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Mercury bioaccumulation in bats reflects dietary connectivity to aquatic food webs[☆]



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ABSTRACT

Mercury (Hg) is a persistent and widespread heavy metal with neurotoxic effects in wildlife. While bioaccumulation of Hg has historically been studied in aquatic food webs, terrestrial consumers can become contaminated with Hg when they feed on aquatic organisms (e.g., emergent aquatic insects, fish, and amphibians). However, the extent to which dietary connectivity to aquatic ecosystems can explain patterns of Hg bioaccumulation in terrestrial consumers has not been well studied. Bats (Order: Chiroptera) can serve as a model system for illuminating the trophic transfer of Hg given their high dietary diversity and foraging links to both aquatic and terrestrial food webs. Here we quantitatively characterize the dietary correlates of long-term exposure to Hg across a diverse local assemblage of bats in Belize and more globally across bat species from around the world with a comparative analysis of hair samples. Our data demonstrate considerable interspecific variation in hair total Hg concentrations in bats that span three orders of magnitude across species, ranging from 0.04 mg/kg in frugivorous bats (*Artibeus* spp.) to 145.27 mg/kg in the piscivorous *Noctilio leporinus*. Hg concentrations showed strong phylogenetic signal and were best explained by dietary connectivity of bat species to aquatic food webs. Our results highlight that phylogeny can be predictive of Hg concentrations through similarity in diet and how interspecific variation in feeding strategies influences chronic exposure to Hg and enables movement of contaminants from aquatic to terrestrial ecosystems.

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Summary

Total mercury was determined in hair from 98 bats from 22 species in Belize, and variation in mercury concentrations was best explained by dietary guild. Frugivorous bats (e.g., *Artibeus* spp.) had the lowest hair mercury ($\mu = 0.04$ mg/kg) while a single sampled

piscivore (*Noctilio leporinus*) showed the highest concentration across our sample (145.27 mg/kg). Hair mercury across 50 bat species from this study and the published literature showed strong phylogenetic signal (Pagel's $\lambda = 0.97$), and a comparative analysis showed that bat species consuming more potentially aquatic prey (e.g., invertebrates, ectotherms, fish) showed the highest hair mercury concentrations.

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1. Introduction

Mercury (Hg) is a persistent and widespread heavy metal with

neurotoxic effects in wildlife (Scheuhammer et al., 2007; Wolfe et al., 1998). Atmospheric deposition and human activities such as gold mining, coal-fired power plants, and slash-and-burn agriculture contaminate soil and water with Hg (Farella et al., 2006; Fitzgerald et al., 1998; López Alonso et al., 2003; Mol et al., 2001). As methylation processes are mostly restricted to aquatic ecosystems (Wiener et al., 2003), Hg bioaccumulates within aquatic food webs (Chen et al., 2005; Chumchal et al., 2011; Lavoie et al., 2013). Terrestrial ecosystems can also receive Hg inputs from trophic transfer (Blais et al., 2007), in which terrestrial consumers are exposed to Hg by feeding on both aquatic organisms and prey species connected by their life histories to aquatic environments (Cristol et al., 2008; Dehn et al., 2006; Rimmer et al., 2010). As one example, spiders become contaminated with Hg by consuming emergent aquatic insects and in turn transfer Hg to terrestrial consumers such as insectivorous songbirds (Jackson et al., 2011; Speir et al., 2014). However, the extent to which dietary connectivity to aquatic ecosystems explains trophic transfer of Hg to terrestrial consumers has not been well studied. This remains a major limitation in understanding how Hg moves between aquatic and terrestrial ecosystems and its potential impacts on terrestrial wildlife.

Bats (Order: Chiroptera) are excellent model systems for examining the trophic transfer of Hg. Many bat species consume food that is the equivalent of a large proportion of their body mass per night while foraging and obtain food from both aquatic and terrestrial ecosystems (Hickey and Fenton, 1996; Salvarina, 2016; Wimsatt and Guerriere, 1962). In particular, bats from the Neotropics exhibit a broad range of dietary strategies, with members of the superfamily Noctilionoidea displaying the greatest dietary diversity among mammals (Teeling et al., 2005; Wetterer et al., 2000). Dietary guilds here range from frugivory and nectarivory to insectivory, sanguivory, and carnivory, alongside several instances of piscivory (Bloedel, 1955; Rojas et al., 2011). Neotropical bat communities thus display feeding strategies reliant almost entirely on either terrestrial (e.g., frugivores) or aquatic food webs (e.g., piscivores) or those that receive contributions from both ecosystems (e.g., insectivores), making them ideal for examining the trophic transfer of Hg. Insectivorous bats are perhaps the most interesting group, as most are thought to be extreme generalists whose diet is dictated more by the habitat they exploit than by preferences for particular prey, and accumulating evidence suggests their diet may be very locally influenced (e.g., Clare et al., 2011, 2014b; Sedlock et al., 2014). As one example, many insectivorous bats forage over aquatic habitats and consume emergent aquatic insects both at and above the water surface (Dietz et al., 2006; Salvarina, 2016), which would repeatedly expose such species to Hg (Little et al., 2015; Wada et al., 2010). Despite this, many bat species can cover large distances in a night while foraging and likely encounter food resources derived from both terrestrial and aquatic habitats and from different trophic levels. Therefore, significant variation in Hg concentrations should be evident across Neotropical bat species.

Exposure to heavy metals, including Hg, has been shown to negatively affect bat health (Karouna-Renier et al., 2014; Nam et al., 2012) and could reduce fitness owing to negative effects on reproduction in this *K*-selected taxon (Barclay et al., 2003; Brasso and Cristol, 2008). Yet research on the distribution of Hg and on risk factors for Hg exposure has been mostly restricted to bat species in North America and Europe (Hickey et al., 2001; Korstian et al., 2017; Lisón et al., 2017; Little et al., 2015; Yates et al., 2013), with limited study in the tropics (Becker et al., 2017a; Syaripuddin et al., 2014; Zukal et al., 2015) where bat species diversity is highest and where widespread sources of Hg include coal burning, gold mining, and deforestation (Almeida et al., 2005; Costa et al., 2012; McCartor and Becker, 2010). Our goal was thus to characterize the

dietary correlates of exposure to Hg across a diverse assemblage of bats in Belize and more globally across bat species using a comparative analysis. We quantified total Hg (THg) from hair as a measure of bioaccumulation and a proxy for methylmercury, which comprises 71–95% of Hg in bat hair (Yates et al., 2013). While THg in hair and blood are highly correlated (Vermeulen et al., 2009; Yates et al., 2013), concentrations in hair are reflective of chronic rather than acute dietary exposure to Hg (Hernout et al., 2016). Our first goal was to test if patterns of Hg bioaccumulation across trophic guilds are similar in bats as in other taxa (e.g., higher Hg in animalivores than herbivores), as some animal-feeding bats have shown low Hg concentrations (Becker et al., 2017a). Our next goal was then to determine if dietary connectivity to aquatic ecosystems explains global patterns of bat Hg concentrations, testing the prediction that Hg would be highest in bat species consuming more prey derived from aquatic food webs.

2. Materials and methods

2.1. Bat capture and sampling

From April 28 to May 4, 2014, we sampled bats from two areas in the Orange Walk District of Belize: Lamanai Archaeological Reserve (LAR) and Ka'Kabish (KK). The LAR is bordered by the New River Lagoon, forest, and agricultural habitat, whereas KK is a site of remnant forest (~20–40 ha) surrounded by agriculture (Fig. 1). At least 55 of the 70 known bat species in Belize have been recorded in this region (Fenton et al., 2001). Bats were captured with mist nets placed at exits of roosts or along flight paths from 19:00 until 22:00; a harp trap was also set along forest trails and gaps in the understorey vegetation from 18:00 until 05:00. Nets were continually monitored and the harp trap was checked at regular intervals. Captures were evenly split between sites (LAR = 44, KK = 54). Only *Chrotopterus auritus*, *Dermanura watsoni*, *Saccopteryx bilineata*, and *Trachops cirrhosus* were captured exclusively at KK, while *Bauerus dubiaquercus*, *Dermanura phaeotis*, *Molossus rufus*, *Myotis elegans*, *Noctilio leporinus*, *Rhogeessa aeneus*, *Rhynchonycteris naso*, and *Sturmira lilium* were captured only at LAR (Table 1). Bats were placed in individual cloth bags until processing, when we trimmed <10 mg of hair from the dorsal posterior or ventral region. Scissors were cleaned with ethanol between processing bats, and samples were stored in individual cryovials or Ziploc bags and kept at room temperature until laboratory analysis. We also assessed sex when possible, as female bats have shown higher THg than males (Yates et al., 2013). All bats were released at their capture site after processing.

All field procedures were approved by the Institutional Animal Care and Use Committees of the University of Georgia (AUP A2014 04-016-Y3-A5) and the University of Western Ontario (AUP-2008-004-04). Bat capture and hair sample collection were authorized by the Belize Forest Department under permits CD/60/3/14(27) and CD/60/3/14(17).

2.2. Hair THg analysis

Bat hair was analyzed for THg at the Texas Christian University Aquatic Ecology Laboratory. Hair was rinsed in a 2:1 chloroform:methanol solution and dried overnight in a fume hood and reported on a fresh weight basis. We quantified hair THg in all samples with a direct Hg analyzer (DMA-80, Milestone, CT, USA) (USEPA, 1998) and analyzed National Research Council Canada reference material DORM 4 (certified value = 0.412 ± 0.036 mg/kg) every 10 samples for quality assurance; mean recovery was $88.5 \pm 1.65\%$. Limited amounts of hair available for analysis resulted in some samples falling below the THg detection limit (0.48 ng,

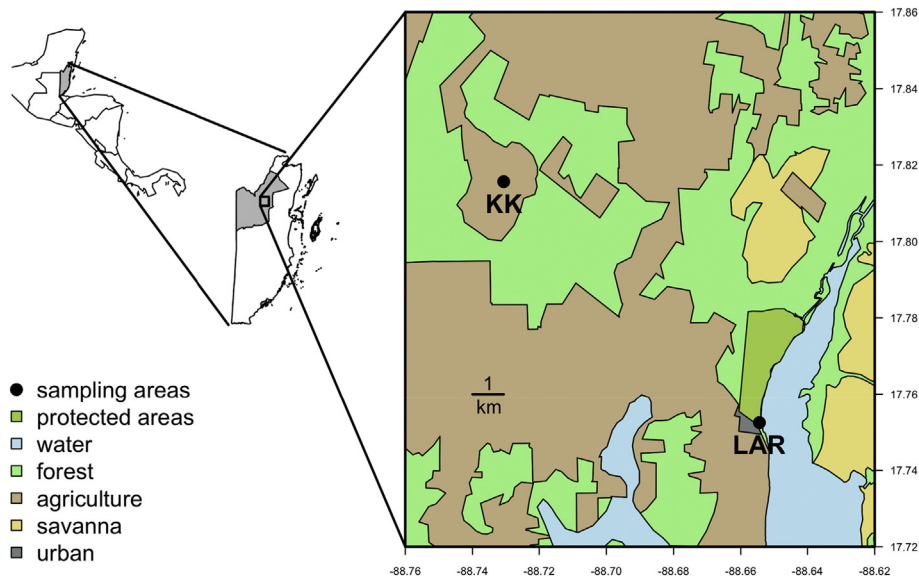


Fig. 1. Map of the sampling regions in Belize. Shaded insets show the location of Belize and Orange Walk District, and colors display ecosystem classifications according to the Biodiversity and Environmental Resource Data System of Belize (Meerman and Clabaugh, 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Sample size per site and dietary guild for the 22 bat species sampled in Belize.

Species name	KK	LAR	Main diet %	Dietary guild
<i>Artibeus intermedius</i>	1	1	Fruit	Frugivore
<i>Artibeus jamaicensis</i>	2	3	Fruit	Frugivore
<i>Artibeus lituratus</i>	1	4	Fruit	Frugivore
<i>Bauerus dubiaquercus</i>	0	3	Invertebrate	Insectivore
<i>Carollia sowelli</i>	2	1	Fruit	Frugivore
<i>Chrotopterus auritus</i>	2	0	Vertebrate/invertebrate	Carnivore
<i>Dermanura phaeotis</i>	0	2	Fruit	Frugivore
<i>Dermanura watsoni</i>	1	0	Fruit	Frugivore
<i>Desmodus rotundus</i>	29	7	Vertebrate	Sanguivore
<i>Eptesicus furinalis</i>	1	1	Invertebrate	Insectivore
<i>Glossophaga soricina</i>	1	1	Fruit/nectar/invertebrate	Omnivore
<i>Molossus rufus</i>	0	3	Invertebrate	Insectivore
<i>Myotis elegans</i>	0	2	Invertebrate	Insectivore
<i>Noctilio leporinus</i>	0	1	Vertebrate/invertebrate	Carnivore
<i>Pteronotus davyi</i>	3	2	Invertebrate	Insectivore
<i>Pteronotus mesoamericanus</i>	2	3	Invertebrate	Insectivore
<i>Rhogeessa aeneus</i>	0	1	Invertebrate	Insectivore
<i>Rhynchonycteris naso</i>	0	3	Invertebrate	Insectivore
<i>Saccopteryx bilineata</i>	4	0	Invertebrate	Insectivore
<i>Sturnira lilium</i>	0	3	Fruit	Frugivore
<i>Trachops cirrhosus</i>	3	0	Vertebrate/invertebrate	Carnivore
<i>Uroderma bilobatum</i>	2	1	Fruit	Frugivore

≈ 0.096 mg/kg; $n = 45$); most such samples were from *Desmodus rotundus* (53%). THg values below detection limit were subsequently estimated as 50% the detection limit (Rainwater et al., 2005). Hair THg was expressed as mg/kg and log transformed prior to statistical analysis; however, we present raw data on a log-scale axis in all figures for ease of interpretability. All data are freely available (Becker et al., 2017b).

2.3. Comparative THg data

To compare hair THg of Neotropical bats against those from other bat species, we compiled data through a systematic search of Google Scholar and Web of Science (Fig. S1; Moher et al., 2009). The search was performed on June 28, 2017 using the following strings: (bat OR Chiroptera OR bats) AND (mercury OR Hg OR THg or “total

mercury” OR “total Hg”). After removing duplicate records, we screened titles and abstracts from 815 studies, resulting in 28 articles that were assessed for eligibility in the full-text. We excluded an additional 17 studies owing to reporting THg in other tissues or to absence of necessary data (mean hair THg). This inclusion process therefore identified 11 studies that reported mean hair THg concentrations (mg/kg), representing 37 records containing 29 bat species (Table S1).

2.4. Bat dietary data

We first grouped bat species into guilds based on the EltonTraits database (Wilman et al., 2014) and a systematic classification of mammal diets (González-Salazar et al., 2014). Guilds were mostly defined by the food groups comprising the majority (>50%) of a

given diet (Bregman et al., 2016). *Glossophaga soricina* was classified as omnivore owing to equal consumption of nectar, fruit, and insects (Clare et al., 2014a). Our sample thus contained five dietary guilds: frugivores, omnivores, insectivores, carnivores, and sanguivores. The one piscivore in our study (*Noctilio leporinus*) was grouped in the carnivore guild for the purposes of statistical analyses, given that only one individual was sampled. To next address the connectivity of these feeding strategies to aquatic food webs (Cristol et al., 2008; Salvarina, 2016), we used EltonTraits data to classify bat species according to if the majority ($\geq 50\%$) of their diet was composed of potentially aquatic prey: invertebrates (including but not limited to aquatic insects, insects with aquatic life stages, and crustaceans), ectotherms (herptiles including reptiles, snakes, amphibians, salamanders), and fish (Wilman et al., 2014). Although some Neotropical mammals are largely aquatic, none that occur in Belize are small enough to be prey for even the largest bats in the region (Reid, 1997). As dietary breadth shows an allometric relationship in bats (Brigham, 1991), we also recorded adult body mass (grams) for each bat species (Wilman et al., 2014); log body mass scales positively with log forearm size across bat species and is thus an acceptable metric of bat body size in comparative analyses (Meng et al., 2016).

2.5. Statistical analysis

We used linear models (LM) and linear mixed models (LMM) with species as a random effect to first test if THg in the Neotropical bat community varied by dietary guild, sex, and sampling site. We compared a set of LMMs with dietary guild, site, and both terms. Models were fit with maximum likelihood (ML) and compared with Akaike information criterion corrected for small sample size (AICc); we considered models within two ΔAICc as competitive (Burnham and Anderson, 2002). We employed model averaging to calculate variable importance. We next refit models using restricted ML and calculated marginal R^2 to quantify how much variation in THg was explained by fixed effects (Nakagawa and Schielzeth, 2013). We repeated this analysis on the subset of data for which sex was determined ($n = 86$, 20 species). To assess pairwise THg differences between these factors, we performed *post hoc* comparisons adjusting for the potentially inflated false-discovery rate using the Benjamini and Hochberg correction (Benjamini and Hochberg, 1995). We used the *lme4*, *multcomp*, and *MuMIn* packages in R for our analyses (Bartoń, 2013; Hothorn et al., 2014; Pinheiro et al., 2011; R Core Team, 2013).

We next used phylogenetic comparative methods to test if connectivity to aquatic food webs could explain interspecific variation in THg across our broader bat species data while accounting for shared evolutionary history. Using the *rotl* and *ape* packages in R (Michonneau et al., 2016; Paradis et al., 2004), we extracted our phylogeny from the Open Tree of Life (OTL) (Hinchliff et al., 2015), resolved polytomies, and calculated branch lengths using Grafen's method (Grafen, 1989). One species (*Rhinolophus chiewkwweae*) absent from the OTL phylogeny was excluded from the analysis. We calculated mean THg for species with multiple records ($n = 39$) and log-transformed THg prior to analyses. We first tested if more closely related bats share similar THg concentrations by estimating Pagel's λ with the *caper* package (Orme, 2013; Pagel, 1999). We then performed likelihood ratio tests to ask whether our estimate of λ differed from a Brownian motion model of evolution ($\lambda = 1$) and a model of phylogenetic independence ($\lambda = 0$). We next used weighted phylogenetic generalized least squares (WPGLS) to test if mean hair THg increased with the proportion of potentially aquatic prey in diet while accounting for phylogeny and variation in sampling effort (Garamszegi and Møller, 2010; Grafen, 1989). We fit models using the *nlme* package, with weights given by the log-

transformed sample size and ML used to optimize λ in residual error for branch length transformation (Garamszegi, 2014; Pinheiro et al., 2011). We compared a set of models with dietary guild and the proportion of potentially aquatic prey in diet, alongside models that included body mass as a covariate and a univariate model with bat family. We refit models with REML and calculated an adjusted R^2 from a weighted regression of observed versus predicted THg values to assess fit.

3. Results

3.1. Neotropical bat THg

We sampled 98 bats from 22 species across LAR and KK (Table 1); sample size per species ranged from 1 to 36 ($\mu = 4.45$). Hair THg was quantified from nine insectivorous species (28 individuals), eight frugivorous species (26 individuals), two carnivorous species (five individuals), one omnivorous species (two individuals), one sanguivorous species (36 individuals), and one piscivorous species (one individual). THg ranged from 0.03 to 145.27 mg/kg ($\mu = 9.71$) across Neotropical bats (Fig. 2A), with species explaining 94% of the variation in THg (LM: $F_{21,76} = 80.01$, $p < 0.001$). Frugivorous bats (e.g., *Artibeus* spp.) had the lowest THg ($\mu = 0.04$). Our single sample from the piscivorous *Noctilio leporinus* showed the highest THg (145.27 mg/kg), ranging from 1–3 orders of magnitude above values from other Neotropical bat species.

The univariate model with dietary guild as a predictor of THg concentrations was the most supported ($\Delta\text{AICc} = 0.00$, $w_i = 0.77$; Table 2); dietary guild here explained 74% of THg variation ($F_{4,15.24} = 17.75$). Adjusting for multiple comparisons revealed that sanguivores only differed from carnivores (including the piscivore) and insectivores; carnivores and insectivores differed from all other dietary guilds; and frugivores differed from all other dietary guilds except the sanguivores and omnivores (Fig. 2A, Table S2). While the relative importance of the dietary guild variable was 100%, that of site was 23%; a univariate model with site had weak support ($\Delta\text{AICc} = 29.04$, $w_i = 0.00$) and explained no variation in THg (Fig. 2B). Sex was also a poor predictor (Table 2) and within a univariate model explained no variation in THg (Fig. 2C).

3.2. Comparative analysis of global bat THg

Mean hair THg ranged from 0.01 to 145.27 mg/kg ($\mu = 7.8$) across the 50 bat species in our global analysis; total sample size per species ranged from 1 to 1304 ($\mu = 39.48$). Bats showed strong phylogenetic signal in log THg (Fig. 3A). Pagel's λ was estimated to be 0.97 and was statistically distinct from models of no phylogenetic signal ($p < 0.001$) and differed slightly from a Brownian motion model ($p = 0.05$). The univariate WPGLS model with the proportion of potentially aquatic prey (i.e., invertebrates, ectotherms, fish) in diet was the most supported ($\Delta\text{AICc} = 0.00$, $w_i = 0.97$; Table 3). This model was far more competitive than models with dietary guild or with log body mass included as a covariate ($\Delta\text{AICc} = 7.70$ – 11.06). While the relative importance of this aquatic diet variable was 97%, that of dietary guild was only 3%. All dietary models were substantially more competitive than bat family alone ($\Delta\text{AICc} = 18.68$). After controlling for residual phylogenetic signal and sampling effort, the relative contribution of potentially aquatic prey explained 54% of the variation in THg ($F_{1,48} = 27.50$, $p < 0.0001$; Fig. 3B). Bats receiving 50% or more of their diet from potentially aquatic prey had higher THg than those species receiving less than 50% of their diet from these food sources ($t = 5.24$, $p < 0.0001$; Fig. 3B).

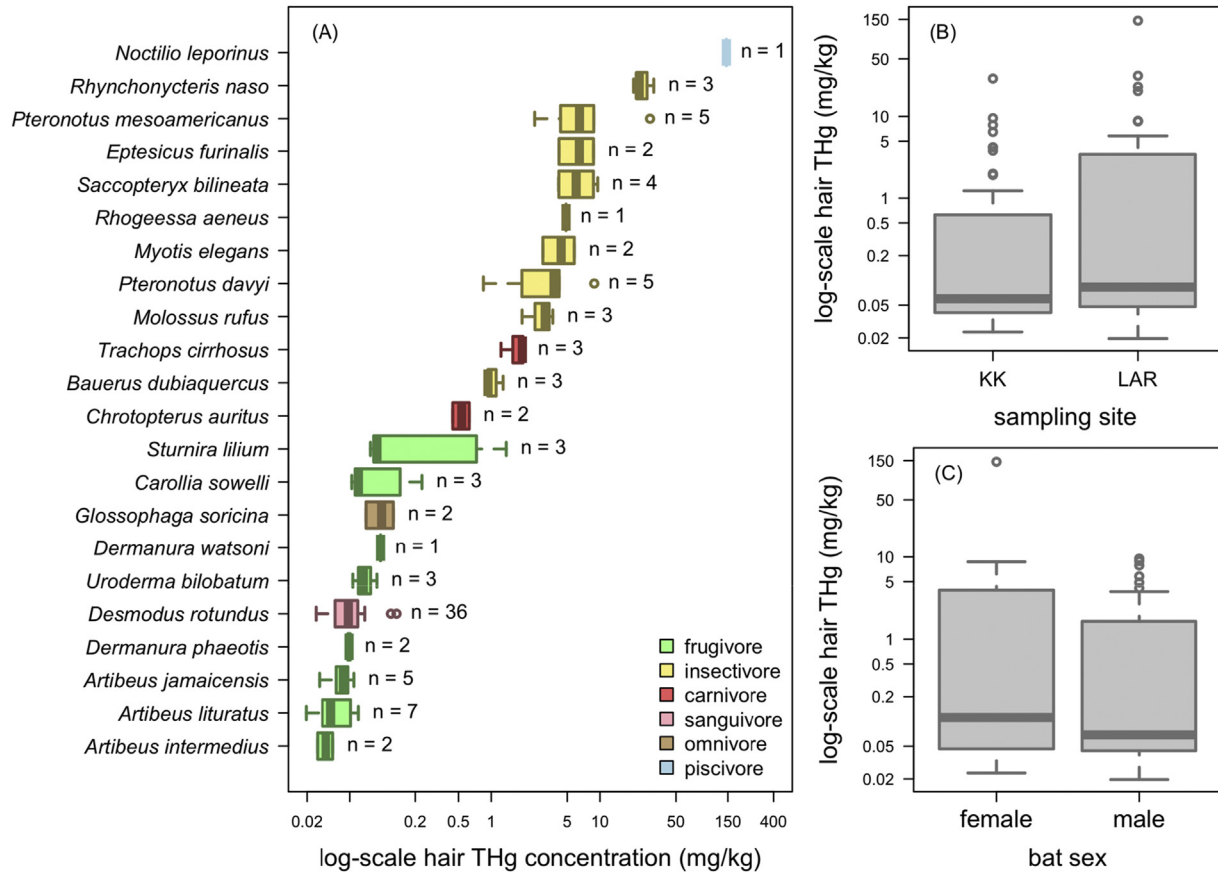


Fig. 2. Distribution of hair THg concentrations (mg/kg, presented on log scale) among Neotropical bats according to (A) species and dietary guild, (B) site, and (C) sex. Boxplots show the median and first and third quartile of THg, whiskers show the range of non-outliers, and circles show potential outliers.

Table 2
Candidate LMMs predicting log hair THg (mg/kg). Models are ranked by ΔAICc with the number of estimated coefficients (k), Akaike weights (w_i), and marginal and conditional R^2 . A random effect of species is denoted by (1|species) in all LMMs.

	Log THg models	k	ΔAICc	w_i	R^2_m	R^2_c
Full data ($n = 98$)	~ dietary guild + (1 species)	5	0.00	0.77	0.74	0.95
	~ dietary guild + site + (1 species)	6	2.37	0.23	0.74	0.95
	~ site + (1 species)	2	29.04	0.00	0.00	0.95
Sex only ($n = 86$)	~ sex + dietary guild + (1 species)	6	0.00	1.00	0.73	0.95
	~ sex + (1 species)	2	24.47	0.00	0.00	0.96
	~ sex + site + (1 species)	3	26.27	0.00	0.00	0.96
	~ sex * site + (1 species)	4	28.58	0.00	0.00	0.96

4. Discussion

Our results demonstrate significant interspecific variation in hair THg concentrations among bats that span three orders of magnitude across species. THg generally increased with bat trophic level but was best explained by the dietary connectivity of bat species to aquatic food webs.

4.1. THg in a neotropical bat community

Hair THg concentrations across our sample of Belizean bats was generally low, with most individuals (93/98) displaying concentrations below putative toxic thresholds of 10 mg/kg (Mahaffey et al., 1997; Nam et al., 2012). Higher values in insectivorous *Rhynchonycteris naso* ($\mu = 24.85$ mg/kg), which typically roosts and forages over water (Bradbury and Vehrencamp, 1976; Fenton et al., 2001), were comparable to hair THg observed in temperate

insectivorous bats such as *Eptesicus fuscus* (28.01 mg/kg) from a Hg-contaminated site along the South River, Virginia (Wada et al., 2010). Hair THg from the single *Noctilio leporinus* (145.27 mg/kg) is among the highest concentration observed in bats; in the South River, Virginia, *Myotis lucifugus*, which are known to forage over water (Clare et al., 2011, 2014b), had THg ranging from 7.3 to 275 mg/kg ($\mu = 132$ mg/kg; Nam et al., 2012). Yet in contrast to these temperate areas, the underlying source of Hg in this part of Belize is unknown. Atmospheric deposition is the most likely source of Hg in the environment (López Alonso et al., 2003). Land use could also exacerbate such Hg inputs; for example, wastewater discharge and agrochemical practices along the Rio Hondo, bordering Belize and Mexico, were speculated to contribute to bioavailable Hg in soil and water (Buenfil-Rojas et al., 2015). Previous work has also reported high Hg in Morelet's crocodile (*Crocodylus moreletii*) eggs, blood, and tail scutes in northern Belize, including in agricultural areas near our sampling sites (Rainwater

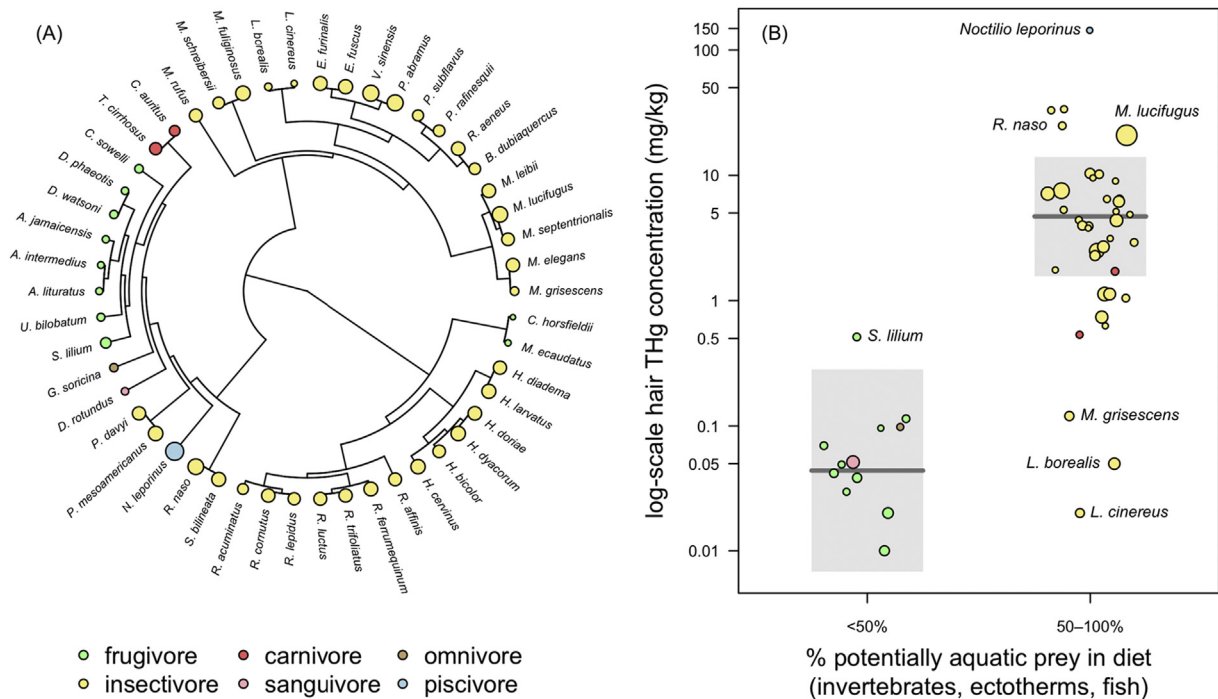


Fig. 3. (A) Phylogeny of all bat species included in the global analysis, with circle size scaled by mean log hair THg concentration and colored by dietary guild. (B) Associations between the proportion of potentially aquatic prey items in diet and THg, with values presented on log scale. Points are scaled by the sample size per species. Grey bands display 95% confidence intervals from WPGLS models, with the mean fit shown with solid lines. To match Open Tree of Life taxonomy, we renamed *Corynorhinus rafinesquii*, *Perimyotis subflavus*, and *Myotis lucifugus* to *Plecotus rafinesquii*, *Pipistrellus subflavus*, and *Myotis lucifugus carissima*, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Candidate WPGLS models predicting log hair THg (mg/kg) while accounting for bat phylogeny and log sample size. Models are ranked by $\Delta AICc$ with the number of estimated coefficients (k), Akaike weights (w_i), and R^2 .

Log THg models	k	$\Delta AICc$	w_i	R^2
~ proportion of potentially aquatic prey in diet	2	0.00	0.97	0.54
~ dietary guild	5	7.70	0.02	0.53
~ dietary guild + log mass	6	9.84	<0.01	0.55
~ proportion of potentially aquatic prey in diet + log mass	3	11.06	<0.01	0.55
~ bat family	9	18.68	<0.001	0.54

et al., 2002, 2007). Yet the lack of a site difference in bat THg suggests a localized point source of Hg contamination is unlikely. Broader agricultural intensification throughout this region of Belize could contaminate water with Hg from agrochemicals and release Hg from soil via slash-and-burn practices (Farella et al., 2007; Patterson, 2016). Assessments of soil and water Hg across habitat types and larger spatial scales could therefore help determine the sources of Hg into the Neotropical bat community.

Patterns of hair THg concentrations across Belizean bat species generally followed patterns of guild-specific bioaccumulation. Frugivores showed low THg given their feeding on basal resources. However, some bats at higher trophic levels showed low THg similar to that of frugivores; for example, the sanguivorous *Desmodus rotundus* had low THg likely due to its propensity to feed on livestock (i.e., terrestrial herbivores) when these prey are available (Voigt and Kelm, 2006). Similarly, the omnivorous *Glossophaga soricina* had lower THg, likely driven by predominantly feeding on nectar and fruit in addition to insects (Clare et al., 2014a; Wilman et al., 2014). As expected, insectivorous, carnivorous, and piscivorous bat species generally had the highest THg. Particularly high

THg in the insectivorous *Rhynchonycteris naso* ($\mu = 24.85$ mg/kg) likely reflects foraging over water and on emergent aquatic insects (Bradbury and Vehrencamp, 1976; Fenton et al., 2001). In contrast, the highest THg concentration observed in *Noctilio leporinus* likely reflects a diet of fish, insects, and crustaceans (Bordignon, 2006; Brooke, 1994). It is important to note that *Rhynchonycteris naso* and *Noctilio leporinus* are also very likely drinking from the same water sources. While other bats may achieve hydration from nectar, fruit, or moisture on foliage (Voigt et al., 2013), we expect many species to drink from standing water and—in these two cases—from the same rivers they forage over. In contrast, THg values of carnivorous *Trachops cirrhosus* and *Chrotopterus auritus* were among the lowest of the animal-feeding dietary guild. As these species were only captured in KK (Table 1), which is located away from water (Fig. 1), these comparatively lower values may reflect a more non-aquatic diet reliant on terrestrial frogs and toads, insects, small rodents, and birds that would contribute low-to-intermediate Hg concentrations (Medellín, 1988; Rodrigues et al., 2014).

Related to the above, we did not detect an effect of sampling site on THg. We observed a trend towards lower THg in KK, although

this is largely due to the absence of *Rhynchonycteris naso* or *Noctilio leporinus*, which had the highest THg concentrations. This suggests these two species are habitat locked, which is consistent with their high THg, and that other species may be more variable in their habitat usage and thus show more variable THg as they encounter a wider range of prey. For example, *Pteronotus mesoamericanus* was sampled from both sites and had the third-highest THg values in Belize species (10.19 mg/kg), suggesting it encounters a mix of both aquatic- and terrestrial-derived prey. Another species of interest is *Bauerus dubiaquercus*, which was only caught at LAR but had the lowest THg for an insectivore (1.05 mg/kg), which suggests it may have a dietary specialization regardless of proximity to a water source. More intensive sampling of Neotropical bats, particularly those species feeding on fish or displaying unexpected THg levels, are necessary to confirm that these THg concentrations are not outliers and to assess if these trends are consistent within these species and dietary guilds. While we have noted individual species of interest, our findings indicate that THg is greatest in insectivorous, carnivorous, and piscivorous bats. These species have a greater propensity to feed on aquatic-derived prey than frugivores, omnivores, and sanguivores, which supports Hg bioaccumulation increasing not only with trophic level but also with dietary connectivity to aquatic ecosystems.

4.2. Connectivity to aquatic ecosystems

Our comparative analysis supports the contention that degree of dietary connectivity to aquatic ecosystems is a key predictor of THg across bats at a global level. Closely related bat species displayed similar hair THg concentrations, likely driven by general phylogenetic similarity in dietary strategies (Cruz-Neto et al., 2001). Bat family membership itself was a poor predictor of interspecific THg, highlighting the importance of instead quantifying bat dietary composition. After accounting for evolutionary history and uneven sampling effort, we found hair THg to be greatest in bats receiving most of their diet from food potentially derived from aquatic ecosystems. Three of the four insectivorous species with the greatest THg concentrations (*Rhynchonycteris naso*, *Myotis lucifugus*, and *Pipistrellus abramus*; all >20 mg/kg) have diets dominated by insects such as dipterans and trichopterans that are either found in aquatic habitats or spend part of their life cycles in water (Anthony and Kunz, 1977; Bradbury and Vehrencamp, 1976; Lee et al., 2005). Some of these bats also feed on spiders (Lee et al., 2005; Whitaker and Lawhead, 1992), which by preying on insects associated with aquatic habitats extend bat food chains and increase the opportunity for Hg biomagnification (Cristol et al., 2008; Speir et al., 2014). In contrast, insectivorous bats with the lowest THg concentrations, such as *Lasiurus borealis* and *Lasiurus cinereus*, feed primarily on lepidopterans (Clare et al., 2009; Valdez and Cryan, 2009), which exhibit low Hg owing to a lower trophic position and having life histories divorced from aquatic ecosystems (Cristol et al., 2008; Rimmer et al., 2010). Yet as some species such as *Vespertilio sinensis* and *Miniopterus fuliginosus* show diets partly composed of lepidopterans but also showed high THg (Fukui and Agetsuma, 2010; Funakoshi and Takeda, 1998; Miura et al., 1978), observed interspecific variation could partly stem from site-specific differences in Hg contamination or from intraspecific variation in diet (e.g., seasonal differences in composition of lepidopterans and dipterans; Fukui and Agetsuma, 2010). While the unknown or poorly quantified dietary composition for many insectivorous bat species examined in our analysis precluded assigning insect prey to either aquatic or terrestrial food webs (Nowak, 1999), more generally our comparative analysis across 50 bat species provides strong evidence that dietary connectivity to aquatic food webs influences trophic transfer of Hg into terrestrial ecosystems (Blais

et al., 2007; Cristol et al., 2008; Dehn et al., 2006; Rimmer et al., 2010).

4.3. Conservation implications and future directions

High phylogenetic signal in THg and greater THg concentrations in bat species with stronger dietary links aquatic ecosystems can also suggest which species may be more vulnerable to health and fitness impacts of long-term Hg exposure, as seen with other taxa in relation to contaminants (Hammond et al., 2012; Larras et al., 2014). The only bat sampled in Belize classified as at risk by the International Union for Conservation of Nature is *Bauerus dubiaquercus* (near threatened) (Hilton-Taylor, 2000), which displayed THg below putative toxicity thresholds. However, given our dietary results, our models could predict high Hg exposure and risk posed to non-sampled Neotropical bats with direct dietary ties to aquatic habitats, such as insectivores that forage over water (e.g., some molossids and emballonurids) and other piscivorous species (e.g., *Noctilio albigentris* and *Myotis vivesi*). Resulting predictions could be important for guiding heavy metal surveillance in bats and better assessing the consequences of chronic Hg exposure for bat population dynamics and their contributed ecosystems services (Kunz et al., 2011).

How chronic Hg exposure impacts bat populations remains an ongoing area of study. Neurochemical alterations in *Myotis lucifugus* were associated with a hair THg threshold of 10 mg/kg (Nam et al., 2012), which was exceeded by five individual bats across our Belize sample and by seven bat species across our global dataset. Yet correlations between much lower THg concentrations and innate immunity were observed in *Desmodus rotundus* from these same sites (Becker et al., 2017a). An important future goal will be to better quantify sensitivity thresholds and the physiological effects of Hg in bats, which remain largely unknown but could be especially important for species listed as vulnerable (e.g., *Balan-tiopteryx io* in Belize), species in decline (e.g., *Vampyrus spectrum*), species threatened by white-nose syndrome (e.g., *Myotis lucifugus*), and species known to be reservoirs for zoonotic pathogens (e.g., *Desmodus rotundus*). While we have here reported the most comprehensive synthesis of the determinants of bat THg concentrations to date, future field and experimental studies are especially needed to understand the individual- and population-level impacts of Hg exposure on bats.

5. Conclusions

Our results demonstrate considerable variation in hair THg concentrations in wild bat species that span three orders of magnitude. Hair THg somewhat followed expected patterns of Hg bioaccumulation with increasing trophic level, although sanguivorous and several carnivorous species showed relatively lower THg concentrations. Hair THg showed strong phylogenetic signal, and interspecific variation in concentrations was best explained by dietary connectivity of bat species to aquatic food webs. Our results highlight that phylogeny can be predictive of Hg concentrations through similarity in diet and how interspecific variation in feeding strategies influences chronic exposure to Hg. More broadly, our results illustrate how trophic connectivity in food webs enables the movement of contaminants from aquatic to terrestrial ecosystems.

Competing interests

We have no competing interests.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.envpol.2017.10.010>.

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