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Foraging Ecology Differentiates Life Stages and Mercury Exposure in Common Terns (*Sterna hirundo*)

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ABSTRACT

Some populations of common terns (*Sterna hirundo*) breeding at inland lakes in North America are declining, including the Laurentian Great Lakes. Terns nesting at inland colonies forage in freshwater during the breeding season and primarily in coastal marine environments during the nonbreeding season. As piscivores, they are susceptible to dietary Hg exposure. To characterize patterns of Hg exposure in this population, we 1) quantified within and among season differences in total mercury (THg) concentrations (μg/g) in blood and feathers at 2 Lake Superior breeding colonies, and 2) documented spatial and temporal variation in exposure by studying adult foraging ecology using geospatial tracking devices and stable isotopes. We used general linear models to assess the relationship between isotopic composition and THg concentrations in bird tissues relative to sex, age, colony location, and season. The THg concentrations were lowest in winter-grown feathers (geometric mean [95% confidence limits]): 1.32 (1.09–1.59) μg/g dw ($n = 60$), higher at the more industrially influenced colony (chick feathers: 4.95 [4.62–5.37] μg/g dw [$n = 20$]), and increased with a riverine-based diet. During the breeding season, Hg exposure varied along a gradient from lake to river, with adult females having lower blood THg concentrations than males (females: 0.83 [0.67–1.03]) μg/g ww ($n = 7$); males: 1.15 (0.92–1.45) μg/g ww ($n = 5$). Stable isotope values suggested adults obtained 42 ± 12% ($n = 12$) of their diet from the river during incubation, which was validated with tracking data. During chick-rearing, chicks obtained 68 ± 19% ($n = 44$) of their diet from the river. Our results indicate colony location, foraging behavior, and season influenced Hg exposure for these Lake Superior colonies and underscores the importance of local contamination with respect to exposure. *Integr Environ Assess Manag* 2020;00:1–13. © 2020 SETAC

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INTRODUCTION

Many wild bird populations worldwide require conservation and management efforts to mitigate the effects of anthropogenic disturbance, such as habitat loss and pollution, to slow population declines. Colonial waterbirds often concentrate in highly urbanized coastal environments where impacts from humans are concentrated but distributed heterogeneously, making conservation and management efforts challenging. Pollution of coastal waters from industrial contaminants negatively affects waterbird populations; however, sources of contamination and pathways of exposure are not well documented for most species (Eagles-Smith et al. 2018). Mercury contamination negatively impacts the breeding success (e.g., lowered hatching success) of many bird species, particularly those that forage in wetlands, where anaerobic microorganisms convert inorganic Hg to MeHg, a potent neurotoxin (Evers 2018). Correlations between Hg exposure and adverse outcomes, such as impaired reproduction, have been documented in many avian species, including common terns (*Sterna hirundo*) (Ackerman et al. 2016).

The common tern is a long-distance migratory waterbird that primarily eats fish. Waterbird populations have been declining in many locations worldwide (Wetlands International 2010), including common tern populations in the North American Laurentian Great Lakes region (hereafter, Great Lakes) (Szczys et al. 2017). Common terns are vulnerable to changes in availability of prey fish, water-level fluctuations, disturbances from coastal development, and contamination from environmental and food-related sources (Cabot and Nisbet 2013). The common tern is a species of

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concern in the Great Lakes, where most active colonies occur at managed sites (Arnold et al. 2020). Estimates of population size indicate this species was common in the region from 1900–1960, with long-term decreases in nest numbers and colony sites occurring since the 1960s (Arnold et al. 2020). Reasons for the decline are not well understood, but habitat loss and degradation are thought to be important factors (Cuthbert et al. 2003; Szczys et al. 2017).

Regional accumulation and bioavailability of Hg in aquatic systems can be influenced by differences in rates of atmospheric deposition, point-source pollution, and habitat type (Wiener et al. 2012). Migration patterns also influence exposure risk, as contaminant accumulation rates and availability vary across ecosystems in space and time (Chételat et al. 2020). The primary source of Hg accumulation in the Great Lakes region is atmospheric deposition (Evers et al. 2011). Despite efforts to reduce Hg emissions, concentrations in some fish and bird species are increasing in some locations in the Great Lakes region, particularly in northern regions where environmental conditions (e.g., low pH and high dissolved organic matter) increase the bioavailability and biomagnification of Hg (Evers et al. 2011). Although the Hg in surface waters of the Great Lakes is low, concentrations exceeding the Great Lakes Initiative aquatic life guidelines (0.77 µg/L) have been measured in Lake Superior near the Duluth-Superior harbor (Dove et al. 2012). The St. Louis River (SLR), a ~4,900 ha waterway, flows through the Duluth-Superior harbor into Lake Superior. The Hg concentrations in secondary consumers from these systems are higher in the SLR versus Lake Superior by ~2:1 (Omara et al. 2015; Jeremiason et al. 2016). Thus, there exists a potential Hg dietary-exposure gradient from high concentrations within the SLR to low concentrations in Lake Superior waters.

Notably, isotopic mixing of riverine to nearshore Lake Superior waters results in a gradient of $\delta^{13}C$ values in the food web from the SLR to Lake Superior, which allows for the assignment of habitat-specific diet contributions along the river-lake continuum (Hoffman et al. 2010). Further, $\delta^{15}N$ values in the riverine portion reflect terrestrial watershed nitrogen inputs, whereas effluent from a municipal wastewater treatment facility (<1.5 km from 1 of the breeding colonies) is highly ^{15}N-enriched, resulting in a distinct isotopic signature near the river mouth, while Lake Superior nitrate is highly ^{15}N-depleted owing to its origin (nitrification in sediments), giving Lake Superior a distinct isotopic signature (Hoffman et al. 2012). In turn, habitat-specific diet contributions can be used to determine whether Hg exposure varies with respect to the diet contribution from inshore (riverine) and nearshore (Lake Superior) habitats.

Although not all bird species exhibit chronic adverse effects associated with dietary Hg exposure (Evers 2018), the impact of Hg on fish and wildlife in the Great Lakes region is a concern, as the number of bird species reported to be adversely affected has increased significantly in recent decades (Evers et al. 2011). Fish-eating birds are known to be at risk of exposure to Hg due to biomagnification (Evers 2018). Assessing the significance of this risk requires knowledge of foraging behavior and how this behavior changes throughout a bird's life. Common terns are generalist foragers and typically feed within ~20 km of their breeding colony (Arnold et al. 2020). In freshwater systems, they almost exclusively consume small prey fish, plunge-diving in open waters, usually within 1 km of the shoreline (Arnold et al. 2020). Biological factors that potentially affect Hg exposure in birds include age, sex, and diet. Mercury concentrations often increase with age, are lower for females, and increase with trophic position (Chételat et al. 2020).

Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) are assimilated in body tissues and can reveal dietary and habitat preferences during different life stages (Chételat et al. 2020). Both $\delta^{13}C$ and $\delta^{15}N$ have been used to identify important avian foraging habitats, particularly in aquatic environments where isotopic signatures vary along a gradient (Chételat et al. 2020). They have also been used to track both local- and large-scale movements of migratory species that travel between isotopically distinct food webs (Hoffman 2016). Trace elements, such as Hg, also concentrate in body tissues and have been shown to be positively correlated with the selection of prey items and their associated locations within aquatic habitats (Chételat et al. 2020). Therefore, avian body tissues are valuable for identifying foraging locations used during different life stages based on $\delta^{13}C$ and $\delta^{15}N$ values and for assessing exposure to trace elements, such as Hg (Chételat et al. 2020). Additionally, geospatial tracking devices such as global positioning system (GPS) tags and solar geolocators can track bird movement at multiple spatial scales (Burger and Shaffer 2008); when coupled with stable isotope data, these technologies can verify habitat use and determine year-round Hg exposure risk of migratory species, including common terns.

Our study system was 2 neighboring common tern colonies in Lake Superior, Interstate Island, in the Duluth-Superior Harbor (Minnesota and Wisconsin, USA) and Ashland Island in Chequamegon Bay, Ashland, Wisconsin, USA. Both are high priority breeding sites in the Great Lakes (Cuthbert et al. 2003), and both are located in areas where historically high levels of industrial activity have led to the contamination and degradation of local ecosystems (Custer et al. 2018).

Study approach

Feathers have been used as bioindicators of exposure to trace elements for many avian species and to assess spatial and temporal variation in contaminant exposure (Evers 2018; Chételat et al. 2020). Feathers are inert tissues that reflect exposure to Hg at the time they were grown, so knowing the molt schedule of a species is crucial to identifying exposure risk (Chételat et al. 2020). The THg concentrations in adult feathers indicate dietary intake at the time of the last molt and can estimate chronic exposure and carryover among seasons (Chételat et al. 2020). Feathers have also been shown to be a reliable indicator of MeHg in

blood (Evers 2018). Chick feathers indicate dietary intake when the feathers are first grown (i.e., during the breeding season, when adults feed their young). Blood, in contrast to feathers, is a metabolically active tissue that indicates short-term Hg exposure (Chételat et al. 2020).

We characterized overwintering habitat use based on $\delta^{13}C$ and $\delta^{15}N$ values measured from adult flight feathers, which are grown during the nonbreeding season (February–April) (Arnold et al. 2020). Stable isotope ratios and THg concentrations from winter-grown feathers were compared between colonies and in reference to known wintering locations (Bracey et al. 2018). We expected seasonal shifts in stable isotope ratios based on differences in marine and freshwater foraging habitats, wherein adult feathers have high $\delta^{13}C$ values, indicative of their marine diet during the nonbreeding season, compared to low $\delta^{13}C$ values in adult blood, indicative of their freshwater diet during the breeding season (Hobson et al. 2000). We also expected adult feather THg concentrations would increase with age due to cumulative effects of exposure but not differ between colony sites because they are part of the same breeding population, and adults spend the winter in similar habitats (Bracey et al. 2018). Additionally, we expected adult females to have lower blood THg concentrations than males because females depurate Hg into eggs (Chételat et al. 2020).

We collected blood from adults nesting at Interstate Island and breast feathers from chicks hatched at both colonies to estimate Hg exposure during the breeding season. In the context of our study, we define exposure as "Hg obtained from diet" and we use chick feathers as a proxy for adult foraging during the chick-rearing phase of the breeding season. We identified foraging locations using 2 complementary tagging methods: geolocation by global positioning system (GPS) (i.e., an external tag) and by $\delta^{13}C$ and $\delta^{15}N$ values (i.e., an intrinsic tag). We subsequently determined if THg concentrations were significantly related to foraging location (as indicated by $\delta^{13}C$ values), trophic level (as indicated by $\delta^{15}N$ values), sex, or age. Between colonies, due to higher levels of historical and present-day industrial activity in the SLR relative to Chequamegon Bay, we expected THg concentrations to be higher in chicks hatched at Interstate Island compared with Ashland Island. Similarly, within the Interstate Island colony, due to the widespread historical sediment Hg contamination in the SLR near the breeding site, we expected that adults or chicks that obtained a greater diet contribution from the SLR (relative to nearshore Lake Superior) would have elevated THg concentrations. We did not expect similar within-colony variation at Ashland Island because a comparable habitat-based difference in Hg contamination does not exist within Chequamegon Bay. Because a distinct isotopic gradient does not exist within Chequamegon Bay (Hoffman et al. 2015a), we could not take an equivalent analytical approach with Ashland Island birds.

Our first objective was to determine if between-colony differences exist in foraging habitat use by adult common terns during the nonbreeding season, and to compare Hg exposure during the nonbreeding season to exposure during the breeding season. To address this objective, $\delta^{13}C$ and $\delta^{15}N$ values were measured in samples reflecting various life stages to associate diet with THg concentrations. Our second objective was to determine if between- or within-colony differences exist in adult foraging habitat use during the breeding season and, if so, whether foraging behavior influenced Hg exposure relative to age, sex, or trophic position. To address this objective, we used the $\delta^{13}C$ and $\delta^{15}N$ values and THg concentrations obtained from blood and feather samples in conjunction with on-bird tracking devices to identify foraging locations and determine habitat-specific exposure.

Identifying the relationship between foraging behavior, foraging habitat use, and Hg exposure provides a rough estimate of risk. Direct comparison of THg concentrations between tissue types is not appropriate, and the use of available conversion equations is tenuous and fraught with interpretive caveats. There are limitations to how we can interpret risk based on our data, as there are both proponents (Zabala et al. 2019) and critics (Chételat et al. 2020) regarding the use of feathers to do so. Therefore, we chose to assess risk based on literature review of tissue-specific concentrations and their associated toxicological risk thresholds simply to provide context in evaluating the potential importance of our results, which could have management and conservation implications for these vulnerable populations.

MATERIALS AND METHODS

Study area

Data were obtained at the only 2 consistently active common tern breeding colonies in Lake Superior (Cuthbert et al. 2003; Bracey et al. 2018), which are ~96 km apart, situated near the western tip of Lake Superior (Supplemental Data Figure S1): Interstate Island (46.75°N, 97.08°W), located in the Duluth-Superior harbor (Minnesota and Wisconsin, USA), and Ashland Island (46.61°N, 90.87°W), located in Chequamegon Bay, Ashland, Wisconsin, USA. While both locations have a legacy of historical pollution, the Duluth-Superior harbor became a major shipping port in the early 1900s that attracted mining, pulp mills, heavy industry, and a relatively large human population (Crane and MacDonald 2003), which has contributed to the present-day Hg burden in the SLR. Interstate Island is a ~2 ha dredge-spoil island that is a designated Wildlife Management Area jointly managed by the Minnesota and Wisconsin Departments of Natural Resources (DNR; Supplemental Data Figure S1). The average number of nesting pairs from 1989 to 2018 ± 1 standard deviation (SD) is 185 ± 50. The number of nesting pairs at Interstate Island has varied from a low of 81 pairs (1989) to a high of 302 pairs (2011), and it is currently in the mid-low 100s. (2015–2020). Ashland Island is a ~0.03 ha reconstructed pier remnant that is managed by the Wisconsin DNR (Supplemental Data Figure S1). The

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average number of nesting pairs from 1984 to 2018 ± SD is 114 ± 29. The number of nesting pairs at Ashland Island has varied from a low of 48 pairs (1980) to a high of 172 pairs (1989), and it is currently in the low 100s (2015–2020).

Biological sampling

During the 2016 breeding season (June–July), adult common terns were captured during incubation using methods described in Bracey et al. (2018) and chicks were captured by hand. Each colony was visited every 5–7 d. All adults captured and included in this study had been previously banded and therefore of known age. Chicks were fitted with a United States Geological Survey (USGS) stainless steel leg band when first encountered, and age was estimated based on plumage characteristics (Wails et al. 2014), using mean age in days for each plumage class. Adults that were fitted with tracking devices were captured and handled twice during peak incubation (from 30 May to 12 June). On first capture, we deployed the tracking devices and on second capture (Interstate Island: 11 June, Ashland Island: 12 June), we removed the tracking devices and took blood and/or feather samples. All other adults were handled once during this time period to draw blood and or take a feather sample. Feather samples were collected from chicks twice from June to July, but only 1 sample per bird was included in the Hg analysis. We included paired feather samples from a subset of individuals ($n = 10$) in the stable isotope mixing model to examine the effect of within-individual variation. Maximum handling time for adults was ~10 min and for chicks was ~3 min.

During the 2016 breeding season, we collected blood samples (Interstate Island; $n = 18$) and second secondary flight feathers (Interstate Island; $n = 39$, Ashland Island; $n = 21$) from adults and breast feathers (Interstate Island; $n = 20$, Ashland Island; $n = 20$) from chicks (Supplemental Data Table S1). Blood and feather samples were collected following the methods of Evers (2009). Adult blood samples were collected by venipuncture of the cutaneous ulnar vein (25 g needle; minimum 0.2 cc of blood per tube, ~3 capillary tubes per bird, stored at −18 °C). Second secondary adult flight feathers were clipped from each wing (2 feathers total per bird), along the calamus. For chicks, ~2 to 3 body feathers were removed from the breast. All feather samples were stored at room temperature in ⅜ × 6″ clasp envelopes. The sex of the adult birds was determined by genetic analysis via a blood sample using the chromo-helicase-DNA binding protein gene (Zoogen Services, Inc., Davis, California, USA). The sex of the chicks was not determined in this study.

During the 2017 breeding season (June–July), we did not collect any additional blood or feather samples from adults. We did collect 2–3 body feathers from chicks (Interstate Island $n = 15$; Ashland Island $n = 14$) using the same methods described earlier. These feather samples were analyzed for stable isotopes only (Supplemental Data Table S1). We also collected intact regurgitated prey fish, which were opportunistically sampled from chicks at both colonies (Supplemental Data Table S2).

Global positioning system (GPS) tag deployment

In 2016, archival GPS tags (*Lotek: PinPoint-50 version V4.16*) were attached to adult terns breeding on Interstate Island ($n = 10$; deployment 30 May to 11 June) and Ashland Island ($n = 9$; deployment 2 June to 12 June). Deployment was restricted to this time period to ensure birds could be reliably recaptured. GPS tags were fitted using a pre-constructed leg-loop harness (Mallory and Gilbert 2008), and the total weight was <3% of the birds' body weight (<4.0 g). Tags recorded discrete daily fixes (i.e., locational data for a specific point) every 30 min from 06:00 to 22:00 CDT. Locational data included latitude, longitude, Greenwich mean time (GMT) and local date and time ([Central Daylight Time [CDT]), dilution of precision (DOP, an indicator of GPS position quality), and number of satellites. The DOP values ≤5 are considered accurate and any estimate >20 poor; fixes with DOP values ≥20 were excluded. Only GPS locations that occurred over water (where birds forage) were included in point density maps, and we assumed the primary purpose for flight from the colony during incubation was for individuals to forage for themselves or for their mates. For Interstate Island, habitat use was estimated as the proportion of GPS fixes in Lake Superior relative to locations in the SLR. Because the breeding site is located in the river mouth, some fixes in the river may be from birds flying from the breeding site to Lake Superior to forage. Therefore, proportions may underrepresent their preference for Lake Superior. As it was not possible to account for behavior, all fixes over water were included. At the Ashland Island colony, all locations were in Chequamegon Bay.

Hg quantification

Laboratory analysis of THg in blood and feather samples was conducted at the Biodiversity Research Institute Toxicology Lab (Portland, Maine, USA), following methods described by Evers et al. (2005). Because common terns have a primarily fish-based diet and most Hg in fish tissue exists in a methylated form (Rai et al. 2002), we used THg concentrations as a proxy for MeHg exposure. Feathers were run whole and not washed prior to analysis, as per Keyel et al. (2020). Blood samples were analyzed wet. Blood and feather THg concentrations were measured using a thermal decomposition and atomic absorption spectrophotometry technique (EPA method 7473) with a direct Hg analyzer (DMA 80, Milestone Incorporated). The DMA 80 was calibrated using Hg standards. Blood THg concentrations are reported as wet weight (μg/g ww), and feather THg concentrations are reported as dry weight (μg/g dw). Certified reference materials (DOLT-5, CE-464; National Research Council, Ontario, Canada) and procedural blanks were analyzed at the start of each sample run and after every 20 samples to ensure consistent analytical precision and accuracy. Mean ± SD of certified reference materials were 0.423 ± 0.013 ppm for DOLT-5 ($n = 25$) and 5.27 ± 0.090 μg/g for CE-464 ($n = 25$). For blood samples, percent recovery of certified reference materials was within 10% (DOLT-5: 99%,

CE-464: 101%) and precision, measured as relative percent differences (RPD) between randomly selected duplicate samples ($n = 1$), was within 10% (8.24%). For feather samples, percent recovery of certified reference materials was within 10% (DOLT-5: 96%, CE-464: 100%) and RPD of duplicates ($n = 6$) was within 10% (range = 0.49% to 9.67%, mean 4.96%). All samples exceeded the method detection limit (0.001 mg/kg).

Stable isotope analysis

Adult common tern blood samples ($n = 12$) from Interstate Island were dried in clean, glass vials (50 °C for >48 h). Feather samples collected from adults (Interstate: $n = 7$; Ashland: $n = 15$) and chicks (Interstate: $n = 14$; Ashland: $n = 21$ [2016: $n = 7$, 2017: $n = 14$]) were cleaned using dichloromethane methanol (2:1 CH_2Cl_2:CH_3OH) and dried in clean, glass vials (50 °C for >48 h). A subsample of regurgitated prey fish species was processed for stable isotope analysis (Supplemental Data Table S2). Fish were stored in a cooler in the field, rinsed in deionized water (DI), placed in glass vials, and stored frozen (−18 °C). Dorsal muscle tissue samples were removed from each fish; rinsed in DI water; dried in clean, glass vials (50 °C for >48 h); and ground. Dried blood, feather, and fish muscle samples were weighed to 1.0 ± 0.1 mg and placed in tin capsules for C and N stable isotope analysis.

Samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (University of California Stable Isotope Facility). Laboratory standards were calibrated against NIST Standard Reference Materials (IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65). The long-term standard deviation of laboratory standards is 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Stable isotope ratios are expressed in standard δ notation and calculated relative to international standards VPDB (Vienna PeeDee Belemnite) and Air for $\delta^{13}C$ and $\delta^{15}N$, respectively. The analytical error, measured as the mean standard deviation (SD) of replicate laboratory reference materials (G- 6, 13, 20, and 21), was <±0.10‰ for both $\delta^{13}C$ and $\delta^{15}N$, confirming samples were within the accepted parameters.

Stable isotope mixing models

We used a 2-stable isotope ratio ($\delta^{13}C$, $\delta^{15}N$) mass balance mixing model (Phillips and Gregg 2001) to describe habitat use by Interstate Island colony birds. Mixing models were used to translate adult blood ($n = 12$) and chick breast feather ($n = 44$) stable isotope data (corrected for diet-tissue isotopic discrimination) into estimates of habitat use based on prey fish consumption. The prey fish data used to estimate model sources were from previous studies (Hoffman et al. 2010, 2015a) and chosen based on 3 criteria: 1) the prey fish species were among those commonly found regurgitated by chicks during this study; 2) the fish were sampled during the breeding season (April–June); and 3) the fish were captured from 1 of 3 isotopically distinct locations (Lake Superior, Superior Bay, and Allouez Bay; Supplemental Data Figure S2A and C), within the areas frequented by adults. Thus, the model sources represent the most probable locations in the river and lake where terns foraged based on GPS and observational data.

For Lake Superior, we used mean $\delta^{13}C$ and $\delta^{15}N \pm SD$ values of rainbow smelt (*Osmerus mordax)* from Lake Superior caught from just outside the SLR mouth and which were identified to have a Lake Superior-specific isotopic composition (Hoffman et al. 2015a) ($n = 19$; $\delta^{13}C = -22.00 \pm 0.87$ and $\delta^{15}N = 5.0 \pm 0.2$). For Allouez Bay, we used data from rainbow smelt caught within Allouez Bay and which were identified to have a bay-specific isotopic composition (Hoffman et al. 2015a) ($n = 6$; mean $\delta^{13}C = -32.00 \pm 0.60$ and $\delta^{15}N = 9.4 \pm 0.5$). For Superior Bay, we used similar data from trout-perch (*Percopsis omiscomaycus*) captured near Interstate Island, which also had a location-specific isotopic composition (Hoffman et al. 2010) ($n = 4$; mean $\delta^{13}C = -27.00 \pm 0.80$ and $\delta^{15}N = 10.8 \pm 0.5$).

The source mean $\delta^{13}C$ and $\delta^{15}N$ values were used in the mixing model to calculate the proportional contribution from each habitat (Lake Superior, Superior Bay, and Allouez Bay) to adult blood and chick feather isotopic ratios. The mixing polygon defined by the source-specific means represents the isotopic range of forage fish available to common terns breeding on Interstate Island (Supplemental Data Figure S3). Prey fish $\delta^{13}C$ values were not lipid corrected because fish tissue samples were low in lipid content (molar C:N < 4.0) (Hoffman et al. 2015b). To correct feather and blood isotopic ratios in the model for diet-tissue isotopic discrimination, we used the mean discrimination value for $\delta^{13}C$ (feather: +0.2‰, blood: –0.3‰) and $\delta^{15}N$ (feather: +3.0‰, blood: +3.1‰) based on captive-raised gulls fed a fish-only diet (Hobson and Clark 1992). To ensure error estimation was properly assessed, we calculated a standard deviation for the contribution from each location, for each blood or chick breast feather sample, using linear error propagation, which accounts for both source and mixture variability (Phillips and Gregg 2001). A few common tern $\delta^{13}C$ and $\delta^{15}N$ values fell outside the mixing polygon; we preferentially fit $\delta^{15}N$ values because small deviations in trophic level have a much larger effect on the consumer's $\delta^{15}N$ value than $\delta^{13}C$ value. The mean absolute fit value for $\delta^{15}N$ was 0.3‰ (SD = 0.1‰, $n = 9$) for feathers and 0.9‰ (SD = 0.7‰, $n = 5$) for blood. No adjustments were necessary for $\delta^{13}C$. Models fit to adult blood or chick breast feather $\delta^{13}C$ and $\delta^{15}N$ values were constrained between 0 to 1. We calculated proportion of "riverine" diet as the sum of Superior Bay and Allouez Bay contributions.

Trophic level is 1 factor that could influence Hg accumulation; therefore, we estimated the trophic level of common tern chicks based on mean $\delta^{15}N$ values of chick breast feathers at each colony relative to the local $\delta^{15}N$ baselines, which was based on particulate organic matter (POM) data sampled near each colony from Hoffman et al. (2015a).

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Estimation of the trophic level of chicks hatched at Interstate Island was restricted to include only feather samples analyzed for THg and with $\delta^{13}C$ values <−26.00, which reflect a riverine diet (Hoffman et al. 2010).

Statistical analyses

The number of samples analyzed for THg and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) varied among sample type (blood or feather), age class (adult or chick), colony location (Interstate or Ashland islands), and year (2016 or 2017; Supplemental Data Table S1). We used general linear models (GLMs) to assess the relationship between natural log-transformed (ln [THg]) concentrations in blood and feathers to isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) and sex and age (when known) for each colony location (Table 1). Sample year was not included as a variable in the GLMs because only data from 2016 were included. In 2017, samples were collected for stable isotope analysis only to inform the Interstate Island mixing model (chick feathers) and to determine trophic status between colonies (prey fish samples). Variable importance was determined using Akaike's Information Criterion, corrected for small sample size (AIC_c), and top models were selected according to minimum AIC_c values (Burnham and Anderson 2002). For the Interstate Island samples, we used the proportion of riverine diet contribution rather than either $\delta^{13}C$ and $\delta^{15}N$ values, since both isotopic ratios were

Table 1. Relative performance of general linear models (GLM)[a]

Candidate models	β	K	logLik	AIC_c	ΔAIC_c	Wt
(A) Nonbreeding—adult feathers						
$\delta^{13}C$	−3.97	3	−14.75	36.84	0.00	1.00
Intercept only	0.25	2	−24.38	53.39	16.55	0.00
Colony	0.35	3	−23.90	55.14	18.30	0.00
$\delta^{15}N$	1.02	3	−24.27	55.88	19.04	0.00
Sex	0.66	4	−23.08	56.51	19.67	0.00
Age (y)	0.33	11	−18.91	86.21	49.37	0.00
(B) Breeding—adult blood						
Proportion river + sex	−0.67	4	6.89	−0.07	0.00	0.69
River	−0.66	3	3.21	2.58	2.65	0.18
Sex	−0.18	3	2.61	3.78	3.85	0.10
Intercept only	−0.05	2	−0.47	6.27	6.34	0.03
Age (y)	−0.09	9	8.08	91.83	91.90	0.00
Proportion river + age	−0.48	10	8.90	222.19	222.26	0.00
Age + sex	−0.23	10	8.60	222.81	222.88	0.00
(C) Breeding—chick feathers Interstate Island						
Proportion river	0.95	3	9.29	−10.18	0.00	0.98
Intercept only	1.55	2	3.54	−1.98	8.20	0.02
Age (d)	1.5	3	3.56	1.27	11.45	0.00
(D) Breeding—chick feathers Ashland Island						
Intercept only	0.74	2	5.22	−3.43	0.00	0.90
Age (d)	1.06	3	5.58	2.85	6.28	0.04
$\delta^{13}C$	−0.71	3	5.37	3.27	6.70	0.03
$\delta^{15}N$	1.42	3	5.33	3.33	6.76	0.03
$\delta^{13}C + \delta^{15}N$	0.04	4	5.39	17.22	20.65	0.00

[a] Models describe the response of natural log-transformed total Hg (ln[THg]) concentrations to isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) relative to sample type (blood or feather), age class (adult or chick), and colony location (Interstate Island, Ashland Island, or both). Models were ranked using Akaike's information criterion, corrected for small sample size (AIC_c). Candidate models are listed in order of ranking (ΔAIC_c), with top models listed first. For each model, the slope (β), number of estimated parameters (K), Log-likelihood (logLik), AIC_c, ΔAIC_c, and Akaike weight (Wt) are provided. Candidate models for (A) adult feathers from both Interstate and Ashland Island colonies ($n = 7$, $n = 15$, respectively), (B) adult blood samples from Interstate Island colony ($n = 12$), (C) chick feathers from Interstate Island colony ($n = 14$), and (D) chick feathers from Ashland Island colony ($n = 7$).

included in the diet contribution calculation. We used *t*-tests to examine differences in (ln [THg]) concentrations between groups (e.g., adult or chick feathers from both colonies). Trophic level was calculated from chick breast feather samples at each colony using the following equation: 1 + (mean δ^{15}N chick feathers – mean δ^{15}N baseline-POM) ÷ 3, where 3 = trophic enrichment factor for feathers (Supplemental Data Table S3). Results are provided as geometric means ±95% confidence intervals (CI) or standard deviations (SD). The THg concentrations in figures represent back-transformed ln (THg) values. Maps were created using the R package tidyverse (Wickham 2017) and ArcGIS software by Esri (ArcMap 10.6.1). The R package MASS (Venables and Ripley 2002) was used for GLM analyses and MuMIn (Barton 2020) for AIC_c model inference. All statistical analyses were conducted in R version 3.6.1 (R Core Team 2019).

RESULTS

Foraging habitat and Hg exposure

Nonbreeding season. Stable isotope data from flight feathers suggest that adults from both colonies foraged in marine environments during the nonbreeding season, indicated by high δ^{13}C values (Figure 1). The top GLM model for adult flight feather THg concentrations, based on AIC_c, included the single variable δ^{13}C, which accounted for 100% Akaike weight (Supplemental Data Figure S4; Table 1). Exclusion of an extreme value did not significantly influence model results ($\beta = -0.30 \pm 0.06$ SE [$n = 22$] vs $\beta = -0.37 \pm 0.09$ SE [$n = 21$]) and was therefore retained in the final model (Supplemental Data Figure S4). Low THg concentrations (geometric mean [95% CL]) = 1.28 (0.92–1.79) µg/g dw ($n = 22$) were associated with high δ^{13}C values, indicating lower Hg exposure during the nonbreeding season (marine diet) than during the breeding season (freshwater diet) for both colonies regardless of age or sex (Table 1). The THg concentrations in all adult flight feathers analyzed for Hg ($n = 60$) did not vary by colony location (Interstate Island: 1.32 [1.04–1.68] µg/g dw [$n = 39$]; Ashland Island: 1.32 [0.95–1.82] µg/g dw [$n = 21$] [$t = -0.02$, $df = 43$, $p = 0.99$; Figure 2]). The mean age and (range) of adult birds (in years) included in our study ($n = 60$) was 9 y (3–16 y).

Breeding season. Based on the stable isotope mixing model fit to adult blood data, adults breeding on Interstate Island obtained (mean ± SD) 42 ± 12% ($n = 12$) of their diet from the river during the incubation period. In contrast, based on the stable isotope mixing model fit to chick breast

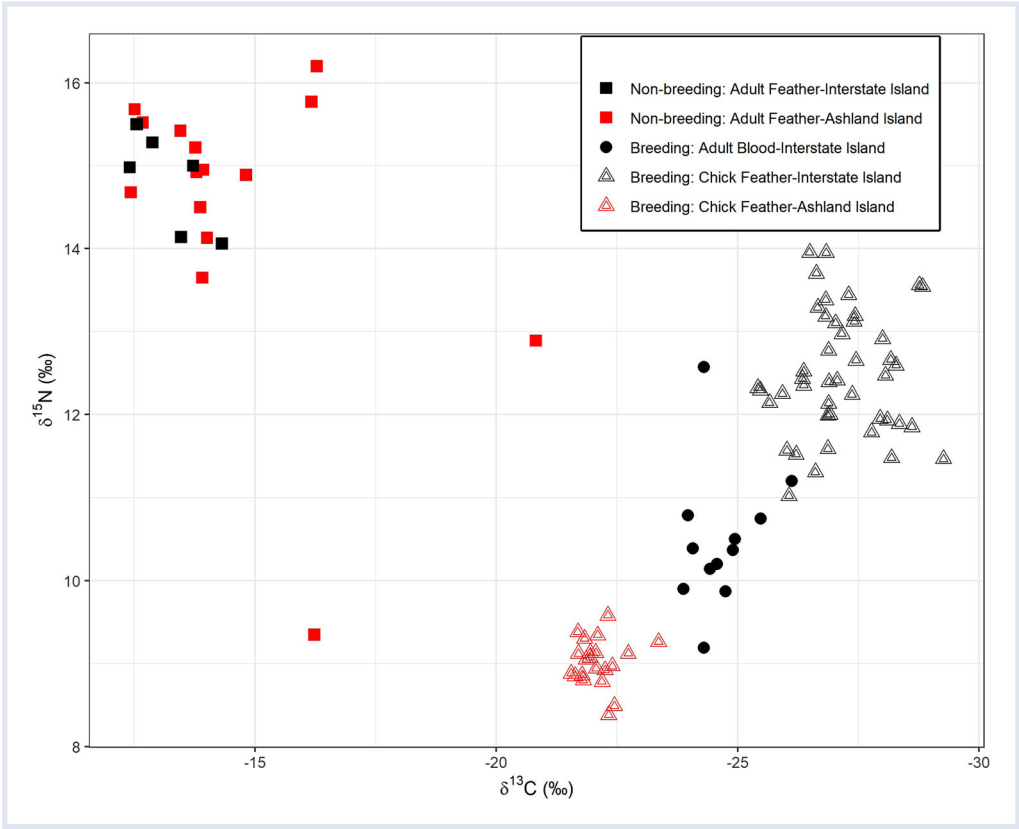

Figure 1. The C and N stable isotope ratios (δ^{13}C and δ^{15}N) by stage (breeding or nonbreeding), age (adult or chick), sample type (feather or blood), and colony location (Interstate Island or Ashland Island). Adult feather samples represent foraging in marine environments during the nonbreeding season (Interstate Island [$n = 7$], Ashland Island [$n = 15$]). Adult blood samples from Interstate Island ($n = 12$) represent foraging in freshwater environments (i.e., in the St. Louis River and western Lake Superior) during the incubation period of the breeding season. Chick feather samples (Interstate Island [$n = 44$], Ashland Island [$n = 21$]) represent parent foraging in freshwater environments during the chick-rearing period of the breeding season.

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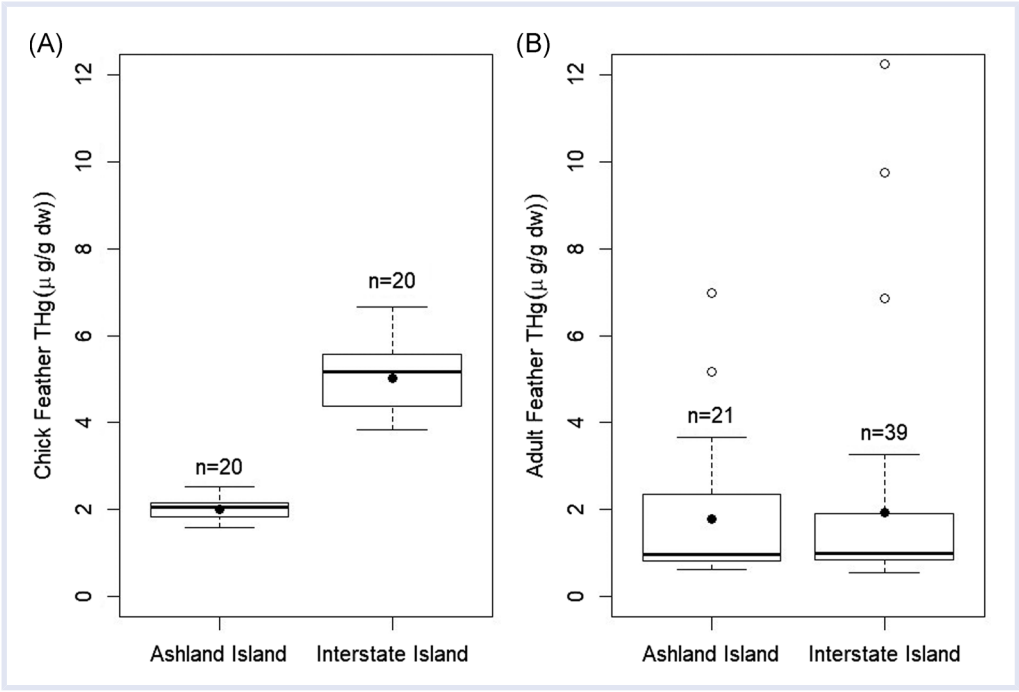

Figure 2. Box plots of total Hg (THg) concentrations measured in (A) chick breast feathers, and (B) adult flight feathers at each nesting colony (Ashland Island and Interstate Island). Midline values represent median geometric THg μg/g dw concentrations, and black dots represent mean geometric THg μg/g dw concentrations. The upper and lower limits of the boxes represent the 75th and 25th quartiles, respectively, with whiskers representing up to 1.5 times the interquartile.

feather data, chicks obtained 68 ± 19% ($n = 44$) of their diet from the river, indicating that during the chick-rearing period, adults foraged more extensively in the river. These stable isotope values suggest that foraging habitat use varied significantly between breeding phases (i.e., incubation and chick-rearing) ($t = 5.56$, $df = 27$, $p = 0.00$).

At Interstate Island, during the incubation period when GPS tags were deployed on adult birds, a total of 987 fixes were recorded. One tag malfunctioned, leaving 9 tags functional. The mean number of fixes per unit was 116 (range: 11–294), the mean number of satellites acquired per fix was 6 (range: 3–11), and the mean DOP was 2.6 (range: 0.8–87.5, mode: 1.2). Of the fixes recorded, 72% occurred over land at the colony. Of the remaining 279 fixes, 77% occurred over Lake Superior, the majority of which were obtained from birds moving along the south shore (Supplemental Data Figure S2). The GPS tags revealed movement up to 35 km from the breeding colony; however, 94% of the fixes occurred within 20 km of the breeding colony and close to shore. The point density maps (Supplemental Data Figure S2) provided useful information about where birds were foraging during the incubation period, and for Interstate Island, locations identified from GPS fixes justified the spatial domain of the stable isotope mixing model (Supplemental Data Figure S3).

At Interstate Island, foraging location was significantly related to THg concentration in both adults and chicks, such that THg concentrations increased with a higher proportion of a riverine diet (Figure 3). We also found differences in blood THg concentrations between males and females, which was expected and consistent based on reproductive biology. The THg concentrations were evidently higher in adult males (1.15 [0.92–1.45] [$n = 5$]) than females (0.83 [0.67–1.03] [$n = 7$]) and increased with proportion riverine diet (Figure 3). The most parsimonious GLM model for adult blood THg concentrations, based on AIC_c, included proportion river and sex (Table 1). The conditional probability (Akaike weight) was 0.69. The top 3 models, all with $\Delta AIC_c < 5.0$, included 2 additional single variable models with proportion river and sex, which collectively accounted for 0.97 Akaike weight. Age did not explain differences in blood THg concentrations among adult birds (Table 1). Because sex was unknown for chicks, we fitted 2 single variable GLM models for chicks, which was proportion riverine diet and age. The model that included proportion river accounted for 0.98 of the model weight, compared to the age and intercept-only models (Table 1). Age did not explain differences in feather THg concentrations among chicks. The mean age and (range) of chicks (in days) included in our study was 20.5 d (10–24 d) for birds at Interstate Island ($n = 20$) and 20.5 d (16.5–23 d) for birds at the Ashland Island colony ($n = 20$).

During the incubation period when GPS tags were deployed on adult birds at Ashland Island, a total of 903 fixes were recorded. Four tags malfunctioned, leaving 5 tags functional. The mean number of fixes per unit was 156 (range: 23–294), the mean number of satellites per fix was 6 (range: 3–10), the mean DOP was 4.6

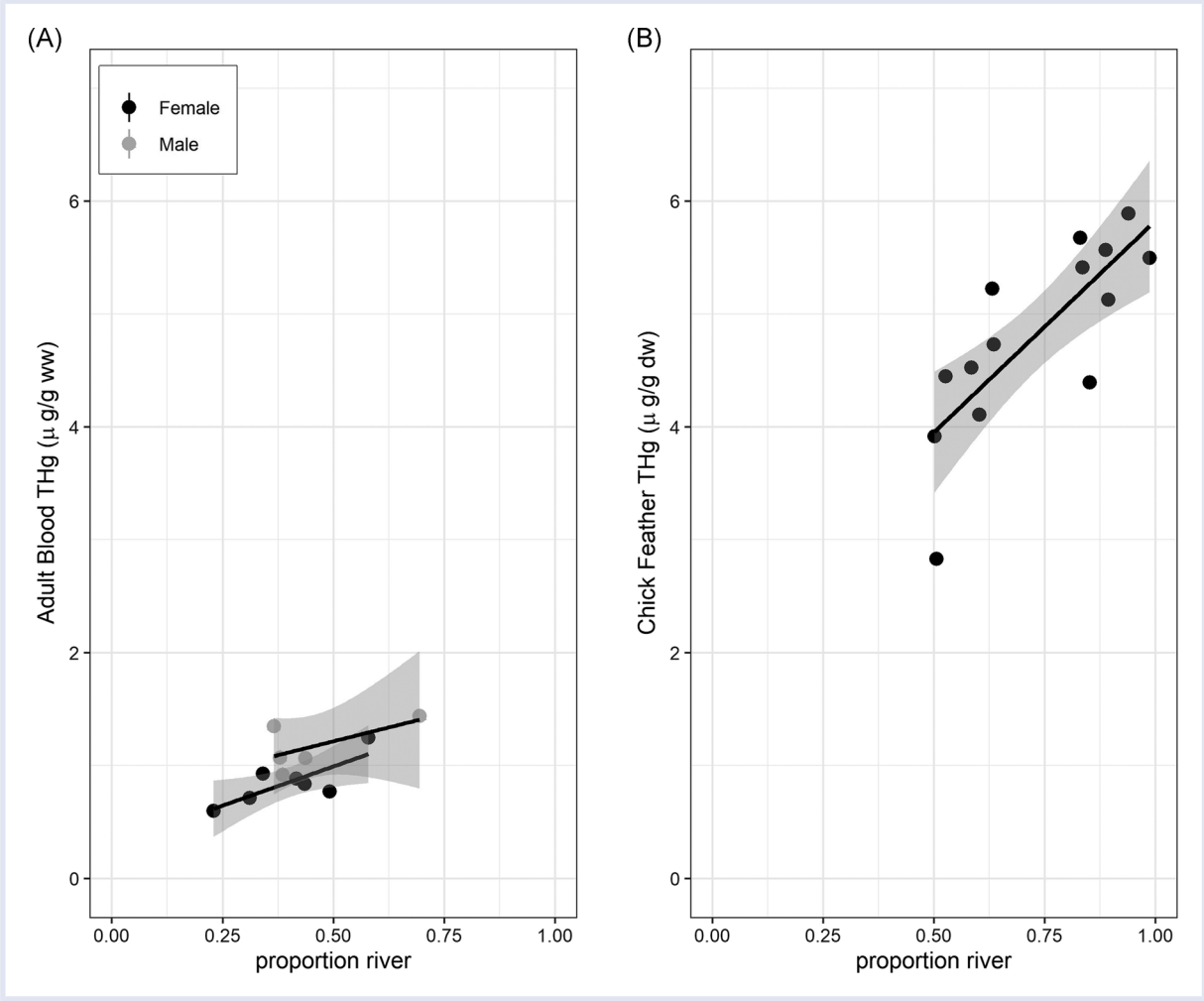

Figure 3. Foraging location was significantly related to total Hg (THg) concentrations in (A) adult blood and (B) chick feathers at the Interstate Island colony. The THg concentrations increased with a higher proportion of a riverine diet. The top GLM model for adult blood THg (μg/g ww) based on AIC_c included proportion riverine diet and sex. The intercept varied by sex, with THg concentrations significantly higher in males than females ($n = 12$). The top GLM model for chick breast feather THg (μg/g dw) based on AIC_c, included proportion riverine diet only ($n = 14$). The fitted lines are estimates of the conditional mean function and 95% confidence limits (CL).

(range: 0.8–504.7; mode: 1.0). Of the fixes recorded, 28% occurred over land at the colony. All other fixes were in Chequamegon Bay, within 15 km of the nesting colony (Supplemental Data Figure S2). Adult birds foraged primarily in Chequamegon Bay during incubation, and likely during the chick-rearing period as well. There was no significant relationship between THg concentrations and $\delta^{13}C$ and $\delta^{15}N$ values for chicks reared at the Ashland Island colony, which was expected based on the lack of a local isotopic gradient (Table 1).

The THg concentrations were significantly higher in chicks hatched on Interstate Island (4.95 [4.62–5.37] μg/g dw, $n = 20$) compared to chicks hatched on Ashland Island (1.99 [1.89–2.11] μg/g dw, $n = 20$) ($t = -20.66$, $df = 35$, $p < 0.01$; Figure 2). The species composition and relative abundance of prey fish collected at both colonies was nearly identical. We collected 27 prey fish of 5 species at the Interstate Island colony and 37 prey fish of 7 species at the Ashland Island colony (Supplemental Data Table S2). Emerald shiner (*Notropis atherinoides*) was the most abundant species collected at both locations, representing >60% of fish collected at either colony (Supplemental Data Table S2). Estimates of trophic level based on $\delta^{15}N$ values show common tern chicks at both colonies were feeding at the same effective trophic level (4.6 and 4.7, respectively; see Supplemental Data Table S3). The stable isotope ratios of prey fish were distinct between the 2 locations (Supplemental Data Table S2), reflecting the underlying isotopic baseline differences; prey fish were ^{13}C-depleted and ^{15}N-enriched at Interstate Island, consistent with a river origin, and ^{13}C-enriched and ^{15}N-depleted at Ashland Island, consistent with a Lake Superior origin (Hoffman et al. 2015a). On average, pooled THg concentrations among age classes at both colonies were lower in adult flight feathers (1.32 [1.09–1.59] μg/g dw, $n = 60$) than in chick breast feathers (3.16 [2.70–3.67] μg/g dw, $n = 40$) ($t = 7.20$, $df = 98$, $p = 0.01$).

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DISCUSSION

Our study is unique as it is the first to integrate Hg and isotopic analyses with geolocation data to study Hg exposure over the annual cycle of the common tern. Based on the life history of common terns breeding in inland freshwater lakes and wintering in marine coastal environments, the use of stable isotopes and on-bird tracking technologies was critical for determining year-round risk of Hg exposure. For common terns breeding at these 2 inland colonies, Hg exposure was associated with geographic location and shifts in foraging behavior and habitat use throughout the year. This demonstrates that piscivorous birds that have small foraging ranges, such as inland nesting common terns, can act as ecological monitors of local Hg exposure.

Foraging habitat and Hg exposure

Nonbreeding season. Stable isotope data from flight feathers supported our prediction that adults from both colonies foraged in marine environments during the nonbreeding season. Previously summarized band recovery and geolocation data demonstrated that common terns breeding in the Great Lakes region winter in coastal areas of central and northwestern South America, concentrating along the Peruvian coast (Bracey et al. 2018; Arnold et al. 2020). Breast feathers collected from seabirds along the coast of southern Peru, where many birds from our study region overwinter, revealed low within- and among-species variability in Hg concentrations, ranging from 0.5 to 2.0 μg/g (Gochfeld 1980). These results suggest winter exposure may be negligible for these birds, consistent with our findings.

Two outlying values associated with adult feather C and N stable isotope ratios (C:N = −16.23: 9.35 and −20.82: 12.89), both sampled from birds breeding at the Ashland Island colony (Figure 1), are more representative of breeding season birds, potentially due to individual variation in molt schedules (e.g., delayed or incomplete molt). Terns have a Complex Alternate molt strategy (i.e., birds replace juvenile plumage in the first year and have an additional molt each year) that is unique and includes inserted molts and repeated replacement of inner primaries and outer secondaries (Arnold et al. 2020). Feather replacement occurs primarily during the nonbreeding season and is considered the primary mechanism for eliminating bioaccumulative trace elements from the body (Arnold et al. 2020).

In our study, THg concentrations in adult flight feathers did not vary by sex or age. The Hg concentrations in feathers of adult common terns breeding in Massachusetts, USA, also did not show an increase in Hg with age (Burger et al. 1994). Although sex and age of adults was not an important factor in our study, it has been found to be important in explaining variation in Hg concentrations in other species (Chételat et al. 2020).

Breeding season. Although sample sizes were small, GPS data from both colonies suggest that common terns utilize relatively local (within 20 km of breeding colony) foraging habitats, consistent with observations from common tern colonies elsewhere (Arnold et al. 2020). Common terns consume a wide variety of fish, with adults choosing larger prey items when feeding mates and smaller prey to match the age and size of chicks posthatching (Arnold et al. 2020). Additionally, foraging locations are typically related to site-specific variables, such as water clarity, and food availability (Arnold et al. 2020). Terns are visual foragers, and visibility is often greater in the near-shore of Lake Superior compared to the SLR (Bellinger et al. 2016). It may be easier for birds to locate and select larger prey fish, such as adult rainbow smelt, for mates in Lake Superior, whereas if young chicks require smaller prey items, locating smaller fish, such as emerald shiner, may require less effort or selectivity, and therefore terns may choose to forage closer to the colony, in the SLR. Adults may also forage more frequently during the chick-rearing period, so foraging nearer the colony would conserve energy. Our results support the findings of previous studies that suggest age-related differences (adult vs chicks) in Hg exposure could be the result of selective allocation of food resources (Arnold et al. 2020). Shifts in foraging strategies have also been associated with competition in foraging flocks (Arnold et al. 2020). Although common terns are not reported to forage in flocks in the Great Lakes, they may cue in on foraging behaviors of other individuals.

Making appropriate inferences about the influence of diet on Hg concentrations detected in birds requires that signal integration times align in tissues chosen for stable isotope and Hg analyses (Chételat et al. 2020). For chicks, breast feathers reflect adult foraging and Hg exposure on the breeding grounds and the same feather samples were used to analyze diet ($\delta^{13}C$ and $\delta^{15}N$) and THg concentrations. Differences in Hg accumulation in chicks between colonies was likely due to variation in Hg exposure of prey fish based on site geochemistry, Hg inputs, and foraging habitats available. These differences also suggest that exposure is greater for prey fish in the SLR than in Chequamegon Bay. Our findings were consistent with a variety of studies that demonstrate site- or habitat-specific differences in Hg concentration influence exposure in seabirds (Chételat et al. 2020). For example, variation in Hg concentration of common terns and other seabirds breeding in the North Sea was predominantly due to local pollution exposure, which showed interspecific and intersite differences (Becker et al. 1993; Furness et al. 1995).

Assessing Hg exposure based on measured Hg concentrations in different tissue types and relating those concentrations to estimates of toxicological risk in wild bird populations is challenging (Evers 2018). For example, a study of Hg concentrations in the blood and feathers of seabird chicks suggested a strong correlation between the 2 tissue types (Renedo et al. 2018). However, Ackerman et al. (2011) found that Hg concentrations in forster's tern (*Sterna forsteri*) chick feathers were not representative of internal concentrations and suggested chick feathers were not a good measure of toxicological risk. These examples suggest there

is likely not 1 common measure or best method for risk assessment across species based on THg concentrations in different tissues. Without species-specific data, using published risk thresholds based on similar species is reasonable for discussing risk in a broad sense. Feather concentrations THg ≥5 μg/g dw have been associated with adverse effects (e.g., in chick growth and development), in tern species, including common tern (Burger and Gochfeld 1997). Mean THg concentrations in adult feathers (nonbreeding signal) from both colonies were <5 μg/g dw, although some individuals exceeded this threshold. Mean THg concentrations in chick feathers and adult blood (breeding signal) at Interstate Island met the toxicological risk thresholds for feathers (5 μg/g dw) and blood (1 μg/g ww) (Burger and Gochfeld 1997; Ackerman et al. 2016), with many individuals exceeding these levels. The ratio of feather THg concentration (dw) to blood (ww) is typically 10 to 20 (Nichols et al. 2010), suggesting that blood-THg concentrations averaged <0.13 μg/g on the wintering grounds compared to mean concentrations of 0.99 ± 0.11 SD on the breeding grounds. This suggests that Hg exposure is greater on the breeding grounds than wintering grounds for adult birds, but warrants further investigation.

From our results, we infer that Hg exposure is higher during the breeding season than the nonbreeding season for adults nesting or chicks hatched at these Lake Superior colonies. Similar to our findings, other studies have found Hg concentrations in avian blood and feathers to be higher and less variable during the breeding season than during the nonbreeding season (Chételat et al. 2020), including studies of common terns breeding in Massachusetts, USA and in the St. Lawrence River (Arnold et al. 2020). We also infer that chicks hatched at Interstate Island had higher exposure than chicks hatched at Ashland Island. Elevated feather-Hg concentrations have been reported in common terns nesting in Lake Winnipeg and the Great Lakes, with highest concentrations occurring in locations downstream of industrial sources (Arnold et al. 2020).

Many contaminant studies fail to identify locations and habitats of greatest exposure throughout the annual cycle, even though such information is required for population-level risk-assessment and for successful management and remediation efforts. Our findings underscore the importance of availability, with respect to both local exposure and risk, and suggest Hg contamination may be an important stressor for both adults and chicks during the breeding season and particularly for individuals at industrially influenced colony locations. It is important to note that local exposure of common terns to Hg at the Interstate Island colony can potentially be mitigated by terns foraging in Lake Superior versus in the SLR. However, conditions that likely influence adult foraging behavior, such as fluctuating water levels and resulting shifts in prey availability, could also influence exposure risk to adults and chicks both annually and over the long term.

Recent estimates suggest steep declines are widespread throughout bird populations in North America, including for gulls and terns, and particularly for species that overwinter in coastal locations in South America (Rosenberg et al. 2019). Further, impacts of climate change (e.g., hydrologic changes and increasing temperatures) are expected to increase the production and bioavailability of MeHg globally and to have the greatest negative impact on bird species overwintering in South America (Culp et al. 2017), potentially increasing future risk to common terns. Although there are multiple factors potentially limiting the Great Lakes common tern population (e.g., habitat loss, predation), documenting chronic and potentially increasing exposure to contaminants such as Hg is important when assessing cumulative risk.

A valuable next step would be to determine whether higher THg concentrations detected in birds at Interstate Island are due to sediment contamination from industrial sources (i.e., legacy and current industrial inputs), higher methylation rates (bioavailability), or both, using Hg isotopes as tracers (Renedo et al. 2018). Further, the methods used in this study can also be used to track exposure to other contaminants of concern that have been associated with decreased fecundity (e.g., organochlorines) (Arnold et al. 2020; Travis et al. 2020). The cumulative effects of exposure to additional contaminants may have consequences to common terns even if effects of Hg exposure are sublethal or chronic. Determining where in the annual cycle vulnerability to environmental hazards, such as contaminant exposure, is greatest can help inform conservation strategies aimed at mitigating exposure risk for this declining Great Lakes population of common terns and for other threatened or endangered species breeding in the region.

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Disclaimer—The authors declare no conflict of interest. We acquired all necessary permitting for handling and marking Common Terns (2016–2018). This project was approved by the USGS Bird Banding Laboratory (permit no. 05322), the Wisconsin Department of Natural Resources Animal Care and Use Committee, and the University of Minnesota Institutional Animal Care and Use Committee (protocol ID 1510-33094A).

Data Availability Statement—Data and associated metadata and calculation tools are available upon request by contacting corresponding author Annie M Bracey (brace005@d.umn.edu).

SUPPLEMENTAL DATA

Figure S1. Location of Common Tern colony study sites.

Figure S2. Point density of global positioning system (GPS) tag fixes occurring on the water.

Figure S3. Mean $\delta^{13}C$ and $\delta^{15}N$ values of source prey fish used to delineate the mixing model polygon, representing tern foraging locations in the St. Louis River Estuary and Lake Superior.

Figure S4. The top model for adult Common Tern flight feather total Hg (THg μg/g) concentrations, based on AIC_c, included the single variable $\delta^{13}C$ (Supplemental Data Table S1).

Table S1. Data used for 1) comparison of total Hg (THg) concentrations, 2) stable isotope (SI) mixing models, and 3) general linear models (GLMs; SI and THg)

Table S2. List of prey fish collected during the 2017 breeding season (June–July) at Interstate and Ashland islands

Table S3. Estimated trophic position of Common Tern chicks.

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