



The impact of mercury on North American songbirds: effects, trends, and predictive factors

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Abstract

Researchers were asked to contribute new results addressing questions about the exposure and effects of mercury (Hg) in North American songbirds, a rapidly declining group of species that is the subject of enduring interest for millions of birdwatchers, the general public and conservation scientists. Important questions to be answered include: Is Hg causing or exacerbating songbird population declines? Which North American songbirds are at most risk and in which landscapes? Are there aspects of songbird natural history that pre-dispose them to risks of Hg exposure and effects, in particular, their migratory behavior? In all, 61 authors contributed 15 studies addressing aspects of these questions. Articles in this special issue address an array of topics including: (1) three studies on health effects in the laboratory using a domesticated songbird model species, the zebra finch; (2) three studies on changes in songbird exposure to Hg over time spans from less than a decade to more than a century; (3) five studies on landscape characteristics or management practices that cause the oft-noted spatial variation in Hg accumulation by resident songbirds, from the subarctic tundra to high-elevation tropical forests; (4) three papers examining the recently recognized role of migration behavior in predicting risk to songbirds from Hg; and (5) one paper on the potential pitfalls of using feather Hg concentration as a bioindicator for Hg exposure. In summary, although there are many questions still to be answered, it is clear that the effects of Hg are persistent long after exposure, Hg exposure of North American songbirds is not improving, predicting exposure requires a detailed understanding of ecosystem processes beyond simply the amount of Hg present at a site, migration behavior predisposes songbirds to risk of Hg exposure and effects, and carefully selecting appropriate bioindicator sites, species, and tissues is critical to any monitoring efforts.

Keywords Bioindicator · Mercury · Methylmercury · Migration · Passerine · Songbird

Importance of understanding mercury exposure for effective conservation

Mercury (Hg) enters ecosystems naturally at low levels, but has been augmented many fold by mining, industrial activity, and the burning of fossil fuels. Once converted by microbes to methylmercury (MeHg), this organic form of Hg can biomagnify to levels of concern in terrestrial species

such as insectivorous songbirds (avian Order Passeriformes, also known as passerines), particularly in wetlands (Jackson et al. 2015; Ackerman et al. 2016) where MeHg concentration in avian invertivores can even exceed those of associated avian piscivores (Evers et al. 2005). This happens because the biomagnification process is related to trophic level amplification of MeHg, which can be elevated in terrestrial systems by predatory invertebrates such as spiders (Cristol et al. 2008). The availability of MeHg can be enhanced in areas with ecosystem sensitivity, such as landscapes with low pH, elevated dissolved organic carbon, water level fluctuations, and vegetated habitats that experience wet-dry cycles during the year (Driscoll et al. 2007). Wetlands, which exhibit all these characteristics, are predisposed to be hotspots of avian Hg exposure.

MeHg potentially threatens all wildlife species, but songbirds may be particularly vulnerable. Most species of birds are songbirds, as this is the most recently evolved and diversified of all avian orders. In general, songbirds are

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declining precipitously, including a combined population decline of three billion birds in North America (Rosenberg et al. 2019). MeHg exposure has already been linked to effects on avian reproduction in industrially polluted sites (Jackson et al. 2011a, b), backed by numerous laboratory dosing studies designed to replicate such exposure (e.g., Heddle et al. 2020). In addition, several studies have correlated avian health with MeHg exposure at non-point-source sites (Ackerman et al. 2016; Whitney and Cristol 2017a; Evers 2018). Many songbirds exhibit phenomenal feats of navigation and endurance during their migratory flights, making them particularly vulnerable to the effects of Hg during this taxing part of the life cycle (Seewagen et al. 2020).

While the legal framework supporting ecotoxicological remediation is most concerned with the effect of contaminants on acute mortality and depression of reproduction that might quickly cause population declines, it is now apparent that environmental MeHg concentrations are high enough to cause sublethal effects to songbird health (Ackerman et al. 2016; Whitney and Cristol 2017a; Evers 2018). Mercury exposure in terrestrial songbirds has been linked to numerous effects in the field and laboratory, including reduced survival (Hallinger et al. 2011), impaired reproduction (Brasso et al. 2008; Hallinger and Cristol 2011), depressed immune and endocrine functions (Hawley et al. 2009; Wada et al. 2009), and altered cognition, sensation and behaviors (Hallinger et al. 2010; Swaddle et al. 2017; Greene et al. 2018; Wolf et al. 2018). Recent research has shown that reproduction in some songbirds can be significantly impaired at Hg levels as low as 0.7 ppm in blood or 2.4 ppm in feathers (Jackson et al. 2011a), providing a framework for estimating adverse effects at a range of concentrations found in wild populations. In addition, laboratory studies have made clear that even brief exposure early in life can have long-lasting fitness effects during adult life (Paris et al. 2018).

As bioindicators for Hg, songbird species offer both advantages and disadvantages over the well-studied loon, seabird, long-legged wading bird and raptor species. Advantages include: (1) they are relatively short-lived, (2) are tied to particular breeding and wintering territories, and (3) depurate Hg rapidly during molt (Whitney and Cristol 2017b). Therefore, they represent a focused spatial and temporal snapshot for Hg contamination in contrast to a long-lived wanderer such as a seabird or raptor. One disadvantage is that in non-resident species, such as neotropical migrants, feather concentrations reflect a mix of body burden and dietary uptake of MeHg at the time of feather growth, which can complicate interpretation of data when feathers are collected months later at locations distant from the source of Hg (Peterson et al. 2019). Another disadvantage is that songbirds are short-lived and Hg can have

significant adverse impacts to reproductive output as it bioaccumulates in older individuals that are in high-risk environments (e.g., common loon (*Gavia immer*); Evers et al. 2008).

The use of wetland-breeding songbirds as bioindicators is of great interest because many species are undergoing major population declines, likely due to a variety of environmental stressors, such as loss of habitat, climate change, acidification, and sea level rise. For example, rusty blackbird populations have declined approximately 90% since the 1960s and some individuals have very high Hg levels for terrestrial songbirds in non-industrially-polluted landscapes (Edmonds et al. 2010). The olive-sided flycatcher, which breeds in similar habitat as the rusty blackbird, but is a long-distance neotropical migrant, overwinters in areas with widespread use of Hg for gold mining and is declining at a similar rate of 78% since 1970. There are very limited data on Hg exposure in this species, so more research is necessary to determine if the availability of MeHg is a driving environmental stressor. How many other species are declining because of MeHg and is that stressor a cause of species declines, or is it merely an additional stressor compounded with other threats such as global climate change?

Special issue articles in context of other recent research

Conversations at the 2017 International Conference on Mercury as a Global Pollutant emphasized: (1) the need for greater understanding about MeHg effects and exposure in songbirds, as well as (2) the importance of identifying species and landscapes at greatest risk, and (3) tools to track trends in MeHg exposure over time within landscapes identified as biological Hg hotspots. The following 15 studies reflect the response of 61 researchers to fill those information gaps. The articles are separated into five content categories, and are briefly summarized below. Further, to build on the findings of the papers from this special issue as well as the existing literature on Hg in songbirds, we have listed all published studies on effects of Hg in songbirds, most of which are also recent. This list of Hg effects on songbirds is organized by species to facilitate use in identifying data gaps and at-risk species (Table 1).

Overview of special issue articles

This special issue on Hg in songbirds presents findings from 15 papers describing laboratory and field studies from across North America. The papers reflect five general

Table 1 Field and laboratory^a studies of songbirds with identification of endpoint effects or no effects (citations from Whitney and Cristol 2017a unless noted)

Species	Effect	Citation
Acadian flycatcher (<i>Empidonax vireescens</i>)	Reproduction	
American dipper (<i>Cinclus mexicanus</i>)	No reproductive effect	
American redstart (<i>Setophaga ruticilla</i>)	No survival effect	Ma et al. (2018a)
Blackpoll warbler (<i>Setophaga striata</i>)	Survival	Ma et al. (2018a)
Carolina wren (<i>Thryothorus ludovicianus</i>)	Behavior (song) Reproduction	
Eastern bluebird (<i>Sialia sialis</i>)	Reproduction Reproduction, condition	
European starling (<i>Sturnus vulgaris</i>)	Organ damage ^b Flight ability ^b	
Great tit (<i>Parus major</i>)	Reproduction	
House wren (<i>Troglodytes aedon</i>)	Likely reproductive effect Behavior (song)	
Nelson's sparrow (<i>Ammodramus nelsoni</i>)	Behavior (song)	
Northern waterthrush (<i>Parkesia noveboracensis</i>)	No behavior effect	
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	No growth, condition effects	
Saltmarsh sparrow (<i>Ammodramus caudacutus</i>)	Neurodevelopment	
Song sparrow (<i>Melospiza melodia</i>)	Behavior (song)	
Tree swallow (<i>Tachycineta bicolor</i>)	No reproductive effect No reproductive effect Nestling growth Likely reproductive effect Reproduction Immune function Endocrine function Endocrine function Reproduction Longevity Reproduction No reproductive effect Nestling survival Behavior (incubation) Flight ability ^b	Hartman et al. (2019)

Table 1 (continued)

Species	Effect	Citation
Yellow-rumped warbler (<i>Setophaga coronata</i>)	Migration departure ^c	Ma et al. (2018b) Seewagen et al. (2019)
Zebra finch (<i>Taeniopygia guttata</i>) (Studies listed for this species are the only ones using dosing in captivity on a domesticated species)	Neurological function Immune function Oxidative stress Endocrine function Reproduction Endocrine function No Immune effect Behavior (foraging) Reproduction Behavior (nesting) Hearing Behavior, cognition Neurological function	Greene et al. (2018) Smith et al. (2018) Paris et al. (2018) Morran et al. (2018) Heddle et al. (2020) Scoville et al. (2020) Spickler et al. (2020)

^aAll studies were in the field with environmental exposures except those noted

^bDosed birds studied in captivity

^cDosed birds studied in the field

categories of research on Hg in songbirds: (1) three studies on health effects in laboratory studies of a domesticated songbird model species, the zebra finch; (2) three studies on historical changes in songbird exposure to Hg; (3) five studies on landscape characteristics or management practices that are often related to spatial variation in Hg accumulation among resident songbirds, from the arctic tundra to high-elevation tropical forests; (4) three papers, two experimental and one a synthetic review, examining the role of migration behavior in predicting risk to songbirds from Hg; and (5) one paper on the potential limitations of using feather Hg concentration as a bioindicator for Hg exposure.

Effects on health and physiology

Title 1: Continuous exposure to mercury during embryogenesis and chick development affects later survival and reproduction of zebra finch (*Taeniopygia guttata*)

Heddle et al. (2020) examines the short and long-term effects of MeHg exposure in a domesticated songbird, the zebra finch. Exposure was either in ovo, as nestlings, or with a combined egg + nestling treatment through injections into eggs and oral dosing of nestlings. In ovo exposure to MeHg reduced hatching success but did not affect nestling growth. In ovo or nestling-only exposure did not have long-term effects on adult reproductive behavior.

However, longer-term effects were seen with combined egg + nestling exposure, in terms of survival, with very few egg + nestling exposed females surviving to breeding age. Females that did survive also had lower overall breeding productivity; a startling delayed fitness effect of Hg also found in another recent study (Paris et al. 2018). This laboratory experiment suggests that combined embryonic and nestling MeHg exposure has compounding latent effects on productivity, likely through a mechanism that reduces the ability of exposed females to lay eggs that hatch.

Title 2: Mercury delays cerebellar development in a model songbird species, the zebra finch

Scoville et al. (2020) describes, for the first time, normal development of the cerebellum in an altricial songbird (zebra finch), and determines the effect on cerebellar maturation of in ovo or egg + nestling exposure to MeHg. These researchers conclude that in this model songbird species, the cerebellum does not mature until the age of fledging, in contrast with what is known from precocial birds that are hatched with mature cerebella. Thus, their finding that all treatments of MeHg caused a delay in cerebellar maturation, when compared to a control group, suggests that early exposure to Hg may delay fledging. Because nests are dangerous places that attract predators, delayed fledging would place nestlings at increased risk of predation. Displaced Purkinje neurons, a pathology typical of MeHg exposure in developing vertebrate brains, including humans with Minamata disease, were more numerous in MeHg-exposed birds, and persisted at least until the age of independence from parents (50 days).

This experimental laboratory result indicates that delays in maturation of the cerebellum, and lasting damage to spatial arrangement of neurons, could delay fledging in altricial bird species and impair survival during the vulnerable juvenile period. It is an example of a careful laboratory study that reveals a result that could have

dramatic effects on wild birds. However, the necessary validation of detecting effects such as cerebellar maturation and fledging delays in the field are challenging to decouple from effects of nest predation and environmental seasonal variability. Studies that merge findings from the laboratory and field are needed.

Title 3: Sexually selected traits as bioindicators: exposure to mercury affects carotenoid-based male bill color in zebra finches

Spickler et al. (2020) examines whether sexually selected traits are sensitive bioindicators of environmental toxicants by assessing the effects of exposure to environmentally relevant dietary concentrations of MeHg on pigment coloration in domestic zebra finches. Like Heddle et al. (2020) and other recent studies, they tested whether effects of MeHg on coloration were influenced by timing of exposure. Birds were either exposed developmentally, as adults, or throughout their entire life. Bill coloration, which is a sexually selected trait, was paler in males with lifetime exposure to MeHg. Neither adult, nor developmental exposure alone, influenced bill color in adult males, with the possible exception of early exposure of nestlings without in ovo exposure. In females, where bill color is not under strong sexual selection, exposure to MeHg had no effect and in both sexes the gray/brown feather color, which is not a sexually selected trait, was unaffected by MeHg exposure.

This dosing experiment found that sexually selected traits may be useful bioindicators of the stress imposed by environmental toxins such as MeHg, as has been reported from recent correlational or theoretical studies. Evolution may have caused these traits to be more sensitive to environmental stressors. This study is an example of how the use of ecotoxicological models can inform basic ecological theory, in this case using an experimental application of MeHg as an environmental stressor.

Temporal trends in Hg

Title 4: Long-term monitoring of mercury in adult saltmarsh sparrows breeding in Maine, Massachusetts and New York, USA, 2000–2017

Lane et al. (2020) conducted a long-term (2000–2017) study of Hg exposure trends in a songbird species of extreme conservation concern (Bateman et al. 2019). This study assessed Hg in blood and feathers of the saltmarsh sparrow (*Ammodramus caudacutus*) breeding in salt marshes across three states, with the goal of determining if exposure was increasing or decreasing. Mercury exposure differed by site and year but there was no consistent temporal trend within or among sites. Blood Hg concentrations declined

only at one site—Rachel Carson National Wildlife Refuge in southeastern Maine, USA. They observed a seasonal variation in blood Hg concentrations in the sparrows, increasing during the breeding season and peaking in July, as recently reported elsewhere (Kopec et al. 2018).

Mercury exposure is hard to predict because mercury moves throughout the regional and global atmosphere, and local methylation conditions vary spatially and temporally. In general, forecasts for warmer temperatures, increased fires and melting polar carbon stores, along with increased use of fossil fuels due to human population growth, suggest that monitoring studies would find an uptick in Hg bioavailability. On the other hand, regional reduction in Hg releases and clean-ups of some contaminated sites might predict a decline in biota. Further trends studies are needed to codify appropriate bioindicator species and to identify vulnerable species.

Title 5: Historical patterns in mercury exposure for North American songbirds

Perkins et al. (2020) examines longer historical trends (~150 years) of Hg in North American songbirds. Researchers measured Hg concentrations in flank feathers of historical museum specimens (1869–2014), as well as feathers plucked more recently from living birds (2008–2017). To exclude inorganic Hg used in the past as preservatives, MeHg was measured in the museum specimens, while total Hg was measured in the living bird feathers. Hg concentrations in feathers collected after 2000 averaged 6.6× greater than historic specimens collected before 1900, clearly indicating a historical increase in exposure. The proportion of individual songbirds with feather concentrations that exceeded modeled toxicity benchmarks increased in samples collected after 1940.

Several songbird species in this study have a vulnerable or near-threatened conservation status, suggesting urgency for actions to identify at-risk species and assess whether Hg is affecting their populations. The greatest increase in feather Hg concentrations was observed for the rusty blackbird, a species that has declined by 90% since the 1960s, yet has not yet been the target of concerted conservation efforts.

Title 6: Patterns of blood mercury variation in two long-distance migratory thrushes on Mount Mansfield, Vermont

Rimmer et al. (2020) explored if Hg exposure is decreasing in long-distance migratory songbirds at a high-elevation forest site in Vermont, USA. They detected no consistent change from 2000–2017 in either atmospheric deposition or blood Hg in Bicknell's thrush (*Catharus bicknelli*) or Swainson's thrush (*C. ustulatus*). Sampling date had the

strongest effect on blood Hg concentration in the thrushes, which declined seasonally. There was an absence of a relationship between local atmospheric deposition and blood Hg concentrations, suggesting that, as found by Shanley et al. (2020), Hg cycling dynamics strongly influence bioavailability and montane forest systems are poorly understood in this regard.

This is one of several articles in this special issue that tackle questions at the frontier of our knowledge about Hg and songbirds, and helps to better address which species are good bioindicators for regional Hg deposition, which processes link atmospheric deposition to bioavailability in the food web, and why Hg concentrations in tissue change across the season (Adams et al. 2020; Kopec et al. 2018).

Landscape and management factors

Title 7: Do songbirds in wetlands show higher mercury bioaccumulation relative to conspecifics in non-wetland habitats?

Brasso et al. (2020) questions the dogma that Hg exposure is higher for songbirds living in wetlands than in non-wetland habitats, with a combined field study and review paper. After comparing blood Hg in tree swallows and eastern bluebirds nesting in artificial cavities placed in both habitats, they found that adult tree swallows breeding in wetlands had significantly higher Hg than those in non-wetland areas. However, adult eastern bluebirds did not differ between wetland and non-wetland sites. Reviewing other studies in which the same species was sampled in wetland or non-wetland sites, they found high variation between wetland sites and did not see an overwhelming pattern of wetland-associated songbirds having higher Hg exposure.

The results of this and other studies in this special issue (e.g., Jackson et al. 2020; Shanley et al. 2020) suggest that no single landscape or other factor can predict risk of Hg bioaccumulation. The authors urge caution against the automatic assumption that songbirds occupying wetlands will have higher Hg exposure than conspecifics living in other habitats.

Title 8: Spatial variation in aquatic invertebrate and riparian songbird mercury exposure across a river-reservoir system with a legacy of mercury contamination

Jackson et al. (2020) examines invertebrate and songbird Hg exposure in a long and complex watershed in Oregon, USA. The watershed starts at a Hg-contaminated Superfund site in the headwaters and includes suspected methylation hotspots such as a reservoir and off-channel wetland complexes. Hg concentrations in both aquatic invertebrates and

the songbirds that feed on them varied spatially among habitat categories and taxa. The highest Hg concentrations occurred near the Superfund site, but Hg did not decline linearly with distance from the source of contamination, rather, habitats more prone to methylation tended to produce food webs with higher Hg availability.

This study shows that Hg risk to riparian songbirds can extend beyond point-source contaminated areas, which has been shown in few other studies (e.g., Jackson et al. 2011b, Howie et al. 2018), highlighting the importance of assessing exposure in surrounding habitats, sometimes far downstream, and including adjacent areas such as reservoirs and wetlands.

Title 9: Resolving a paradox—high mercury deposition, but low bioaccumulation in northeastern Puerto Rico

Shanley et al. (2020) resolves an apparent paradox: atmospheric Hg deposition was remarkably high at a montane Mercury Deposition Network site in Puerto Rico, but assimilation into the local avian food web was low, relative to nearby lowlands or North American continental songbird Hg exposure levels. Avian blood Hg concentrations from eight species in five foraging guilds was no more than 0.03 ppm, despite elevated atmospheric deposition of Hg. Avian Hg was significantly greater at a low-elevation site near a wetland compared to an upland montane site. Potential rates of demethylation were 3 to 9× greater than those for Hg(II)-methylation, but rates of change of ambient MeHg pools showed a slight net positive Hg(II)-methylation.

The resolution of the apparent paradox is that MeHg degradation approximately keeps pace with MeHg production in surface soil and sediment at this site. Further, high rainfall flushes any net production of MeHg. The interplay between hydrology and microbial processes appears to shield the local food web from adverse effects of high atmospheric Hg deposition. This scenario may be representative of other humid tropical ecosystems as well, but it is difficult to evaluate because coordinated studies of Hg deposition, methylation, and trophic uptake have rarely been conducted in the tropics.

Title 10: A preliminary assessment of mercury in the feathers of migratory songbirds breeding in the North American subarctic

Stenhouse et al. (2019) quantifies Hg exposure in feathers of 12 migratory songbird species breeding at subarctic latitudes, in Denali National Park, interior Alaska, USA. Feathers were collected throughout the breeding season, and, in most species, represented Hg accumulation in the breeding range. Overall, Hg exposure, as measured through feathers, was relatively low for songbirds breeding in the subarctic, with only a few individuals exceeding concentrations associated with deleterious effects.

Most published research on Hg in songbirds has been carried out at temperate latitudes on a relatively small number of well-studied species, or with a laboratory model songbird, the zebra finch. If Hg is indeed a threat to songbird populations, as suggested by some of the papers in this special issue, it will be imperative to carry out more studies like this one, in remote regions, on under-represented landscapes, and with poorly studied species.

Title 11: Wetland water-management may influence mercury bioaccumulation in songbirds and ducks at a mercury hotspot

Winder et al. (2020) makes use of a water-level manipulation to examine the role of four water management classifications on Hg bioaccumulation in two songbird species (common yellowthroats, *Geothlypis trichas*, and Nelson's sparrows, *Ammodramus nelsoni*) and three waterfowl species at a National Wildlife Refuge complex, in North Dakota, USA. Nelson's sparrow blood Hg concentrations were elevated and similar to those reported six years previously for the same population, indicating no reduction in exposure. Mercury in songbird blood and duck eggs varied among wetland water-management classifications. Songbirds and ducks had lower Hg concentrations in wetlands that were drawn down compared to individuals occupying isolated-depressional wetlands, with no outflow. In addition, songbirds within impounded and partially drawn-down wetlands had lower blood Hg concentrations than those in isolated, depressional wetlands with no outflow.

This study suggests that, although wetlands are often hotspots for songbird exposure to MeHg, even far from point sources of pollution, water management can have significant effects on methylation and bioaccumulation. Applied research like this study, on efficacy of management techniques in altering Hg bioavailability, is surprisingly scarce and needed.

Migration

Title 12: Mercury exposure in migrating songbirds: correlations with physical condition

Adams et al. (2020) asked whether a suite of migrating songbirds show effects of Hg exposure and whether this changes over time. Over a 4-year study, they examined migrants at a stopover site on Key Biscayne, Florida, USA and tested for correlations between measures of physiological condition and Hg concentrations in blood (spring) or feathers (fall). They found that blood Hg concentration decreased in birds sampled later in the day, and feather Hg varied across the fall migration, being high in early migrants of some species and late arriving individuals of other

species. The relationship between Hg concentrations in songbird blood and feathers and body condition was complex and deserves further study. This was especially true in fall, when breeding ground Hg (measured in feathers) could have devastating effects on first-time migrants. In spring, there was evidence suggesting that Hg exposure and physical condition are weakly correlated but the effect was not significant when examining fat score or pectoral muscle thickness. However, even minor losses in weight could have profound effects on survival during migration, as well as carryover effects during breeding.

This study is one of several that are attempting the difficult task of interpreting seasonal or temporal changes in Hg concentrations with respect to what it means for individuals. Longitudinal studies would be preferable, but at this point the technology is not available to track and resample large numbers of small birds so we must interpret individual fitness effects from population-level patterns.

Title 13: The threat of global mercury pollution to bird migration: potential mechanisms and current evidence

Seewagen (2020) synthesizes the literature on the physiological effects of Hg in non-migrating birds and taxa other than birds to form hypotheses on potential mechanisms by which Hg might hinder songbird migration and affect survival. Mercury, through its destabilizing effect on proteins, especially those forming enzymes, has potential to disrupt many essential physiological processes that make long-distance migration possible, including navigation, magnetoreception, flight endurance, oxidative balance, and stop-over refueling. Migration performance and possibly survival might also be limited by the effects of Hg on the immune system at a time when exposure to novel pathogens and parasites is at its greatest.

Mercury pollution is likely to be further challenging the songbird annual cycle, potentially contributing to global declines in migratory bird populations. This synthetic review sounds the alarm for the importance of considering migration behavior and its associated physiological and neurological adaptations as ecotoxicological risk factors, and recent empirical studies (e.g., Ma et al. 2018a, b) have already provided supporting evidence to bolster this case.

Title 14: Explaining variation in Colorado songbird blood mercury using migratory behavior, foraging guild, and diet

Knutsen and Varian-Ramos (2020) examines interspecific variation in blood Hg levels in songbirds of various foraging guilds in a single watershed in Colorado and discovers that certain species had blood Hg concentrations over 75 times higher than other species. Trophic level was an important factor, with invertivores having the highest blood

Hg levels, but ground foragers and long-distance migrants also had higher Hg concentrations than other species.

Studies that compare a suite of species in the same geographic area (e.g., Keller et al. 2014) are surprisingly scarce, and very valuable because they can be used to start to piece together relative risk of each species, something not possible when comparing species sampled from different landscapes, years or seasons. This study can inform biologists which species to select as indicators of Hg pollution in future projects, and similar to other studies in this special issue, points to migration as an emerging risk factor.

Use of songbirds as bioindicators

Title 15: Songbird feathers as indicators of mercury exposure: high variability and low predictive power suggest limitations

Low et al. (2020) examines the reliability of feathers for Hg monitoring and concludes that despite their widespread current use in the literature (e.g., Peterson et al. 2019), feathers are sometimes not a suitable sampling matrix for Hg monitoring in songbird species. All birds used in this study died from accidents such as car and window collisions in Oregon, USA. Researchers examined variation in Hg among tissues including feathers from six tracts, nails, liver, and muscle; in thrushes and sparrows, and concluded that Hg concentrations in all feather tracts and nails were higher than in the liver and muscle, and Hg was higher in the thrushes than in the sparrows. Variation between feather tracts on the same bird was high, and feathers were not reliable predictors of internal tissue Hg concentrations. Because the birds were not collected at the site where feathers were grown, dispersal and migration likely increased the complexity for using feathers as biomonitoring tissues.

Toenails better predicted internal tissue Hg concentrations in the thrushes and sparrows than did feathers. Nails are more commonly used to monitor Hg in mammals and reptiles but may not be an effective sampling option for songbirds because the collection of sizable nail mass could be harmful. This study underscores the care that must be taken in choosing proper tissues for monitoring, and also the importance of understanding geographic variation and species life history and behavior when interpreting Hg exposure and predicting deleterious effects.

Application: songbirds as bioindicators of mercury in the environment

With the emergence of a better understanding of Hg in songbirds (in part based on this special issue), appropriate

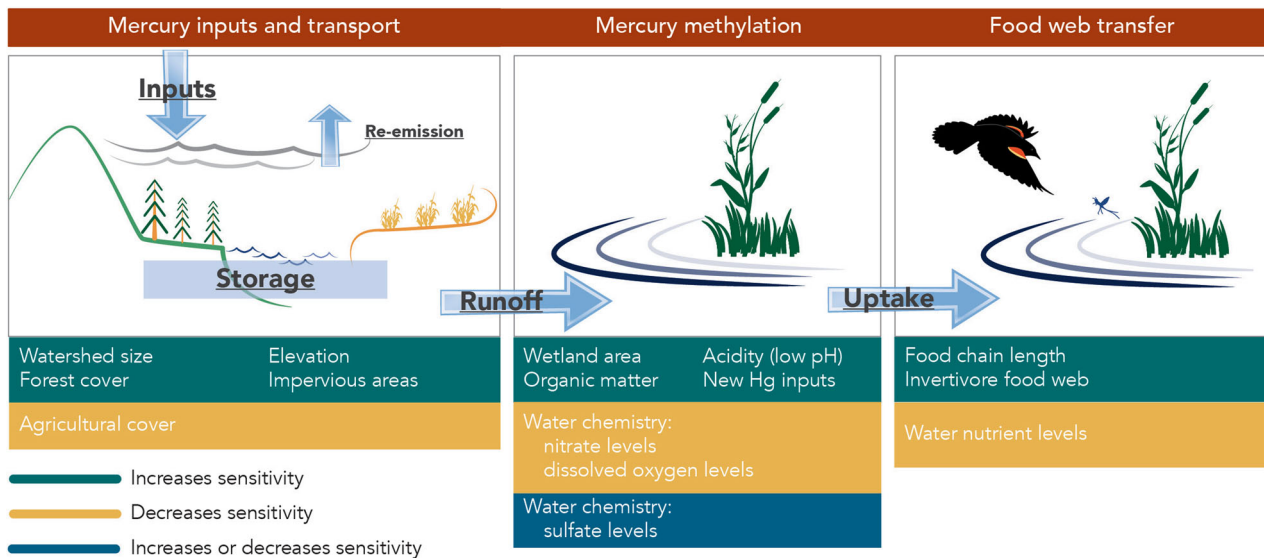


Fig. 1 Watershed Hg sensitivity connects landscape features related to Hg input and transport, methylation potential, and food web transfer

bioindicators can be identified for properly assessing risk and tracking Hg in the environment. An ability to standardize the use of bioindicators is key for policymaking and landscape management needs. An important facet for the use of bioindicators is the knowledge of effect levels. Based on studies to date, there are 20 laboratory studies that have identified adverse impacts from MeHg, including immune and endocrine functions, neurological impacts, and reproduction (Table 1). These laboratory studies have been important in relating findings to field conditions, where 24 studies have identified adverse impacts from MeHg to body condition and immune function (Table 1).

The findings in this special issue combine with the existing literature to provide a basis for creating and defining a ranking matrix that could be used to identify risk to songbird species. Variables that have been identified as important for assessing the suitability of a bioindicator include: (1) habitats used during either the breeding or non-breeding seasons; (2) foraging preferences during either the breeding or non-breeding seasons; and (3) migration distance.

The type of habitat use during the breeding season has an important influence on the methylation process and subsequent Hg availability in food webs. Moist habitats, such as wetlands, have a far greater propensity for Hg to methylate than xeric habitats, and therefore species that are foraging within wetland habitats tend to be exposed to MeHg at the highest levels within a landscape (Evers et al. 2005; Jackson et al. 2015), although wetlands are variable in methylation abilities (Hall et al. 2020). Additionally, forested habitats have a greater ability to scavenge air Hg and increase dry deposition over non-forested habitats in both temperate (Driscoll et al. 2007; Jackson et al. 2015) and tropical systems (A. Gerson, unpublished data). So,

forested landscape combined with wetlands that regularly include wet-dry cycles (intra- and inter-season) and are acidic with organic matter have greater MeHg availability than alkaline and agricultural areas (Fig. 1).

The biomagnification of MeHg is closely related to trophic level because MeHg concentrations are highest in the upper trophic levels and in terrestrial ecosystems, and invertivorous songbirds often occupy some of the highest trophic levels (Evers et al. 2005; Abeyasinghe et al. 2017; Luo et al. 2020). Songbirds that regularly forage on predatory invertebrates (e.g., spiders; Cristol et al. 2008) are at the highest trophic level and therefore maintain the greatest body burdens of MeHg.

High body burdens of Hg may be exacerbated by migration, and we predict that the greater the distance the more chance that Hg will interact negatively with the demands of migration (Seewagen 2020). While the initial Hg body burden of a neotropical or palaeotropical migrant is important for a songbird's fitness level for completing its migration, the levels of MeHg bioavailability at the destination habitat are also important within a bird's annual cycle. While the exposure to MeHg in temperate areas is increasingly understood as an important risk to certain breeding songbird populations and species, the exposure in their non-breeding areas is not. And, for many long-distance migrants, winter habitats are increasingly becoming Hg hotspots because of emerging activities related to artisanal small-scale gold mining, such as in Peru (Markham and Sangermano 2018; Diringer et al. 2019), and legacy or ongoing contamination from industrial sources, such as in China (Abeyasinghe et al. 2017).

Ultimately, the selection of songbird bioindicators for assessing and monitoring environmental Hg loads is

dependent on a number of factors including: (1) objective (e.g., to identify spatiotemporal trends or assess conservation concern), (2) ecological attributes such as landscapes occupied (e.g., breeding, migration and non-breeding), and geographical distribution across its annual life cycle, and (3) potential ability for bioaccumulation over the individual's lifetime. The choice of indicator biota is actively being assessed now to fulfill the long-term obligations of a global multilateral treaty, the Minamata Convention on Mercury (Evers and Sunderland 2019), and to connect biotic dietary uptake of MeHg with differing source types of Hg (using Hg isotopes; Tsui et al. 2018). The findings of this special issue significantly further that goal.

Compliance with ethical standards

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

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