varian-Ramos et al. 2013).

Songbirds (avian order Passeriformes) are the most numerous avian order, with over 5,000 species, occurring in almost every terrestrial ecosystem on earth. As such, they may be suitable as potential sentinels of Hg contamination in diverse terrestrial ecosystems of eastern North America (Osborne et al. 2011; Evers et al. 2012). Whereas other sentinel species, such a mink or osprey, are singular species with a wide geographic distribution (Basu et al. 2007; Grove et al. 2009), "songbirds" as a group represent a diversity of taxonomic and distributional characteristics that can complicate interpretation of contaminants data or use of songbirds in risk assessment. Because of this, most songbird Hg studies have focused on a single species or suite of species living in a particular habitat type, including riparian corridors (Evers et al. 2005; Custer et al. 2007; Cristol et al. 2008, Jackson et al. 2011b), tidal estuaries (Warner et al. 2010; Lane et al. 2011; Winder and Emslie 2011), freshwater bogs (Edmonds et al. 2012), upland forests of the southern Appalachians (Keller et al. 2014) and high elevation forests (Rimmer et al. 2005, 2010; Townsend et al. 2014). Research that integrates data from these distinct habitats is lacking, and a lack of understanding of differences among habitats limits the effectiveness of using songbirds as sentinels of Hg across terrestrial ecosystems.

Eastern North America has a well-documented portfolio of point-source (e.g., historic chlor-alkali plants) and atmospheric Hg inputs (e.g., current coal-fired power plants) leading to biological hotspots of Hg exposure and risk (Evers et al. 2007). In response to documentation of elevated exposure in natural resources across the country, paired with recognition of Hg releases through fossil fuel combustion, the USEPA promulgated the Mercury and Air Toxics Standards (MATS) Rule in 2011 to in-part reduce Hg emissions by 90 % from United States coal-fired power plants by 2015–2016 (USEPA 2011). Therefore, understanding current baseline conditions across diverse ecosystems is important for documenting biological responses to these emission reductions. In collaboration with a number of active songbird monitoring and research activities, spanning four ecological regions (see below) across the eastern United States and Canada (Fig. 1), we here document the trends in Hg exposure occurring within

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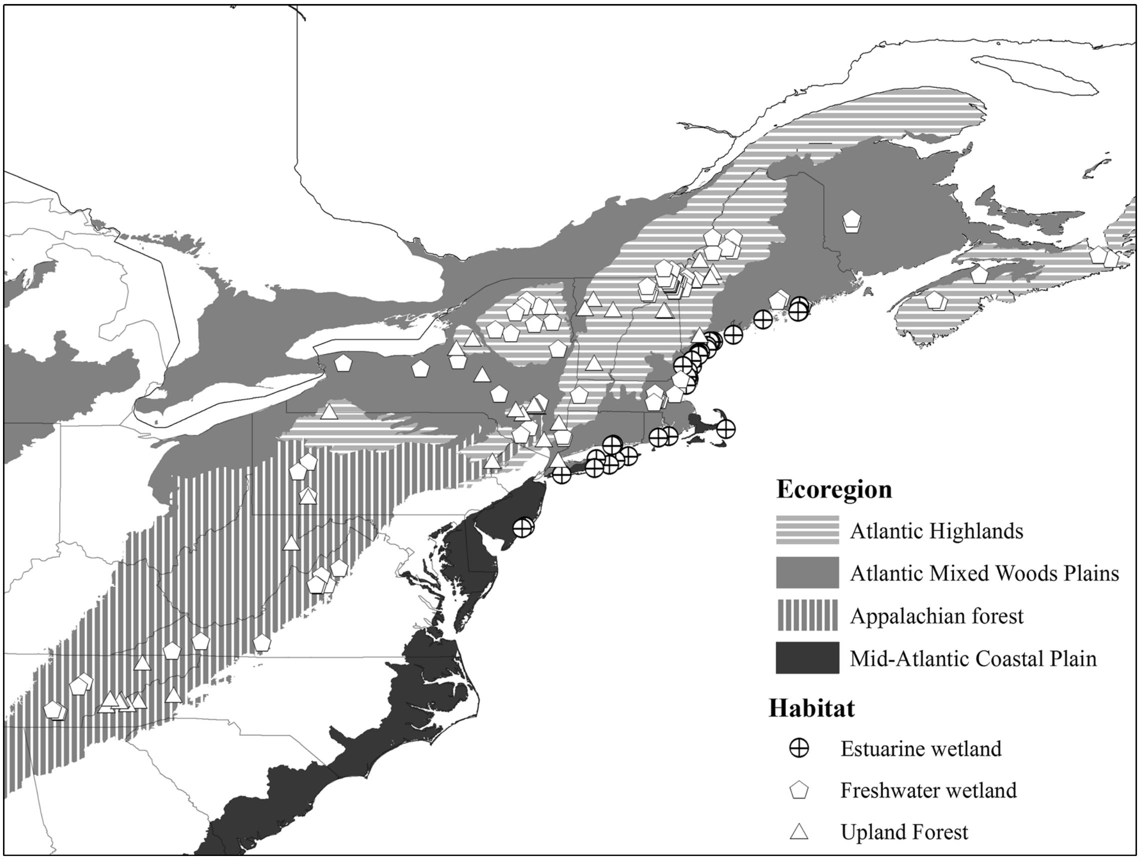


**Fig. 1** Songbird capture sites during 1999–2012, illustrating differences in habitat types (freshwater wetlands, estuarine wetlands, and upland forests) and ecoregion (Mid-Atlantic Coastal Plain, Atlantic Mixed Wood Plains, Atlantic Highlands, and Appalachian Forests). Detailed descriptions of sites are available in Supplemental Table 1

songbirds in the decade prior to implementation of the MATS rule. Songbirds were sampled in three broad habitat types—freshwater wetlands (including palustrine and lacustrine), tidal or estuarine wetlands, and upland forests. Our goals were twofold. First, to elucidate the factors affecting bioaccumulation of Hg in songbirds, we modeled Hg exposure as a function of age, foraging guild and habitat across all species in all ecoregions. Second, we used information from our model to highlight potential sentinel species of terrestrial Hg in future risk assessments. We provide summary information for blood Hg concentrations in these species, to aid in future comparisons after the anticipated MATS Hg emission reductions.

## Materials and methods

Samples were collected opportunistically from 1999 to 2012 in association with a variety of projects across a wide geographic area (Fig. 1). Site locations and characteristics are outlined in Supplementary Table 1. Because we were interested in linking habitat characteristics of breeding territories with recent Hg exposure, we selected blood, which is strongly influenced by recent local exposure, as the tissue of most relevance. Blood was collected only during breeding seasons. At the southern sites (Virginia, Tennessee, North Carolina, and West Virginia) we classified breeding season as beginning on 20 March, while the more northerly sites were sampled only after 1 May to account for the later nesting. By restricting sampling to the breeding season, we focused on the life history stage at which most species of songbirds are restricted to small breeding territories and Hg in their blood is likely to have accumulated locally.

All mist netting, banding and sampling followed appropriate state and federal permits. Although specific sample collection methods varied among researchers, in general, birds were captured using mesh mist nets at each site and species, age, and sex were determined by external characteristics. Because of the difficulty in determining age at high resolution for many species, we limited age classification to either juvenile (hatch-year) or adult (after hatch-year). We were unable to include sex as a factor in this analysis because we would have had to remove over

1,900 records to exclude birds of unknown sex. Samples for which sex was known consisted of 2,900 females and 3,629 males.

Blood samples were collected by puncturing the cutaneous ulnar vein with a sterile 26- to 28-gauge needle and placing a heparinized capillary tube at the puncture site to gather the blood. Between 30 and 150 µl of blood was collected depending on the size of the bird, which was always less than 1 % of the bird's weight, as recommended (Fair et al. 2010); birds were released unharmed. Once the blood was collected, researchers sealed tubes at both ends with Crito-caps® and placed them in labeled 10 ml glass vacutainers (BD, Franklin Lakes, NJ, USA) and a zipped plastic bag to prevent breakage or desiccation. All samples were kept on ice after sampling, and then frozen at approximately −20 °C later the same day for preservation until analysis.

Data used for this multi-year synthesis were generated at a number of laboratories. Although there were some differences in sample preparation and analytical methods, all analyses included quality control samples to allow evaluation of accuracy and precision, and all laboratories utilized atomic absorption spectroscopy to measure total Hg concentrations. Labs used either USEPA method 7473 (Trace Elements Research Lab at Texas A&M, Biodiversity Research Institute, College of William and Mary, Acadia University, Center for Environmental Systems Engineering at Syracuse University) or USEPA method 1631 modified (Brooks Rand, CEBAM). Total Hg was measured as a proxy for MeHg as bird blood had previously been found to be >90 % MeHg (Rimmer et al. 2005; Edmonds et al. 2010). Although the specific analytical protocols may have varied at each lab, all sample runs included, at minimum, analytical blanks, sample replicates, and certified reference materials (DORM and/or DOLT) with every batch of 20–30 samples. All labs and analyses reported their relative percent difference for replicates to be <10 %. All samples were above the minimum detection limits and recovery of standard reference material was 90 to 110 %.

We assigned each of the 102 species sampled to one of two trophic categories (invertivore or omnivore) based upon individual species accounts of their diets during the breeding season (Poole and ed 2013). The 59 species classified as invertivores were those that consume >90 % insect and invertebrate prey during the breeding season, whereas the 43 omnivores consumed 30–90 % invertebrates during the breeding season with the remainder comprised of plant matter (Table 1; includes scientific names of all species).

We distinguished sites with known Hg point sources nearby (hereafter "contaminated") from those without known point sources (hereafter "uncontaminated"). Many of the sites where point-source contamination is an issue have already been summarized elsewhere (Jackson et al. 2011a, b; Cristol et al. 2008; Folsom and Evers 2008; Franceschini et al. 2009). The designation of "contaminated" can be fairly arbitrary since sites in the Northeast with high atmospheric deposition are classified as "uncontaminated" even though Hg loading may be higher than sites with small or localized point sources (which would be classified as "contaminated"). The purpose of this analysis is not to assess differences between contaminated and uncontaminated sites, but to instead consider our questions of interest about how Hg varies between habitats, ages, and guilds. We, therefore, accounted for differences in Hg loading among sites, by nesting site within contamination regime as a random effect in all models. We include geometric mean Hg concentrations for contaminated and uncontaminated birds in Supplementary Table 2.

We used the USEPA Level II Ecoregions to group sites into one of four ecoregions: (1) Ozark, Ouachita-Appalachian Forest, hereafter Appalachian forest, (2) Mixed Woods Plains, where our samples were restricted to a subsection of this ecoregion, so more accurately described as Atlantic Mixed Woods Plains, (3) Mid-Atlantic Coastal Plain and (4) Atlantic Highlands (Commission for Environmental Cooperation Working Group 1997). Within each of these ecoregions, Hg cycling was hypothesized to vary based on proximity to aquatic habitat. We characterized the dominant habitat type associated with each site into one of three broad groups based on criteria that could be reliably distinguished from field notes, global positioning system (GPS) locations and site visits. Based on Cowardin et al. (1979), the three broad habitat groups to which we could reliably assign sites were (1) estuarine or tidal wetlands, (2) freshwater wetlands (including emergent, scrub–shrub, and forested wetlands bordering rivers, streams, lakes, ponds and bogs), and (3) uplands (forest or open habitats without dominant water features nearby) (Table 2).

## Modeling effects of guild, age, and habitat

Although a strength of using songbirds as sentinels is that one species or another occurs in nearly every habitat type, few species were—or could have been—sampled across all habitats (Table 1). Because our modeling effort could not, therefore, focus on species differences, we combined species into foraging guilds, while accounting for species differences by nesting species within guild as a random effect. Similarly, we accounted for site and any known point source contamination by including a random effect of site nested within contamination status (contaminated or uncontaminated). Sites were also classified by EPA Level II Ecoregion, which was included as a random effect. We examined habitat type and individual bird age class as main

**Table 1** Sample sizes for each species sampled in each habitat type

| Species code[a] | Species common name[a] | Species scientific name[a] | Foraging guild | Total (N) | Estuarine wetland (N) | Freshwater wetland (N) | Upland forest (N) |
|---|---|---|---|---|---|---|---|
| ACFL | Acadian Flycatcher | *Empidonax virescens* | Invertivore | 16 | | 16 | |
| ALFL | Alder Flycatcher | *Empidonax alnorum* | Invertivore | 2 | | 2 | |
| AMRE | American Redstart | *Setophaga ruticilla* | Invertivore | 24 | | 11 | 13 |
| AMRO | American Robin | *Turdus migratorius* | Omnivore | 41 | | 26 | 15 |
| BAOR | Baltimore Oriole | *Icterus galbula* | Invertivore | 8 | | 8 | |
| BARS | Barn Swallow | *Hirundo rustica* | Invertivore | 15 | 9 | 6 | |
| BAWW | Black-and-White Warbler | *Mniotilta varia* | Invertivore | 19 | | 13 | 6 |
| BCCH | Black-capped Chickadee | *Poecile atricapillus* | Omnivore | 43 | | 41 | 2 |
| BGGN | Blue-gray Gnatcatcher | *Polioptila caerulea* | Invertivore | 6 | | 6 | |
| BHCO | Brown-headed Cowbird | *Molothrus ater* | Omnivore | 3 | | 3 | |
| BHNU | Brown-headed Nuthatch | *Sitta pusilla* | Omnivore | 1 | | 1 | |
| BHVI | Blue-headed Vireo | *Vireo solitarius* | Invertivore | 17 | | 9 | 8 |
| BITH | Bicknell's Thrush | *Catharus bicknelli* | Invertivore | 71 | | | 71 |
| BLJA | Blue Jay | *Cyanocitta cristata* | Omnivore | 7 | | 7 | |
| BLPW | Blackpoll Warbler | *Setophaga striata* | Invertivore | 25 | | 2 | 23 |
| BOBO | Bobolink | *Dolichonyx oryzivorus* | Omnivore | 4 | 4 | | |
| BOCH | Boreal Chickadee | *Poecile hudsonicus* | Omnivore | 3 | | 3 | |
| BRCR | Brown Creeper | *Certhia americana* | Invertivore | 2 | | 2 | |
| BRTH | Brown Thrasher | *Toxostoma rufum* | Omnivore | 8 | | 7 | 1 |
| BTBW | Black-throated Blue Warbler | *Setophaga caerulescens* | Invertivore | 16 | | 8 | 8 |
| BTNW | Black-throated Green Warbler | *Setophaga virens* | Invertivore | 10 | | 3 | 7 |
| CACH | Carolina Chickadee | *Poecile carolinensis* | Omnivore | 166 | 1 | 165 | |
| CARW | Carolina Wren | *Thryothorus ludovicianus* | Invertivore | 512 | | 510 | 2 |
| CAWA | Canada Warbler | *Cardellina canadensis* | Invertivore | 21 | | 21 | |
| CERW | Cerulean Warbler | *Setophaga cerulea* | Invertivore | 3 | | 3 | |
| CHSP | Chipping Sparrow | *Spizella passerina* | Omnivore | 5 | 1 | 3 | 1 |
| CLSW | Cliff Swallow | *Petrochelidon pyrrhonota* | Invertivore | 16 | | 16 | |
| COGR | Common Grackle | *Quiscalus quiscula* | Omnivore | 25 | | 25 | |
| COYE | Common Yellowthroat | *Geothlypis trichas* | Invertivore | 56 | 3 | 51 | 2 |
| CSWA | Chestnut-sided Warbler | *Setophaga pensylvanica* | Invertivore | 4 | | 2 | 2 |
| DOWO | Downy Woodpecker | *Picoides pubescens* | Omnivore | 8 | 1 | 6 | 1 |
| EABL | Eastern Bluebird | *Sialia sialis* | Invertivore | 756 | | 756 | |
| EAKI | Eastern Kingbird | *Tyrannus tyrannus* | Omnivore | 7 | | 7 | |
| EAPH | Eastern Phoebe | *Sayornis phoebe* | Invertivore | 32 | | 29 | 3 |
| EATO | Eastern Towhee | *Pipilo erythrophthalmus* | Omnivore | 10 | | 10 | |
| EAWP | Eastern Wood-Pewee | *Contopus virens* | Invertivore | 9 | | 8 | 1 |
| EUST | European Starling | *Sturnus vulgaris* | Omnivore | 1 | | 1 | |
| FISP | Field Sparrow | *Spizella pusilla* | Omnivore | 12 | | 12 | |
| GCFL | Great Crested Flycatcher | *Myiarchus crinitus* | Invertivore | 16 | | 15 | 1 |
| GRCA | Gray Catbird | *Dumetella carolinensis* | Omnivore | 99 | 5 | 91 | 3 |
| GRSP | Grasshopper Sparrow | *Ammodramus savannarum* | Omnivore | 2 | | 2 | |
| HAWO | Hairy Woodpecker | *Picoides villosus* | Omnivore | 6 | | 4 | 2 |
| HETH | Hermit Thrush | *Catharus guttatus* | Omnivore | 238 | | 157 | 81 |
| HOFI | House Finch | *Haemorhous mexicanus* | Omnivore | 1 | | 1 | |
| HOWA | Hooded Warbler | *Setophaga citrina* | Invertivore | 14 | | 9 | 5 |
| HOWR | House Wren | *Troglodytes aedon* | Invertivore | 319 | 1 | 317 | 1 |
| INBU | Indigo Bunting | *Passerina cyanea* | Omnivore | 100 | | 99 | 1 |

**Table 1** continued

| Species code[a] | Species common name[a] | Species scientific name[a] | Foraging guild | Total (N) | Estuarine wetland (N) | Freshwater wetland (N) | Upland forest (N) |
|---|---|---|---|---|---|---|---|
| KEWA | Kentucky Warbler | *Geothlypis formosa* | Invertivore | 2 | | 2 | |
| LEFL | Least Flycatcher | *Empidonax minimus* | Invertivore | 1 | | | 1 |
| LISP | Lincoln's Sparrow | *Melospiza lincolnii* | Omnivore | 88 | | 88 | |
| LOWA | Louisiana Waterthrush | *Parkesia motacilla* | Invertivore | 59 | | 37 | 22 |
| MAWA | Magnolia Warbler | *Setophaga magnolia* | Invertivore | 26 | | 19 | 7 |
| MAWR | Marsh Wren | *Cistothorus palustris* | Invertivore | 23 | 22 | 1 | |
| MOWA | Mourning Warbler | *Geothlypis philadelphia* | Invertivore | 1 | | | 1 |
| MYWA | Myrtle Warbler | *Setophaga coronata* | Omnivore | 19 | | 13 | 6 |
| NAWA | Nashville Warbler | *Oreothlypis ruficapilla* | Invertivore | 31 | | 29 | 2 |
| NESP | Nelson's Sparrow | *Ammodramus nelsoni* | Invertivore | 126 | 123 | 3 | |
| NOCA | Northern Cardinal | *Cardinalis cardinalis* | Omnivore | 91 | | 91 | |
| NOFL | Northern Flicker | *Colaptes auratus* | Omnivore | 1 | | 1 | |
| NOPA | Northern Parula | *Setophaga americana* | Invertivore | 5 | | 5 | |
| NOWA | Northern Waterthrush | *Parkesia noveboracensis* | Invertivore | 9 | | 9 | |
| NRWS | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* | Invertivore | 34 | | 34 | |
| OROR | Orchard Oriole | *Icterus spurius* | Invertivore | 7 | | 7 | |
| OVEN | Ovenbird | *Seiurus aurocapilla* | Invertivore | 122 | | 60 | 62 |
| PAWA | Palm Warbler | *Setophaga palmarum* | Invertivore | 66 | | 66 | |
| PIWA | Pine Warbler | *Setophaga pinus* | Invertivore | 2 | | 2 | |
| PRAW | Prairie Warbler | *Setophaga discolor* | Invertivore | 1 | | 1 | |
| PROW | Prothonotary Warbler | *Protonotaria citrea* | Invertivore | 3 | | 3 | |
| PUFI | Purple Finch | *Haemorhous purpureus* | Omnivore | 3 | | 3 | |
| RBGR | Rose-breasted Grosbeak | *Pheucticus ludovicianus* | Omnivore | 1 | | | 1 |
| RBNU | Red-breasted Nuthatch | *Sitta canadensis* | Omnivore | 9 | | 9 | |
| RBWO | Red-bellied Woodpecker | *Melanerpes carolinus* | Omnivore | 19 | | 19 | |
| REVI | Red-eyed Vireo | *Vireo olivaceus* | Invertivore | 328 | | 197 | 131 |
| RUBL | Rusty Blackbird | *Euphagus carolinus* | Invertivore | 75 | | 75 | |
| RWBL | Red-winged Blackbird | *Agelaius phoeniceus* | Omnivore | 107 | 7 | 100 | |
| SALS | Saltmarsh Sparrow | *Ammodramus caudacutus* | Invertivore | 1,126 | 1,126 | | |
| SAVS | Savannah Sparrow | *Passerculus sandwichensis* | Omnivore | 4 | 2 | 2 | |
| SCJU | Slate-colored Junco | *Junco hyemalis* | Omnivore | 65 | | 1 | 64 |
| SCTA | Scarlet Tanager | *Piranga olivacea* | Omnivore | 13 | | 10 | 3 |
| SESP | Seaside Sparrow | *Ammodramus maritimus* | Invertivore | 38 | 38 | | |
| SOSP | Song Sparrow | *Melospiza melodia* | Omnivore | 370 | 20 | 348 | 2 |
| SWSP | Swamp Sparrow | *Melospiza georgiana* | Omnivore | 60 | 7 | 53 | |
| SWTH | Swainson's Thrush | *Catharus ustulatus* | Omnivore | 111 | | 33 | 78 |
| TRES | Tree Swallow | *Tachycineta bicolor* | Invertivore | 2,155 | 116 | 2,038 | 1 |
| TRFL | Traill's Flycatcher | *Empidonax spp.* | Invertivore | 16 | | 16 | |
| TUTI | Tufted Titmouse | *Baeolophus bicolor* | Omnivore | 52 | | 49 | 3 |
| VEER | Veery | *Catharus fuscescens* | Omnivore | 106 | | 27 | 79 |
| WAVI | Warbling Vireo | *Vireo gilvus* | Invertivore | 13 | | 13 | |
| WBNU | White-breasted Nuthatch | *Sitta carolinensis* | Omnivore | 8 | | 6 | 2 |
| WEVI | White-eyed Vireo | *Vireo griseus* | Invertivore | 9 | | 7 | 2 |
| WEWA | Worm-eating Warbler | *Helmitheros vermivorum* | Invertivore | 20 | | 20 | |
| WIFL | Willow Flycatcher | *Empidonax traillii* | Invertivore | 10 | | 10 | |
| WIWA | Wilson's Warbler | *Cardellina pusilla* | Invertivore | 3 | | 3 | |
| WIWR | Winter Wren | *Troglodytes hiemalis* | Invertivore | 3 | | | 3 |

**Table 1** continued

| Species code[a] | Species common name[a] | Species scientific name[a] | Foraging guild | Total (N) | Estuarine wetland (N) | Freshwater wetland (N) | Upland forest (N) |
|---|---|---|---|---|---|---|---|
| WOTH | Wood Thrush | *Hylocichla mustelina* | Omnivore | 126 | | 49 | 77 |
| WTSP | White-throated Sparrow | *Zonotrichia albicollis* | Omnivore | 67 | | 32 | 35 |
| YBCH | Yellow-breasted Chat | *Icteria virens* | Omnivore | 2 | | 2 | |
| YBCU | Yellow-billed Cuckoo | *Coccyzus americanus* | Invertivore | 1 | | 1 | |
| YBFL | Yellow-bellied Flycatcher | *Empidonax flaviventris* | Invertivore | 3 | | 1 | 2 |
| YEWA | Yellow Warbler | *Setophaga petechia* | Invertivore | 19 | | 19 | |
| YTVI | Yellow-throated Vireo | *Vireo flavifrons* | Invertivore | 3 | | 3 | |
| YTWA | Yellow-throated Warbler | *Setophaga dominica* | Invertivore | 5 | | 5 | |

[a] Based on American Ornithologists' Union Check-list of North American birds, 7th edition

**Table 2** Blood mercury sample size for each all songbirds captured in each ecoregion and habitat type

| Guild | Age | Atlantic highlands | | Mid-Atlantic coastal plain | Atlantic mixed woods plains | | | Appalachian forests | | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Freshwater wetlands | Upland forest | Estuarine wetlands | Estuarine wetlands | Freshwater wetlands | Upland forest | Freshwater wetlands | Upland forest | |
| Invertivore | Adult | 359 | 291 | 188 | 1,129 | 238 | 9 | 2,539 | 64 | 4,817 |
| | Juvenile | 52 | 11 | 9 | 112 | 110 | 0 | 1,211 | 12 | 1,517 |
| Omnivore | Adult | 344 | 328 | 10 | 14 | 184 | 21 | 799 | 67 | 1,767 |
| | Juvenile | 55 | 35 | 8 | 16 | 93 | 3 | 132 | 3 | 345 |
| | Total | 810 | 665 | 215 | 1,271 | 625 | 33 | 4,681 | 146 | 8,446 |

effects, because these have been hypothesized to affect Hg exposure in other avian taxa (Evers et al. 2005; Eagles-Smith et al. 2009). Blood Hg data were natural log-transformed to meet assumptions of parametric tests and to normalize residuals. All analyses were conducted in R (R Development Core Team 2012). Unless specified otherwise, all model-generated results are presented as back-transformed least squares mean blood Hg concentrations in µg/g (or ppm, wet weight) with 95 % confidence intervals (R Package "lmerTest", Kuznetsova et al. 2014).

In the first tier of this analysis, we evaluated the effects of habitat type (freshwater wetland, estuarine wetland, or upland), age (juvenile or adult), and foraging guild (invertivore or omnivore) using linear mixed-effects models, with species nested within guild, site nested within contamination status, and ecoregion as random effects (R Package "lme4", Bates et al. 2013). We also included all two-way interactions (habitat × age, habitat × guild, age × guild) in the global model. Models with significant interaction terms ($p < 0.05$) confounded our ability to properly interpret the importance of main effects. Therefore, we conducted a second tier analysis where we divided the data by guild and ran a mixed-effects model with main effects of habitat, age, and habitat × age, and species nested within guild, site nested within contamination regime, and ecoregion were again included as random effects. Pairwise differences between ages and habitats were assessed using Tukey's honest significant difference (HSD) test (R Package "lsmeans", Lenth 2014).

## Potential sentinels for Hg

Our second objective was to provide Hg concentrations in songbird sentinel species in each of the habitat and ecoregion we sampled. We are using the term sentinel in the broadest sense, to highlight songbird species with robust data in our database that can be used for future comparisons. To do this, we selected only sites that were not point-source contaminated—and were thus most likely to be influenced primarily by atmospheric emissions—in order to provide Hg concentrations for these species before the MATS rule goes into effect. Model results indicated that juvenile birds bioaccumulated Hg in blood at lower concentrations than adults; therefore, only the analysis results from data obtained from adult birds were used when considering sentinel candidates. After isolating species with robust sample sizes (i.e., sample sizes greater than 20) in each habitat-ecoregion pair, we ranked each species in terms of mean Hg concentration. We highlight the top ten highest mean Hg levels in freshwater wetland and upland habitats and the top three highest in estuarine habitats, where species richness was low. We include descriptive statistics of blood Hg concentrations for future comparisons to these sentinels in Table 3; descriptive statistics of

Hg concentrations for all birds used in the large model are shown in Supplementary Table 2.

## Results

### Modeling approach

Analysis of the mixed-effects model with species nested within guild and site as random effects revealed that blood Hg concentrations were significantly influenced by age ($F_{1,8444} = 536.3$, $p < 0.001$) and marginally influenced by habitat ($F_{2,8443} = 2.9$, $p = 0.067$) and guild ($F_{1,8444} = 3.5$, $p = 0.064$). However, the significant habitat × guild ($F_{2,8443} = 5.8$, $p = 0.003$), habitat × age ($F_{2,8443} = 58.7$, $p < 0.001$), and guild × age ($F_{1,8444} = 384.6$, $p < 0.001$) interactions confounded our ability to interpret the main effects. Sample sizes for each guild, age and habitat are shown in Table 2.

We simplified our approach by separately analyzing invertivores and omnivores (Fig. 2). Invertivore songbird blood Hg concentrations were influenced by age ($F_{1,6332} = 425.6$, $p < 0.001$) and an interaction of habitat × age ($F_{2,6331} = 79.4$, $p < 0.001$) but not habitat alone ($F_{2,6331} = 0.4$, $p = 0.67$). Adult invertivores in freshwater wetland exhibited 1.97 times higher blood Hg concentrations than adult invertivores in upland forests ($t = 4.4$, $p = 0.0003$) (Fig. 2a). Similarly, adult invertivores in estuarine wetland habitats had 1.65 times higher blood Hg concentrations than adult invertivores in upland forests; however, the difference was not significant ($t = 2.1$, $p = 0.3$) (Fig. 2a). Adult invertivores living in both wetland habitat types exhibited higher Hg concentrations than juvenile invertivores living in the same habitats; adult Hg levels were 7.01 times higher than juveniles in freshwater wetlands ($t = 81.7$, $p < 0.0001$) and 3.92 times higher than juveniles in estuarine wetlands ($t = 20.9$, $p < 0.0001$).

Hg levels in omnivores were influenced by age ($F_{1,2110} = 38.2$, $p < 0.001$) and a habitat × age interaction ($F_{2,2109} = 3.9$, $p = 0.02$). Unlike adult invertivores, significant differences in blood Hg did not occur consistently among the wetland and upland habitats; adults in freshwater wetlands were 1.99 times higher than adults in upland forest ($t = 4.4$, $p = 0.0004$) but this trend was not significant for estuarine wetlands (Fig. 2b). There were no significant differences between adults and juveniles living in wetland habitats but adults in upland forest had significantly higher Hg concentrations than juveniles in upland forests ($t = 3.2$, $p = 0.02$).

### Sentinel species

We identified ten sentinel species for freshwater wetlands in both Atlantic Highlands (Fig. 3a) and Appalachian forests (Fig. 3b) but only four sentinel species in Atlantic Mixed Woods Plains (Fig. 3c). The candidate sentinel species for freshwater wetlands varied between ecoregion and we identified only one species, Tree Swallow, with suitable sample sizes across all ecoregions to be considered a cross-region common sentinel. Red-eyed Vireo was found in each ecoregion but limited sample size in Atlantic Mixed Woods plains precluded comparison. Song Sparrow and Hermit Thrush occurred in only two out of the three ecoregions and regionally unique species, such as the Carolina Wren in Appalachian forests and the Rusty Blackbird and Palm Warbler in Atlantic Highlands, cannot be compared to other ecoregions.

In the upland habitat type, we could identify ten sentinel species in the Atlantic Highlands (Fig. 4a) but only two in the Appalachian forests (Fig. 4b). Only Wood Thrush and Red-eyed Vireo were considered common across the Atlantic Highlands and Appalachian forests and regionally unique species included Bicknell's Thrush and Blackpoll Warbler in the Atlantic Highlands. Estuarine habitats were relatively species poor and only the Saltmarsh Sparrow met our criteria in both Mid-Atlantic Coastal Plain and Atlantic Mixed Woods Plains ecoregions (Fig. 5). Descriptive statistics for all adults in each of these sentinel species at uncontaminated sites are summarized in Table 3, while descriptive statistics for all 102 species included in our model (across contamination regime, ages, habitats and ecoregions) are summarized in Supplementary Table 2.

## Discussion

Mercury pollution is expected to decrease incrementally in the next few years, following the implementation of the MATS rule, as the approximately 1,400 coal- and oil-fired electric generating units at the 600 power plants in the United States reduce emissions through the installation of updated control technologies (USEPA 2011). Our dataset, spanning the decade before the MATS Rule is implemented, shows that across all studied ecoregions, foraging guild, habitat, and age can influence Hg exposure in songbirds. As expected, ecoregions were inhabited by different species, and we used the dataset to generate a list of potential Hg sentinel species in each, along with baseline blood Hg concentrations to aid in future comparisons after the MATS Hg emissions reductions go into effect.

Our modeling results illustrate that, even at the coarse designations described here, foraging guild, habitat, and age were all related to songbird blood Hg concentrations and should be accounted for when comparing across species or locations. In general, invertivores had higher blood Hg concentrations than omnivores and habitat type was important for some age and guild groups; for example,

**Table 3** Descriptive statistics for blood Hg concentrations (μg/g, ww) for adult sentinel species on uncontaminated sites in each habitat-ecoregion pair

| Habitat | Ecoregion | Species | N | Arithmetic mean | Arithmetic SE | Geometric mean | Geometric SE[a] | Maximum |
|---|---|---|---|---|---|---|---|---|
| Freshwater wetlands | Atlantic highlands | Hermit Thrush | 106 | 0.157 | 0.025 | 0.098 | 0.008 | 1.900 |
| | | Lincoln's Sparrow | 80 | 0.232 | 0.020 | 0.168 | 0.016 | 0.821 |
| | | Nashville Warbler | 28 | 0.094 | 0.013 | 0.074 | 0.010 | 0.254 |
| | | Ovenbird | 36 | 0.068 | 0.005 | 0.058 | 0.006 | 0.124 |
| | | Palm Warbler | 51 | 0.607 | 0.065 | 0.497 | 0.043 | 2.815 |
| | | Red-eyed Vireo | 70 | 0.236 | 0.025 | 0.169 | 0.017 | 1.313 |
| | | Rusty Blackbird | 47 | 0.642 | 0.044 | 0.573 | 0.042 | 1.544 |
| | | Swainson's Thrush | 32 | 0.098 | 0.006 | 0.092 | 0.006 | 0.191 |
| | | Tree Swallow | 28 | 0.338 | 0.022 | 0.320 | 0.020 | 0.640 |
| | | White-throated Sparrow | 25 | 0.063 | 0.008 | 0.052 | 0.007 | 0.161 |
| | Appalachian forest | Carolina Chickadee | 20 | 0.071 | 0.008 | 0.062 | 0.007 | 0.140 |
| | | Carolina Wren | 142 | 0.246 | 0.016 | 0.207 | 0.010 | 1.660 |
| | | Eastern Bluebird | 98 | 0.102 | 0.006 | 0.089 | 0.004 | 0.418 |
| | | Gray Catbird | 55 | 0.131 | 0.028 | 0.097 | 0.008 | 1.571 |
| | | House Wren | 21 | 0.122 | 0.012 | 0.111 | 0.011 | 0.269 |
| | | Indigo Bunting | 22 | 0.138 | 0.075 | 0.040 | 0.012 | 1.670 |
| | | Northern Cardinal | 20 | 0.056 | 0.014 | 0.038 | 0.007 | 0.293 |
| | | Red-eyed Vireo | 27 | 0.148 | 0.035 | 0.102 | 0.015 | 0.923 |
| | | Song Sparrow | 93 | 0.119 | 0.008 | 0.092 | 0.007 | 0.373 |
| | | Tree Swallow | 723 | 0.147 | 0.003 | 0.136 | 0.002 | 1.290 |
| | Atlantic mixed woods plains | Black-capped Chickadee | 12 | 0.151 | 0.023 | 0.136 | 0.017 | 0.347 |
| | | Common Yellowthroat | 14 | 0.245 | 0.060 | 0.168 | 0.042 | 0.880 |
| | | Hermit Thrush | 21 | 0.177 | 0.024 | 0.141 | 0.023 | 0.382 |
| | | Red-eyed Vireo | 8 | 0.338 | 0.044 | 0.307 | 0.060 | 0.480 |
| | | Red-winged Blackbird | 47 | 0.212 | 0.027 | 0.157 | 0.017 | 0.821 |
| | | Song Sparrow | 31 | 0.166 | 0.026 | 0.114 | 0.018 | 0.522 |
| | | Swamp Sparrow | 5 | 0.419 | 0.119 | 0.366 | 0.092 | 0.864 |
| | | Traill's Flycatcher | 7 | 0.152 | 0.019 | 0.142 | 0.023 | 0.212 |
| | | Tree Swallow | 67 | 0.275 | 0.026 | 0.192 | 0.021 | 0.996 |
| | | Yellow Warbler | 6 | 0.094 | 0.042 | 0.050 | 0.028 | 0.288 |

**Table 3** continued

| Habitat | Ecoregion | Species | N | Arithmetic mean | Arithmetic SE | Geometric mean | Geometric SE[a] | Maximum |
|---|---|---|---|---|---|---|---|---|
| Upland forest | Atlantic highlands | Bicknell's Thrush | 64 | 0.097 | 0.006 | 0.087 | 0.005 | 0.286 |
| | | Blackpoll Warbler | 23 | 0.058 | 0.003 | 0.056 | 0.003 | 0.082 |
| | | Hermit Thrush | 64 | 0.064 | 0.004 | 0.058 | 0.003 | 0.173 |
| | | Ovenbird | 52 | 0.047 | 0.003 | 0.043 | 0.003 | 0.096 |
| | | Red-eyed Vireo | 94 | 0.079 | 0.005 | 0.066 | 0.004 | 0.266 |
| | | Slate-colored Junco | 38 | 0.052 | 0.004 | 0.049 | 0.003 | 0.151 |
| | | Swainson's Thrush | 76 | 0.088 | 0.005 | 0.080 | 0.004 | 0.238 |
| | | Veery | 56 | 0.055 | 0.004 | 0.049 | 0.003 | 0.165 |
| | | White-throated Sparrow | 34 | 0.041 | 0.004 | 0.036 | 0.003 | 0.153 |
| | | Wood Thrush | 40 | 0.080 | 0.006 | 0.072 | 0.006 | 0.180 |
| | Appalachian forests | American Redstart | 4 | 0.062 | 0.008 | 0.060 | 0.009 | 0.072 |
| | | American Robin | 4 | 0.196 | 0.134 | 0.106 | 0.063 | 0.597 |
| | | Black-and-White Warbler | 2 | 0.226 | 0.086 | 0.208 | 0.084 | 0.312 |
| | | Black-throated Blue Warbler | 4 | 0.054 | 0.006 | 0.053 | 0.006 | 0.067 |
| | | Blue-headed Vireo | 3 | 0.119 | 0.023 | 0.114 | 0.024 | 0.153 |
| | | Ovenbird | 2 | 0.090 | 0.037 | 0.082 | 0.036 | 0.127 |
| | | Red-eyed Vireo | 30 | 0.113 | 0.014 | 0.083 | 0.013 | 0.300 |
| | | Slate-colored Junco | 16 | 0.044 | 0.006 | 0.039 | 0.005 | 0.088 |
| | | Veery | 13 | 0.095 | 0.025 | 0.073 | 0.015 | 0.372 |
| | | Wood Thrush | 24 | 0.099 | 0.008 | 0.091 | 0.008 | 0.204 |
| Estuarine wetlands | Mid-Atlantic coastal plain | Marsh Wren | 10 | 0.744 | 0.060 | 0.723 | 0.059 | 1.134 |
| | | Saltmarsh Sparrow | 79 | 0.954 | 0.039 | 0.882 | 0.041 | 1.888 |
| | | Seaside Sparrow | 12 | 1.060 | 0.058 | 1.041 | 0.060 | 1.328 |
| | Atlantic mixed woods plains | Tree Swallow | 107 | 0.230 | 0.010 | 0.209 | 0.009 | 0.698 |
| | | Nelson's Sparrow | 120 | 0.511 | 0.023 | 0.464 | 0.018 | 2.270 |
| | | Saltmarsh Sparrow | 892 | 0.888 | 0.017 | 0.773 | 0.014 | 3.746 |

Scientific names are shown in Table 1

[a] Calculated using the delta method

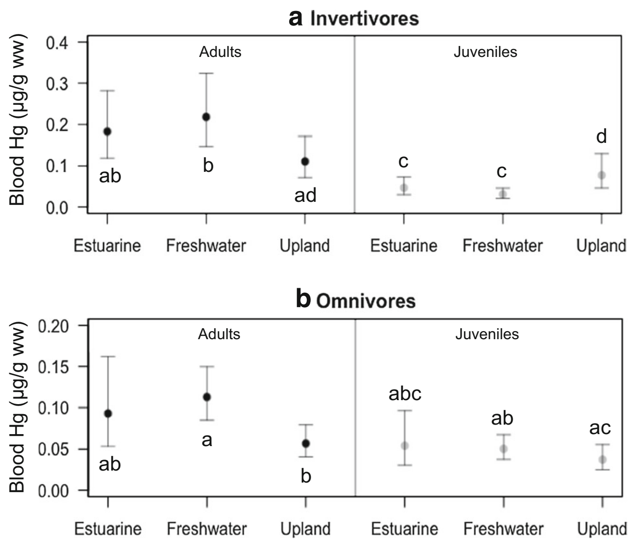


**Fig. 2** Songbird blood Hg concentrations (µg/g, ww) for each age class in each habitat type for **a** invertivores and **b** omnivores [back-transformed µg/g wet weight (ww), from the second tier mixed effects model, accounting for site and species effects]. *Error bars* represent 95 % confidence intervals; *different letters* indicate statistically significant Tukey HSD differences between pairwise groups

adult invertivores exhibited consistently higher blood Hg exposure in wetland habitats than in upland habitats. Generally, adults had higher blood Hg concentrations than juveniles within each habitat type and the strongest relationships between habitat and avian blood Hg were found in adult invertivores. Other studies have found similarly complex relationships of Hg exposure across habitats, but never across multiple species and broad geographic areas (Winder and Emslie 2011; Alberts et al. 2013).

Invertivores likely show elevated Hg concentrations over omnivores because a larger percentage of their diet comes from higher trophic levels in the food web (Poole 2013), thereby, providing more opportunity for biomagnification of MeHg in their prey. Invertivores in wetland habitats likely also exploit the aquatic subsidy of emergent aquatic insects that accumulate Hg directly from sediments (Gray 1993; Nakano and Murakami 2001). Because MeHg production occurs largely in aquatic-associated habitats (Driscoll et al. 2013), birds foraging on emergent aquatic insects rather than seeds and fruit are likely exposed to more MeHg (Jackson et al. 2011b). Birds do not need to feed directly on emergent aquatic insects to be exposed; spiders, and other predatory invertebrates also effectively transfer, and most importantly biomagnify, aquatic MeHg into the terrestrial food web, either from floodplain biota or sediment-dwelling aquatic emergent insects (Cristol et al. 2008). This link has also been demonstrated with other environmentally persistent contaminants, such as PCBs (Walters et al. 2008, 2010).

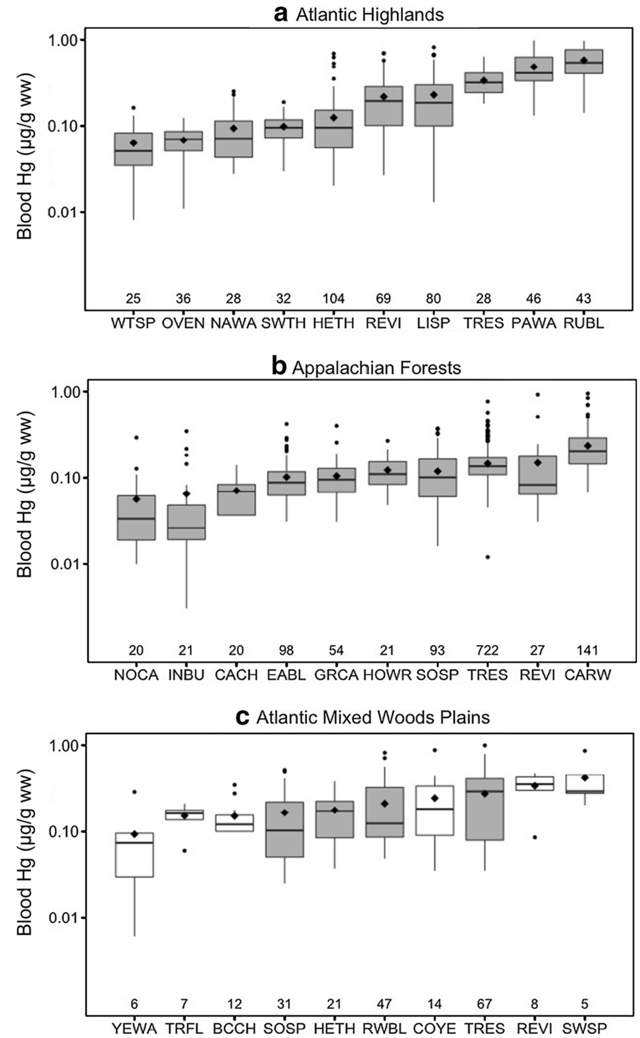


**Fig. 3** Blood Hg concentrations (µg/g, ww) of adult freshwater wetland songbird sentinel species in **a** Atlantic Highlands, **b** Appalachian Forests, and **c** Atlantic Mixed Woods Plains, plotted on a log-scale. *Gray shaded boxes* identify suitable Hg sentinel species for each ecoregion (N > 20). *Diamonds* indicate mean blood Hg concentrations for each species. *Bottom* and *top* of *boxes* indicate first and third quartiles, respectively. *Upper* and *lower whiskers* indicate the highest and lowest values that are within 1.5 times the interquartile range. Data outside of this range are plotted as *points*. Common and scientific names of species are listed in Table 1

Adult and juvenile songbirds exhibited differences in Hg exposure across habitats and guilds. The disparity between adult and juvenile blood Hg concentrations is likely driven by the complex dynamics of blood MeHg concentrations in chicks as they reduce their blood burdens of MeHg through somatic growth and depuration through feather growth (Condon and Cristol 2009). In rapidly growing young birds, mass accretion can exceed or dampen MeHg accumulation, which manifests as lower body Hg concentrations compared to non-growing birds with identical Hg exposure (French et al. 2010). Although the juvenile birds

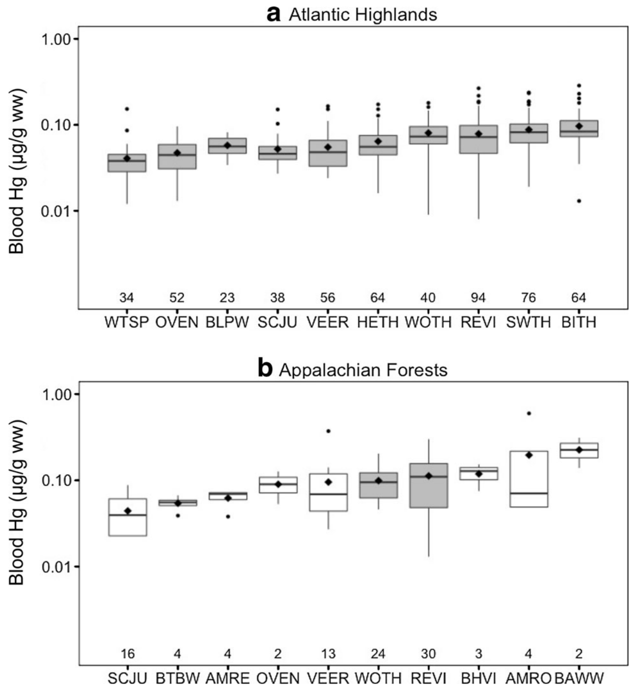


**Fig. 4** Blood Hg concentrations (μg/g, ww) of adult upland songbird sentinel species in **a** Atlantic Highlands and **b** Appalachian Forests, plotted on a log-scale. *Gray shaded boxes* identify suitable Hg sentinel species for each ecoregion (N > 20). *Diamonds* indicate mean blood Hg concentrations for each species. *Bottom* and *top* of *boxes* indicate first and third quartiles, respectively. *Upper* and *lower whiskers* indicate the highest and lowest values that are within 1.5 times the interquartile range. Data outside of this range are plotted as *points*. Common and scientific names of species are listed in Table 1

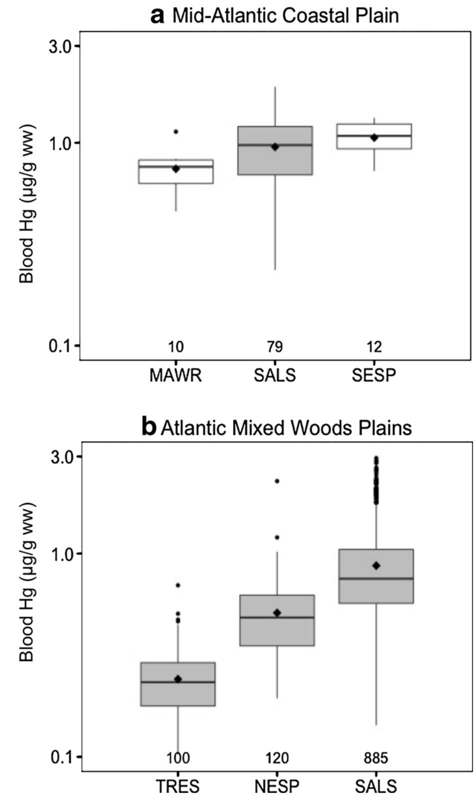


**Fig. 5** Blood Hg concentrations (μg/g, ww) of adult estuarine wetland songbird sentinel species in **a** Mid-Atlantic Coastal Plain and **b** Atlantic Mixed Woods Plains, plotted on a log-scale. *Gray shaded boxes* identify suitable Hg sentinel species for each ecoregion (N > 20). *Diamonds* indicate mean blood Hg concentrations for each species. *Bottom* and *top* of *boxes* indicate first and third quartiles, respectively. *Upper* and *lower whiskers* indicate the highest and lowest values that are within 1.5 times the interquartile range. Data outside of this range are plotted as *points*. Common and scientific names of species are listed in Table 1

we sampled were full grown, early-life MeHg dynamics could influence Hg concentrations into the fledgling time period and beyond. Perhaps the most important mechanism responsible for the disparity between juvenile and adult birds is the strong influence of feather growth in young birds. As new feathers grow, MeHg from the blood and muscle tissue binds to the keratin in the growing feather, which is then permanently sequestered in feather tissue, effectively eliminating it from internal tissues such as blood and organs (Condon and Cristol 2009). Because songbirds experience multiple molts during their juvenile stage, many of the blood samples for juveniles are likely obtained from birds that recently depurated a large amount of Hg into growing feathers.

Our findings allow a qualitative examination of species and habitats at risk for Hg bioaccumulation in the eastern United States. The suite of well-sampled species from each habitat type offers a baseline for the variation seen in Hg concentrations at uncontaminated sites (i.e. those without a known point source of contamination). A wide range of variation among individuals of the same species was observed and average concentrations varied by an order of magnitude among some species within a habitat type. For the freshwater wetland habitat type, this variation might be driven by the wide diversity of vegetative structure and associated hydrology along with greater trophic complexity that may significantly influence methylation rates (Shanley and Bishop 2012).

In estuarine wetlands there is high potential for elevated methylation and transport through the food web to high trophic level species (Lane et al. 2011). These habitats have low species diversity compared to the range of species supported by diverse freshwater and upland habitats. While species diversity might be lower, multiple species are of particular concern because they are obligate estuarine specialists and are subject to a host of conservation issues ranging from sea level rise and urbanization to contaminant exposure. For example, Saltmarsh and Nelson's Sparrows show some of the highest blood Hg concentrations in our dataset and these species are also exhibiting population declines across their ranges (Lane et al. 2011).

Some invertivore songbirds of regional conservation concern that prefer wetland breeding habitats are conspicuously missing from our analysis. This is because they are rare or difficult to sample. In the future, we recommend also sampling wetland-dependent songbird species that are experiencing significant population declines, such as the Olive-sided Flycatcher (*Contopus cooperi*) and Canada Warbler (*Cardellina canadensis*), to expand upon the information presented here and to help determine if Hg is an important adverse stressor to their health, reproduction, and survival. Environmental Hg loads originating from the deposition of atmospheric Hg may already be causing widespread reproductive harm for some species of high conservation concern, such as the Rusty Blackbird (Edmonds et al. 2010, 2012).

Although we report the most comprehensive dataset on songbird Hg exposure to date, further investigations are needed to fully understand the impact of Hg exposure on songbirds in eastern North America. For example, we focused on breeding season Hg concentrations, but we should be concerned about Hg exposure throughout a bird's life cycle, especially for neotropical migrants that overwinter in tropical areas with elevated environmental Hg loads. Our sampling design does not provide an ability to connect songbird blood Hg concentrations to abiotic environmental Hg levels, an important step in understanding if songbirds can serve as bioindicators of Hg loading to an ecosystem. We lack a detailed understanding of the effects of Hg on songbirds at a population level. Although short-term fieldwork on wild songbirds has determined Hg effects on reproductive success (Jackson et al. 2011a; Brasso and Cristol 2008), obtaining Hg estimates from sites with long-term banding operations would provide a better understanding of potential population-level impacts of Hg exposure. Promulgation of the MATS rule by the USEPA is an important step toward reducing atmospherically generated loads of Hg across the North American landscape and therefore potentially reducing harmful body burdens in birds. Our findings provide a foundation from which to gauge songbird response to the new MATS regulations and an important step forward in assessing the risk of environmental Hg exposure to songbirds.

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

## References

Alberts JM, Sullivan SMP, Kautza A (2013) Riparian swallows as integrators of landscape change in a multiuse river system: implications for aquatic-to-terrestrial transfers of contaminants. Sci Total Environ 463–464:42–50. doi:10.1016/j.scitotenv.2013.05.065

Basu N, Scheuhammer AM, Bursian SJ, Elliot J, Rouvinen-Watt K, Chan HM (2007) Mink as a sentinel species in environmental health. Environ Res 103:130–144

Bates D, Maechler M, Bolker B, Walker S (2013) lme4: linear mixed-effects models using Eigen and S4. R package version 1.0-5. http://CRAN.R-project.org/package=lme4. Accessed 28 Nov 2014

Beeby A (2001) What do sentinels stand for? Environ Pollut 112:285–298

Bossart GD (2006) Marine mammals as sentinel species for oceans and human health. Oceanography 19:134–137

Brasso RL, Cristol DA (2008) Effects of mercury exposure on the reproductive success of tree swallows (*Tachycineta bicolor*). Ecotoxicology 17:133–141. doi:10.1007/s10646-007-0163-z

Brown CL, Luoma SN (1995) Use of the euryhaline bivalve *Potamocorbula amurensis* as a biosentinel species to assess trace metal contamination in San Francisco Bay. Mar Ecol Press Series 124:129–142

Bundy JG, Keun HC, Sidhu JK, Spurgeon DJ, Svendsen C, Kille P, Morgan AJ (2007) Metabolic profile biomarkers of metal contamination in a sentinel terrestrial species are applicable across multiple sites. Environ Sci Technol 41:4458–4464

Burger J, Gochfeld M (2004) Marine birds as sentinels of environmental pollution. EcoHealth 1:263–274

Carlson JR, Cristol D, Swaddle JP (2014) Dietary mercury exposure causes decreased escape takeoff flight performance and increased molt rate in European starlings (*Sturnus vulgaris*). Ecotoxicology. doi:10.1007/s10646-014-1288-5

Commission for Environmental Cooperation Working Group (1997) Ecological regions of North America—toward a common perspective. Commission for Environmental Cooperation, Montreal 71p

Condon AM, Cristol DA (2009) Feather growth influences blood mercury level of young songbirds. Environ Toxicol Chem 28:395–401. doi:10.1897/08-094.1

Cowardin LM, Cater V, Golet FC, LaRoe ET (1979) Classification of wetlands and deepwater habitats of the United States. Department of the Interior, Fish and Wildlife Service, Washington, U.S

Cristol DA, Brasso RL, Condon AM, Fovargue RE, Friedman SL, Hallinger KK, Monroe AP, White AE (2008) The movement of aquatic mercury through terrestrial food webs. 320:335. doi:10.1126/science.1154082

Custer CM, Custer TW, Hill EF (2007) Mercury exposure and effects on cavity-nesting birds from the Carson River, Nevada. Arch Environ Contam Toxicol 52:129–136. doi:10.1007/s00244-006-0103-6

Drewett DVV, Willson JD, Cristol DA, Chin SY, Hopkins WA (2013) Inter- and intraspecific variation in mercury bioaccumulation by snakes inhabiting a contaminated river floodplain. Environ Toxicol Chem 32:1178–1186

Driscoll CT, Mason RP, Chan HM, Jacob DJ, Pirrone N (2013) Mercury as a global pollutant: sources, pathways, and effects. Environ Sci Technol 47:4967–4983

Eagles-Smith CA, Ackerman JT, De La Cruz SEW, Takekawa JY (2009) Mercury bioaccumulation and risk to three waterbird foraging guilds is influenced by foraging ecology and breeding stage. Environ Pollut 157:1993–2002

Edmonds ST, Evers DC, Cristol DA, Mettke-Hoffman C, Powell LL, McGann AJ, Armiger JW, Lane OP, Tessler DF, Newell P, Heyden K, O'Driscoll NJ (2010) Geographic and seasonal variation in mercury exposure of the declining rusty blackbird. Condor 112:789–799

Edmonds ST, O'Driscoll NJ, Hillier NK, Atwood JL, Evers DC (2012) Factors regulating the bioavailability of methylmercury to breeding rusty blackbirds in northeastern wetlands. Environ Pollut 171:148–154. doi:10.1016/j.envpol.2012.07.044

Evers DC (2006) Loons as biosentinels of aquatic integrity. Environ Bioindic 1:18–21

Evers DC, Burgess NM, Champoux L, Hoskins B, Major A, Goodale WM, Taylor RJ, Poppenga R, Daigle T (2005) Patterns and interpretation of mercury exposure in freshwater avian communities in northeastern North America. Ecotoxicology 14:193–221

Evers DC, Han Y-J, Driscoll CT, Kamman NC, Goodale MW, Lambert KF, Holsen TM, Chen CY, Clair TA, Butler T (2007) Biological mercury hotspots in the Northeastern United States and Southeastern Canada. Bioscience 57:29–43

Evers DC, Jackson AK, Tear TH, Osborne CE (2012) Hidden risk: mercury in terrestrial ecosystems of the northeast. BRI Report #2012-07. http://www.briloon.org/uploads/BRI_Documents/Mercury_Center/Hidden%20Risk/HiddenRisk_lr.pdf. Accessed 28 Nov 2014

Fair JM, Paul E, Jones J, Clark AB, Davie C, Kaiser G (2010) Chapter 6: Minor manipulative procedures. In: Guidelines to the use of wild birds in research. Ornithological Council, Washington. www.nmnh.si.edu/BIRDNET/guide. Accessed 22 Oct 2014

Folsom SB, Evers DC (2008) Assessment of mercury contamination and effects in songbirds on the North Fork of the Holston River, Virginia 2007. BRI Report #2008-01 Submitted to the U.S. Fish and Wildlife Service, Gloucester, Virginia. Biodiversity Research Institute, Gorham, Maine

Franceschini MD, Lane OP, Evers DC, Reed JM, Hoskins B, Romero LM (2009) The corticosterone stress response and mercury contamination in free-living tree swallows, Tachycineta bicolor. Ecotoxicology 18:514–521

French JB, Bennett RS, Rossmann R (2010) Mercury in the blood and eggs of American kestrels fed methylmercury chloride. Environ Toxicol Chem 29:2206–2210. doi:10.1002/etc.284

Gray LJ (1993) Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. Am Midl Nat 129:288–300

Grove RA, Henny CJ, Kaiser JL (2009) Osprey: worldwide sentinel species for assessing and monitoring environmental contamination in rivers, reservoirs, and estuaries. J Toxicol Environ Health Part B 12:25–44

Hallinger KK, Zabransky DJ, Kazmer KA, Cristol DA (2010) Birdsong differs between mercury-polluted and reference sites. Auk 127:156–161

Jackson AK, Evers DC, Etterson MA, Condon AM, Folsom SB, Detweiler J, Schmerfeld J, Cristol DA (2011a) Mercury exposure affects the reproductive success of a free-living terrestrial songbird, the Carolina wren (*Thryothorus ludovianus*). Auk 128:759–769

Jackson AK, Evers DC, Folsom SB, Condon AM, Diener J, Goodrick LF, McGann AJ, Schmerfeld J, Cristol DA (2011b) Mercury exposure in terrestrial birds far downstream of an historical point source. Environ Pollut 159:3302–3308. doi:10.1016/j.envpol.2011.08.046

Keller RH, Xie L, Buchwalter DB, Franzreb KE, Simons TR (2014) Mercury bioaccumulation in southern Appalachian birds, assessed through feather concentrations. Ecotoxicology 23(2):304–316. doi:10.1007/s10646-013-1174-6

Kuznetsova A, Brockhoff PB, Christensen RHB (2014) lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-6. http://CRAN.R-project.org/package=lmerTest. Accessed 28 Nov 2014

Lane OP, O'Brien KM, Evers DC, Hodgman TP, Major A, Pau N, Ducey MJ, Taylor R, Perry D (2011) Mercury in breeding saltmarsh sparrows (*Ammodramus caudacutus caudacutus*). Ecotoxicology 20:1984–1991

Lenth R (2014) lsmeans: least-squares means. R package version 2.00-5. http://cran.r-project.org/web/packages/lsmeans/lsmeans.pdf. Accessed 28 Nov 2014

Lewis CA, Cristol DA, Swaddle JP, Varian-Ramos CW, Zwollo P (2013) Decreased immune response in zebra finches exposed to sublethal doses of mercury. Arch Environ Contam Toxicol 64:327–336. doi:10.1007/s00244-012-9830-z

McKay JL, Maher CR (2012) Relationship between blood mercury levels and components of male song in Nelson's sparrows (*Ammodramus nelsoni*). Ecotoxicology 21:2391–2397

Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc Natl Acad Sci 98:166–170

National Research Council (1991) Animals as sentinels of environmental health hazards. Committee on Animals as Monitors of Environmental Hazards, National Academy Press, Washington

Newman MC, Xu X, Condon A, Liang L (2011) Floodplain methylmercury biomagnification factor higher than that of the contiguous river (South River, Virginia USA). Environ Poll 159:2840–2844

Osborne CE, Evers DC, Duron M, Schoch N, Yates D, Buck D, Lane OP, Franklin J (2011) Mercury contamination within terrestrial ecosystems in New England and Mid-Atlantic states: profiles of soil, invertebrates, songbirds, and bats. BRI Report #2011-09. http://www.briloon.org/uploads/BRI_Documents/Mercury_Center/Hidden%20Risk/BRI_2011-09_Osborne.etal.2011.pdf. Accessed 28 Nov 2014

Poole A (eds) (2013) The birds of North America online: Cornell Laboratory of Ornithology, Ithaca. http://bna.birds.cornell.edu/BNA/. Accessed 3 Jan 2013

Rimmer CC, McFarland KP, Evers DC, Miller EK, Aubry Y, Busby D, Taylor RJ (2005) Mercury concentrations in Bicknell's thrush and other insectivorous passerines in montane forests of northeastern North America. Ecotoxicology 14:223–240

Rimmer CC, Miller EK, McFarland KP, Taylor RJ, Faccio SD (2010) Mercury bioaccumulation and trophic transfer in the terrestrial food web of a montane forest. Ecotoxicology 19:697–709. doi:10.1007/s10646-009-0443-x

Scheuhammer AM, Meyer MW, Sandheinrich MB, Murray MW (2007) Effects of environmental methylmercury on the health of wild birds, mammals, and fish. Ambio 36:12–18

Scheuhammer AM, Basu N, Evers DC, Heinz GH, Sandheinrich MB, Bank MS (2012) Ecotoxicology of mercury in fish and wildlife: Recent Advances. In: Bank MS (ed) Mercury in the environment: pattern and process. Univ. California Press, Berkeley, pp 223–238

Scoville SA, Lane OP (2013) Cerebellar abnormalities typical of methylmercury poisoning in a fledged saltmarsh sparrow, *Ammodramus caudacutus*. Bull Environ Contam Toxicol 90:616–620

Shanley JB, Bishop K (2012) Mercury cycling in terrestrial watersheds. In: Bank MS (ed) Mercury in the environment: pattern and process. Univ. California Press, Berkeley, pp 119–142

Stahl RG (2008) Can mammalian and non-mammalian "sentinel species" data be used to evaluate the human health implications of environmental contaminants? Human Ecol Risk Assess 3:329–335

Townsend JM, Driscoll CT, Rimmer CC, McFarland KP (2014) Avian, salamander, and forest floor mercury concentrations increase with elevation in a terrestrial ecosystem. Environ Toxicol Chem 33:208–215

United States Environmental Protection Agency (USEPA) (2011). "Mercury and Air Toxics Standards (MATS) for Power Plants."

Van der Schalie WH, Gardner HS, Bantle JA, De Ross CT, Finch RA, Reif JS, Reuter RH, Backer LC, Buger J, Folmar LC, Stokes WS (1999) Animals as sentinels of human health hazards of environmental chemicals. Environ Health Perspect 107:309–315

Varian-Ramos CW, Swaddle JP, Cristol DA (2013) Mercury reduces avian reproductive success and imposes selection: an experimental study with adult- or lifetime-exposure in zebra finch. PLoS ONE 9:e95674

Wada H, Cristol DA, McNabb FMA, Hopkins WA (2009) Suppressed adrenocortical responses and thyroid hormone levels in birds near a mercury-contaminated river. Environ Sci Technol 43:6031–6038

Walters DM, Fritz KM, Otter RR (2008) The dark side of subsidies: adult stream insects export organic contaminants to riparian predators. Ecol Appl 18:1835–1841

Walters DM, Mills MA, Fritz KM, Raikow DF (2010) Spider-mediated flux of PCBs from contaminated sediments to terrestrial ecosystems and potential risks to arachnivorous birds. Environ Sci Technol 44:2849–2856. doi:10.1021/es9023139

Warner SE, Shriver WG, Pepper MA, Taylor RJ (2010) Mercury concentrations in tidal marsh sparrows and their use as bioindicators in Delaware Bay, USA. Environ Monit Assess 171:671–679. doi:10.1007/s10661-010-1312-z

Wiener JG (2013) Mercury exposed: advances in environmental analysis and ecotoxicology of a highly toxic metal. Environ Toxicol Chem 32:2175–2178

Winder VL, Emslie SD (2011) Mercury in breeding and wintering Nelson's sparrows (*Ammodramus nelsoni*). Ecotoxicology 20:218–225. doi:10.1007/s10646-010-0573-1

Wren CD, Harris S, Harttrup N (1995) Ecotoxicology of mercury and cadmium. In: Hoffman DJ, Rattner BA, Burton GA, Cairns J (eds) Handbook of Ecotoxicology. Lewis Publishers, Boca Raton, pp 392–423

Yates DE, Adams EM, Angelo SE, Evers DC, Schmerfeld J, Moore MS, Kunz TH, Divoll T, Edmonds ST, Perkins C, Taylor R, O'Driscoll NJ (2014) Mercury in bats from the northeastern United States. Ecotoxicology 23:45–55