Disentangling interactions between mercury, immunity, and infection in a Neotropical bat community

Daniel J. Becker[1,2*], Kelly A. Speer[3-5], Jennifer M. Korstian[6], Dmitriy V. Volokhov[7], Hannah F. Droke[8], Alexis M. Brown[9], Catherene L. Baijnauth[10], Ticha Padgett-Stewart[11], Hugh G. Broders[12], Raina K. Plowright[11], Thomas R. Rainwater[13-15], M. Brock Fenton[16], Nancy B. Simmons[17], Matthew M. Chumchal[18]

[1]Department of Biology, Indiana University, Bloomington, IN, USA
[2]Center for the Ecology of Infectious Disease, University of Georgia, Athens, GA, USA
[3]Richard Gilder Graduate School, American Museum of Natural History, New York, NY, USA
[4]Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
[5]Center for Conservation Genomics, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, D.C., USA
[6]Department of Biological Sciences, Texas Tech University, Lubbock, TX, USA
[7]Center for Biologics Evaluation and Research, Food and Drug Administration, Silver Spring, MD, USA
[8]Department of Global and Planetary Health, University of South Florida, Tampa, FL, USA
[9]Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, USA
[10]Sackler Institute of Comparative Genomics, American Museum of Natural History, New York, NY, USA
[11]Department of Microbiology and Immunology, Montana State University, Bozeman, MT, USA
[12]Department of Biology, University of Waterloo, Waterloo, ON, Canada
[13]Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA
[14]Baruch Institute of Coastal Ecology and Forest Science, Clemson University, Georgetown, SC, USA
[15]Tom Yawkey Wildlife Center, Georgetown, SC, USA
[16]Department of Biology, Western University, London, Ontario, Canada

31 [17]Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural
32 History, New York, NY, USA
33 [18]Department of Biology, Texas Christian University, Fort Worth, TX, USA
34 [*]Corresponding author, danbeck@iu.edu
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Abstract

1. Contaminants such as mercury are pervasive and can have immunosuppressive effects on wildlife. Impaired immunity could be important for forecasting pathogen spillover risks, as many land-use changes that generate mercury contamination can also bring wildlife reservoir hosts into close contact with humans and domestic animals. However, the interactions between contaminants, immunity, and infection are difficult to study in natural systems, and empirical tests of possible directional relationships remain rare.
2. We capitalized on extreme mercury variation in a diverse Neotropical bat community in Belize to test association between contaminants, immunity, and infection. By comparing a previous dataset of bats sampled in 2014 with new data from 2017, we first confirmed bat species with more aquatic prey in their diet had higher fur mercury. We then tested covariation between mercury and cellular immunity and determined if such relationships mediated associations between mercury and common bacterial pathogens (hemoplasmas and *Bartonella*). Lastly, as bat ecology can dictate exposure to mercury and pathogens, we also assessed species-specific patterns in these mercury–infection relationships.
3. Across the bat community, individuals with higher mercury had fewer neutrophils but not lymphocytes, suggesting stronger associations with innate immunity. However, the odds of infection for both pathogens were generally lowest in bats with high mercury, and relationships between mercury and immunity did not mediate infection patterns. When considering species-specific relationships between mercury and infection, mercury was associated with especially low odds for *Pteronotus mesoamericanus* and *Dermanura phaeotis* for hemoplasmas. Yet for *Bartonella*, mercury was associated with particularly low odds in the genus *Pteronotus* but especially high odds within the Stenodermatinae.
4. *Synthesis and application*: Lower infection risk in bats with high mercury despite weaker innate defense suggests contaminant-driven loss of pathogen habitat (i.e., anemia) or vector mortality as possible causal mechanisms. Strong positive associations between mercury and *Bartonella* in the Stenodermatinae, however, alongside negative associations between mercury and neutrophils in this clade, suggest these bats could be especially vulnerable to immunosuppression. Greater attention to these potential causal pathways could help disentangle the complex relationships between environmental contaminants, immunity, and infection in natural systems and forecast disease risks.

Introduction

Wildlife are commonly exposed to a range of contaminants that are ubiquitous in the environment, including heavy metals, organic compounds, and pesticides (Smith et al., 2007). Contaminants can be novel stressors that have direct impacts such as mortality (Davidson, 2004) and more subtle consequences such as immunosuppression (Grasman, 2002). For example, even relatively low concentrations of mercury (Hg), a neurotoxic heavy metal, can impair wildlife immunity (Scheuhammer, Meyer, Sandheinrich, & Murray, 2007). When immunosuppression manifests in increased susceptibility to pathogens, environmental gradients of contaminants could increase infection prevalence or intensity in wild hosts (Becker, Albery, et al., 2020). These elevated infection risks could be especially relevant in the context of environmental changes such as gold mining and agricultural land clearing, both of which allow contaminants like Hg to bioaccumulate in aquatic and terrestrial food webs (Almeida, Lacerda, Bastos, & Herrmann, 2005; Palheta & Taylor, 1995). As land conversions such as these also facilitate novel interactions between wildlife, domestic animals, and humans, impaired immunity could further increase pathogen spillover risks (Borremans, Faust, Manlove, Sokolow, & Lloyd-Smith, 2019).

The interactions between contaminants, immunity, and infection are notoriously difficult to study in natural systems, and empirical tests of possible directional relationships remain rare (Ross, 2002). Without captive or field experiments, natural systems must demonstrate sufficient variation in contaminant exposure and infection status to permit inference, and these criteria may be hard to meet in practice. For example, recent work on urbanized bobcats demonstrated strong effects of anticoagulant exposure on immunity in ways that should increase susceptibility, but pathogens of clinical relevance were generally rare, making it difficult to draw epidemiological inferences (Serieys et al., 2018). Additionally, effects may be difficult to detect if contaminant concentrations have low variance or are below toxicity thresholds (Fisk et al., 2005). Other examples suggest contaminants may instead decrease infection risks (Prüter et al., 2018), but the degree to which such patterns might be mediated by contaminant effects on immunity are unclear. Field-based assessments of how variable contaminant concentrations are associated with both immunity and common pathogens are necessary to disentangle directional relationships.

Here, we capitalized on high variation in Hg and infection across species in a diverse Neotropical bat community in Belize to test associations between contaminants, immunity, and infection. Although Hg concentrations are typically highest in aquatic animals owing to

100 bioaccumulation (Chumchal et al., 2011), such contaminants can transfer into terrestrial
101 ecosystems through diet (Cristol et al., 2008). Neotropical bats are ecologically diverse (Gunnell
102 & Simmons, 2012; Rojas, Vale, Ferrero, & Navarro, 2011), and their diet variation enables
103 strong heterogeneity in Hg exposure. Specifically, the degree to which species feed on aquatic
104 prey (or prey with at least some life stages linked to aquatic ecosystems) determines bat fur
105 concentrations of Hg, such that insectivores and species feeding on amphibians and fish have
106 greater diet exposure than frugivores and sanguivores (Becker, Chumchal, et al., 2018). Such
107 variation should produce strong associations with immunity, as even sublethal Hg concentrations
108 correlate with immunity (Becker et al., 2017). Because bats can be vulnerable to extracellular
109 pathogens and can also harbor viral and bacterial zoonoses (Brook & Dobson, 2015), immune
110 differences driven by dietary variation in Hg could have health implications for disease risks to
111 and from bats. This sampled region in Belize is also undergoing intensive land clearance for
112 agriculture similar to much of Latin America (Patterson, 2016), and thus analyses of Hg,
113 immunity, and infection can also help assess how land use affects wildlife and human health.
114 Here we built upon our prior studies of Hg and of infectious disease in Neotropical bats
115 (e.g., Becker, Chumchal, et al., 2018; Becker, Speer, et al., 2020) to address three study aims.
116 First, we assessed whether bat dietary connectivity to aquatic ecosystems is the primary driver of
117 Hg bioaccumulation despite spatiotemporal variation. We combined historic and new data on Hg
118 concentrations in bat fur, an indication of long-term metal exposure (Flache et al., 2015), and
119 compared contaminant load over a three-year period and two sites. Second, we tested whether
120 elevated bat Hg is correlated with impaired cellular immunity, using blood samples. Third, we
121 examined how infection with two common bacterial pathogens is associated with Hg and tested
122 if patterns were mediated by immunological relationships. We predicted long-term Hg exposure
123 would be highest in bats more reliant on aquatic food webs and that individuals of these species
124 would have lower measures of cellular immunity, which could manifest in higher infection risks.
125

126 **Methods**

127 *Bat sampling*

128 During April 28 to May 4 2014 and April 24 to May 6 2017, we sampled 249 bats from 29
129 species captured in two areas of the Orange Walk District of Belize: Lamanai Archeological
130 Reserve (LAR) and Ka'Kabish (KK). The LAR is bordered by the New River Lagoon, forest,

131 and agriculture, while KK is a remnant forest patch surrounded by agriculture located 10 km
132 away. At least 44 of the 70 bat species in Belize have been recorded in this region (Herrera,
133 Duncan, Clare, Fenton, & Simmons, 2018; Reid, 1997). Bats were captured with mist nets from
134 19:00 until 22:00, and harp traps were also set from 18:00 to 05:00.
135 Bats were placed in individual cloth bags until processing and were identified to species
136 based on morphology (Reid, 1997). For Hg analysis, we trimmed <10 mg of fur from the dorsal
137 or ventral region. Scissors were cleaned with ethanol between processed bats, and samples were
138 stored in individual cryovials or Ziploc bags. From a subset of bats sampled in 2017, we
139 collected 3–30 μL of blood by lancing the propatagial vein with sterile needles, followed by
140 collection using heparinized capillary tubes. Thin blood smears were prepared on glass slides and
141 stained with Wright–Geimsa (Astral Diagnostics Quick III) to characterize cellular immunity.
142 Remaining blood was stored on Whatman FTA cards (room temperature) or RNAlater (room
143 temperature for four weeks and then –20°C) to preserve bacterial DNA. All bats were released
144 after processing. Sampling followed guidelines for safe and humane handling of bats issued by
145 the American Society of Mammalogists (Sikes, Care, & Mammalogists, 2016) and was approved
146 by the University of Georgia Animal Care and Use Committee (A2014 04-016-Y3-A5).
147 Sampling was authorized by the Belize Forest Department under permits CD/60/3/14(27),
148 WL/2/1/17(16), and WL/2/1/17(19). Sample size for Hg varied by year (2014=98, 2017=148)
149 and by site (LAR=163, KK=83) and ranged from 1–58 individuals per species ($\bar{x}$=30 ± 29 SE).
150
151 *Fur Hg analysis*
152 Bat fur was analyzed for total Hg (THg) at the Texas Christian University Aquatic Ecology
153 Laboratory. THg data from 2014 were published previously (Becker, Chumchal, et al., 2018).
154 Fur samples were rinsed in a 2:1 chloroform:methanol solution and dried overnight in a fume
155 hood and reported on a fresh weight basis. We quantified THg with a direct Hg analyzer (DMA-
156 80, Milestone, CT, USA) and analyzed National Research Council Canada reference material
157 DORM 4 (certified value = 0.412 ± 0.036 mg/kg) every 10 samples for quality control; mean
158 recovery was 94.32 ± 0.96% for 2017 data. Limited fur resulted in some samples falling below
159 detection limit (DL), which was higher in 2014 (~0.48 ng). THg values below DL were
160 estimated as 50% DL, and we used the 2014 DL to standardize concentrations (Rainwater et al.,

2005). Fur THg was expressed in mg/kg and $\log_{10}$-transformed prior to statistical analyses. THg is a proxy for methylmercury, which comprises 71-95% of Hg in bat fur (Yates et al., 2013).

Statistical analysis of fur THg

To first link bats to aquatic food webs (i.e., the primary source of dietary Hg exposure; Becker, Chumchal, et al., 2018), we used the EltonTraits database to classify bat species according to the proportion of diet consisting of potentially aquatic prey: invertebrates, ectothermic tetrapods, and fish (Wilman et al., 2014). We used phylogenetic generalized linear mixed models (GLMMs) to test how THg varied with bat diet, site (LAR and KK), and year (2014 and 2017). We fit candidate models that considered all fixed effects and their two- and three-way interactions. We fit the phylogenetic GLMM using the *brms* package in R, default priors, and Gaussian errors (Bürkner, 2017). We included random effects for species and phylogeny, the latter of which used a phylogenetic covariance matrix derived from the Open Tree of Life through the *rotl* and *ape* packages (Michonneau, Brown, & Winter, 2016; Paradis, Claude, & Strimmer, 2004). We ran four chains for 20,000 iterations with a burn-in period of 10,000, thinned every 10 steps, for a total 4,000 samples. We compared GLMMs using leave-one-out cross-validation (LOOIC) and assessed fit with a Bayesian R^2, including the total modeled variance and that attributed to only the fixed effects (Gelman, Goodrich, Gabry, & Vehtari, 2019; Vehtari, Gelman, & Gabry, 2017). We then estimated fixed effects per predictor (means and 95% highest density intervals [HDI]) and visualized fitted values with 100 random draws from the GLMM posterior distribution.

Quantifying immunity and bacterial infection

Using blood smears, we first estimated total white blood cell (WBC) counts as the mean number of leukocytes from 10 fields of view (400X) with a light microscope (Schneeberger, Czirják, & Voigt, 2013). We next used differential WBC counts (1000X) to quantify the relative abundance of neutrophils and lymphocytes from 100 leukocytes. Neutrophils are components of the innate immune system, whereas lymphocytes are involved in adaptive responses like immunoglobulin production (Lanier, 2013). We derived absolute leukocyte counts by multiplying the total and differential WBC data. Elevated absolute WBC counts can indicate a more robust cellular defense or an inflammatory response to acute infection (French, Fokidis, & Moore, 2008).

To detect bacterial pathogens, we extracted genomic DNA from blood using QIAamp DNA Investigator Kits and DNeasy Blood and Tissue Kits (Qiagen). Before extracting RNAlater-preserved blood, samples were vortexed with 1 mL 1X phosphate-buffered saline and centrifuged, from which 200 µL from the bottom of the tube was used for extraction. We used PCR to test for hemoplasmas (targeting the 16S rRNA gene) and *Bartonella* spp. (targeting the *gltA* gene) using previous diagnostic protocols (Bai, Gilbert, Fox, Osikowicz, & Kosoy, 2016; Volokhov et al., 2017). Both pathogens are commonly in Neotropical bats (Ikeda et al., 2017), and infection status can strongly correlate with bat immunity (Becker, Czirják, et al., 2018). Hemoplasma data and sequences have been published previously (Becker, Speer, et al., 2020).

Analyses of THg, immunity, and infection

We used phylogenetic GLMMs to test the overall relationship between THg and both absolute neutrophil and lymphocyte counts. Each model included THg as the fixed effect, with species and phylogeny as random effects. We used a Gaussian distribution for $\log_{10}$-transformed WBC counts. We next fit phylogenetic GLMMs with binomial errors to test associations between THg and infection with hemoplasmas and *Bartonella*. We then used causal mediation analyses to test support for directional relationships between THg, immunity, and infection (Imai, Keele, & Tingley, 2010). This estimates how much of a directional relationship (i.e., outcome model) is mediated indirectly by a third variable (i.e., mediator model). Mediator models were each of the GLMMs predicting immunity by THg. For outcome models, we fit two GLMMs per pathogen; each modeled infection as a function of THg and each WBC count. We used the *brms* package to estimate the proportion of the relationship between THg and infection mediated by immunity.

Because bat ecology likely dictates exposure to contaminants and pathogens, we assessed species-specific patterns in Hg–infection relationships. We fit logistic regressions for each bat species and pathogen when sample sizes were sufficient (e.g., $n>2$). As small samples can bias odds ratio estimates, we used the *logistf* package to implement Firth's bias reduction (Heinze & Schemper, 2002). For species with no variance in infection, we assigned log odds of zero. We estimated phylogenetic signal (Pagel's λ) in the log odds using the *caper* package and used phylogenetic generalized least squares to test if log odds covaried with sample size (Orme, 2013). We lastly used phylogenetic factorization to identify clades with different log odds at various taxonomic depths. We used the *taxize* and *phylofactor* packages to obtain taxonomic

222 information for each bat species and to partition the log odds as a Gaussian response in a GLM
223 (Chamberlain & Szöcs, 2013; Washburne et al., 2019). We weighted by sample size per species
224 and used Holm's sequentially rejective test to determine the number of significant bat clades.
225
226 **Results**
227 *Neotropical bat fur THg*
228 Expanding our initial studies of fur Hg across this Neotropical bat community in 2014, we found
229 that THg varied up to five orders of magnitude across species, sites, and years (Fig. 1). Our top
230 model included interactions between diet and year and between year and site (Table 1). The
231 proportion of potentially aquatic prey in diet positively predicted THg but more so in 2014
232 (β=0.019, 95% HDI: 0.011–0.026) than in 2017 (β=0.016, 95% HDI: 0.008–0.023; Fig. 2A). We
233 also identified strong spatiotemporal variation, such that fur THg increased between 2014 and
234 2017 for KK ($\tilde{x}$=0.46 to 0.66) but slightly decreased for LAR ($\tilde{x}$=0.52 to 0.49).
235
236 *Associations with immunity and infection*
237 Across bats sampled in 2017 with Hg and WBC data (*n*=52), higher THg was associated with
238 fewer neutrophils (β=–0.48, 95% HDI:–0.89 to –0.12) but not lymphocytes (β=–0.36, 95% HDI:
239 –0.83 to 0.03; Fig. 2B). However, higher THg was also associated with lower odds of infection
240 for hemoplasmas (OR=0.19, 95% HDI: 0.04–0.79, *n*=134) and *Bartonella* (OR=0.18, 95% HDI:
241 0.03–0.84, *n*=117; Fig. 3A). Accordingly, the relationship between THg and leukocytes did not
242 mediate relationships between THg and infection.
243 When we analyzed relationships between THg and infection per species and pathogen,
244 we only found significant protective effects for *Pteronotus mesoamericanus* and hemoplasmas
245 after adjusting for multiple comparisons (ln(OR)=–10.20, *p*=0.001; Table 2). We also detected a
246 strong negative association between THg and *Bartonella* in this species (ln(OR)=–3.34), but no
247 log odds were significantly different from zero after adjustment. Most species instead had null
248 relationships between THg and infection (i.e., 36% for hemoplasmas and 43% for *Bartonella*) or
249 relatively weaker negative effects (e.g., *Dermanura phaeotis*, ln(OR)=–7.58 for hemoplasmas; *P.*
250 *fulvus*, ln(OR)=–3.35 for *Bartonella*). These negative THg–infection associations were identified
251 for 29% of species for both pathogens. We also estimated similar proportions of positive THg
252 associations for hemoplasmas (36%) and *Bartonella* (29%). *Desmodus rotundus* had the

253 strongest positive THg effect size for hemoplasma infection (ln(OR)=2.40), whereas *Dermanura*
254 *watsoni* had the largest positive THg effect size for *Bartonella* infection (ln(OR)=8.9).
255 Comparative analyses of the log odds ratios across bat species revealed no phylogenetic
256 signal for the relationship between THg and hemoplasmas (λ=0) but strong phylogenetic signal
257 for the relationship between THg and *Bartonella* (λ=0.84). Log odds ratios were not associated
258 with sample size for hemoplasmas ($F_{1,12}$=1.46, p=0.25) or *Bartonella* ($F_{1,12}$=0.25, p=0.63).
259 Phylogenetic factorization further identified species-specific or taxonomic patterns in the
260 magnitude and direction of effect size. For hemoplasmas, the odds of infection were significantly
261 lower for *Pteronotus mesoamericanus* and *Dermanura phaeotis* when compared to the remaining
262 sampled bat phylogeny. For *Bartonella*, however, the odds of infection were significantly lower
263 for the genus *Pteronotus* (mean ln(OR)=–3.34) and significantly higher for the subfamily
264 Stenodermatinae (*Dermanura* spp. and *Sturnira parvidens*, mean ln(OR)=5.79; Fig. 3B). Post-
265 hoc GLMs showed that bats in the Stenodermatinae had especially negative associations between
266 THg and neutrophils (β=–2.14, p=0.001) but not lymphocytes (β=–0.43, p=0.63), but these
267 analyses were limited by small sample size (n=7).
268
269 **Discussion**
270 Interactions between contaminants, immunity, and infection are difficult to disentangle in natural
271 systems, but quantifying their proposed causal relationships can inform how land-use change
272 affects wildlife health and human disease risks. By capitalizing on a diverse Neotropical bat
273 system with high variation in Hg bioaccumulation and bacterial pathogens, we found higher THg
274 was associated with fewer neutrophils but also lower odds of infection. Our species-specific and
275 taxonomic analyses showed THg had protective effects for hemoplasmas and *Bartonella* in the
276 genus *Pteronotus*, whereas THg was associated with fewer neutrophils and elevated infection in
277 the subfamily Stenodermatinae. These contrasting relationships suggest contaminant-driven loss
278 of pathogen habitat (i.e., anemia) or vector mortality versus immunosuppression as possible
279 causal mechanisms, respectively, and identify clades of Neotropical bats that may be especially
280 resilient or vulnerable to infection risks stemming from long-term Hg exposure.
281 Expanding our prior analyses of this Neotropical bat community and global patterns of
282 THg in bat fur (Becker, Chumchal, et al., 2018) with larger within-species sample sizes, we first
283 demonstrated that Hg exposure increases as a function of potentially aquatic prey (or prey with at

284 least some life stages linked to aquatic ecosystems) in diet despite spatial and temporal variation
285 in THg. Consistent positive associations with diets linked to aquatic ecosystems across sites and
286 years provides additional support for trophic transfer of Hg through foraging (Cristol et al., 2008;
287 Speir et al., 2014). This diet-mediated connectivity to aquatic ecosystems likely underlies other
288 cases of guild-specific Hg bioaccumulation in bat communities (Carrasco-Rueda, Loiselle, &
289 Frederick, 2020; Korstian, Chumchal, Bennett, & Hale, 2018). In many of these regions, bat diet
290 exposure to Hg is driven by land-use changes such as gold mining and agriculture (Carrasco-
291 Rueda et al., 2020; Costantini, Czirják, Bustamante, Bumrungsri, & Voigt, 2019), whereas
292 atmospheric deposition is often the primary source of Hg in regions located further from
293 anthropogenic point sources (Chételat et al., 2018; Korstian et al., 2018). The latter is a likely
294 source of Hg in the Belize system (Becker, Chumchal, et al., 2018), although intensified
295 agriculture and slash-and-burn practices in this region could provide other Hg inputs and may
296 explain why bat THg increased between 2014 and 2017 in KK but not LAR (Patterson, 2016).
297 Across bat species, fur THg was negatively correlated with neutrophil counts, which
298 mirrors captive results and suggests impaired innate immunity (Lalancette, Morin, Measures, &
299 Fournier, 2003). Previously, vampire bats sampled in Belize with high fur THg had weaker
300 innate defense (i.e., bacterial killing ability; Becker et al., 2017). Wrinkle-lipped free-tailed bats
301 with higher Hg exposure also had weaker innate immunity (i.e., bacterial killing ability,
302 lysozyme and haptoglobin concentrations; Costantini et al., 2019). Most individual bats for
303 which we had both Hg and immunity data showed THg below toxicity and subclinical thresholds
304 of 5–10 mg/kg (Nam et al., 2012), which suggests innate immunity could be weakened at
305 sublethal contaminant concentrations (Lewis, Cristol, Swaddle, Varian-Ramos, & Zwollo, 2013).
306 Alternatively, sublethal effects of THg could combine with other stressors (e.g., reproduction,
307 food and roost availability) to impair immunity. Additional immune measures across broader
308 land-use gradients would help characterize functional differences in defense in relation to THg
309 concentrations in anthropogenic habitats (Becker, Albery, et al., 2020; Costantini et al., 2019).
310 Although neutrophils were lowest in bats with high Hg exposure, the odds of infection
311 with hemoplasmas and *Bartonella* decreased with fur THg. As in other mammals, bats
312 challenged with bacteria produce neutrophils as part of the innate immune response (Weise,
313 Czirják, Lindecke, Bumrungsri, & Voigt, 2017). Elevated neutrophil counts could be protective,
314 as implied through negative associations between innate immunity and these two pathogens in

vampire bats (Becker, Czirják, et al., 2018). Accordingly, relationships between THg and immunity did not mediate the relationships between THg and infection, which likely indicates immunosuppression is not a causal mechanism. One alternative may involve contaminant-mediated pathogen mortality; for example, lead exposure likely caused helminth mortality in avian hosts (Prüter et al., 2018). As intracellular pathogens, hemoplasmas and *Bartonella* both rely on red blood cells. Hg can lower erythrocyte counts (Shaw, Dash, & Panigrahi, 1991), which could reduce resources available to both bacteria. We did not measure anemia or Hg in blood; however, fur THg strongly correlates with blood THg, despite the former being orders of magnitude higher than the latter (Wada, Yates, Evers, Taylor, & Hopkins, 2010). As *Bartonella* and possibly hemoplasmas likely depend in part on vector-borne transmission (Becker, Bergner, et al., 2018; Willi et al., 2007), ectoparasite mortality from contaminants in hosts or the environment could also explain observed infection patterns (e.g., as found for some avian ectoparasites; Eeva & Klemola, 2013). Lastly, we did not reliably age bats, but older animals typically have higher fur THg (Korstian et al., 2018). If older bats also have stronger adaptive immunity (e.g., antibody titers in *Saccopteryx bilineata*; Schneeberger, Courtiol, Czirják, & Voigt, 2014), age could explain negative associations between THg and infection.

Our species-specific analyses suggested that possibly protective effects of THg on infections primarily occurred in the genus *Pteronotus*, with strong negative effects for *P. mesoamericanus* for both pathogens. Both sampled species in this genus had high THg, being insectivores that often eat dipterans and coleopteran (Salinas-Ramos, Herrera Montalvo, León-Regagnon, Arrizabalaga-Escudero, & Clare, 2015). Given this strong clade-based signal, *Pteronotus* bats may be particularly resilient to disease impacts of Hg exposure. Such effects could be in part mediated by high host-specificity of bat flies for this genus (Ter Hofstede, Fenton, & Whitaker, 2004), particularly if high THg increases vector mortality or if aspects of bat fly biology impact vector competence (Weiss & Aksoy, 2011). In contrast, we also identified several species with positive relationships between THg and infection. For hemoplasmas, higher THg was associated with hemoplasma risk in vampire bats. As this species frequently feeds on humans and livestock (Streicker & Allgeier, 2016), focused pathogen surveillance would be particularly important in habitats that are contaminated by agriculture or mining. Additionally, the Stenodermatinae displayed strong positive associations between THg and *Bartonella*. These frugivorous bats also showed negative correlations between THg and neutrophils, suggesting Hg-

346 mediated immunosuppression. Such species may be especially vulnerable to infection from Hg
347 exposure and could play key roles in maintaining *Bartonella* infection cycles between bats and
348 ectoparasites in environments with high Hg contamination (Judson, Frank, & Hadly, 2015).
349 From another perspective, because the Stenodermatinae and *Pteronotus* had lower and higher fur
350 THg, respectively, low Hg exposure could increase susceptibility while higher concentrations
351 instead cause anemia and facilitate protective effects against erythrocyte-dependent pathogens.
352 Beyond bats and their pathogens, our study more broadly emphasizes the need to assess
353 potential causal relationships between contaminants and infectious diseases in natural systems. In
354 particular, we provide a novel perspective on integrating approaches from ecotoxicology with
355 those of disease ecology to disentangle the complex relationships between contaminants,
356 immunity, and infection. Future work that carefully integrates data on contaminant exposure,
357 multiple immune measures, and pathogen diversity (e.g., using metagenomics approaches;
358 Bergner et al., 2019) across site gradients of anthropogenic intensity could help identify
359 particular habitats, host species, and infections for which disease risks are highest.
360

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365

366 **Data accessibility**
367 Data from 2017 will be deposited in Dryad Digital Repository upon acceptance. Data from 2014
368 have been published previously (Becker, Chumchal, et al., 2018).
369

370 **Author contributions**
371 DJB, KAS, AMB, HGB, and NBS collected samples; JMK, DJB, KAS, DVV, AMB, CLB, HD,
372 and TPS analyzed samples; DJB analyzed the data; and HGB, RKP, TRR, MBF, NBS, and
373 MMC provided funding and logistical support. DJB wrote the paper with input from authors.
374
375

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Tables

Table 1. Competing phylogenetic GLMMs predicting log fur THg concentrations across the Belize bat community (n=249). Models are ranked by ΔLOOIC with LOOIC SE, Akaike weights (w_i) and Bayesian R^2 estimates. All models include random effects for species and phylogeny.

Fixed effects	**LOOIC**	**SE**	**ΔLOOIC**	w_i	R^2_m	R^2_c
~ diet + year + site + year:site + diet:year	76.21	38.83	0.00	0.39	0.80	0.92
~ diet + year + site + year:site + diet:year + diet:site	77.22	38.12	1.01	0.24	0.79	0.92
~ diet * year * site	77.64	37.03	1.43	0.19	0.79	0.92
~ diet * year + site	78.78	39.63	2.57	0.11	0.80	0.92
~ diet + year + site + diet:site + diet:year	79.57	38.96	3.36	0.07	0.79	0.92
~ diet + year + site + diet:site + year:site	86.87	33.20	10.66	>0.01	0.77	0.91
~ diet + year * site	89.33	33.93	13.13	>0.01	0.78	0.91
~ diet *site + year	89.97	33.94	13.77	>0.01	0.77	0.91
~ diet + year + site	94.43	34.22	18.23	>0.01	0.78	0.91

397 Table 2. Results of species-specific logistic regressions (using Firth's bias reduction method)

398 between bat fur THg concentrations and infection status per each bacterial pathogen.

	Hemoplasmas				***Bartonella***			
Bat species	**ln(OR)**	***p***	σ^2	***n***	**ln(OR)**	***p***	σ^2	***n***
Eptesicus furinalis	-1.545	0.4569	0.214	8	0	1	0	7
Bauerus dubiaquercus	0	1	0	3	0	1	0	3
Dermanura watsoni	-0.128	0.984	0.267	6	8.904	0.3177	0.167	6
Dermanura phaeotis	-7.578	0.2562	0.278	9	4.27	0.5789	0.214	8
Sturnira parvidens	1.099	0.7923	0.257	15	4.198	0.4613	0.194	9
Carollia sowelli	0.213	0.9427	0.178	10	-1.987	0.5159	0.233	10
Trachops cirrhosus	0	1	0	3	0	1	0	3
Chrotopterus auritus	0	1	0	3	0	1	0	3
Glossophaga soricina	0.665	0.8421	0.218	11	-2.373	0.4911	0.194	9
Desmodus rotundus	2.395	0.3328	0.208	22	0.178	0.933	0.208	22
Pteronotus mesoamericanus	-10.201	0.0001	0.227	22	-3.339	0.0159	0.25	16
Pteronotus fulvus	1.653	0.65	0.25	4	-3.346	0.4073	0.25	4
Rhynchonycteris naso	0	1	0	4	0	1	0	3
Saccopteryx bilineata	0	1	0	8	0	1	0	8

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Figures and legends

Figure 1. THg concentrations in bat fur across Neotropical bat species sampled in 2014 and 2017 across two sites in Belize. Boxplots are colored by the proportion of potentially aquatic prey in bat diets from the EltonTraits database. THg concentrations are displayed on a $\log_{10}$ scale.

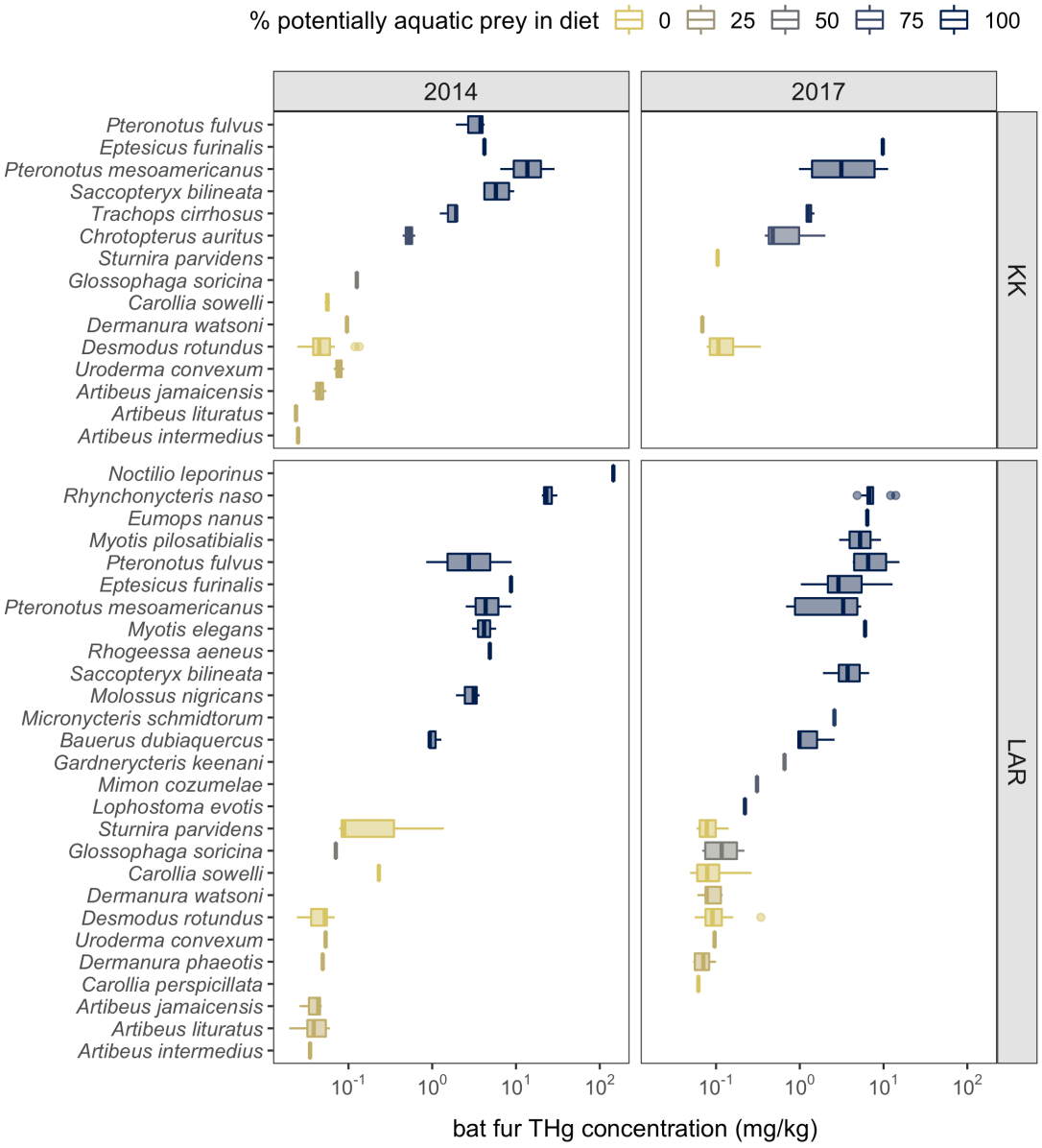


Figure 2. Dietary drivers of THg concentrations in Neotropical bat fur (A) and cellular immunity correlates of THg (B). Points indicate individual bats and are colored by sampling year in Belize. Lines display 100 random draws from the posterior distribution of the main phylogenetic GLMMs. THg concentrations and absolute leukocyte counts are displayed on a $\log_{10}$ scale.

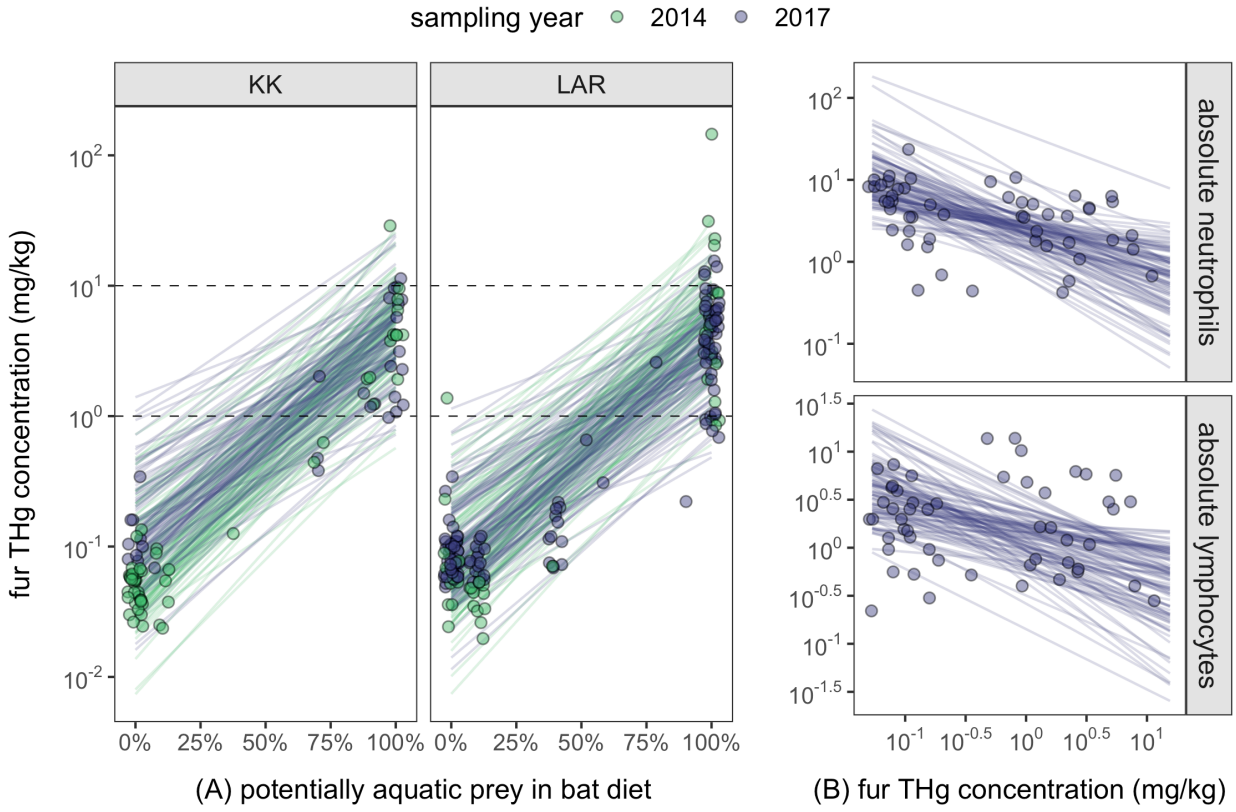
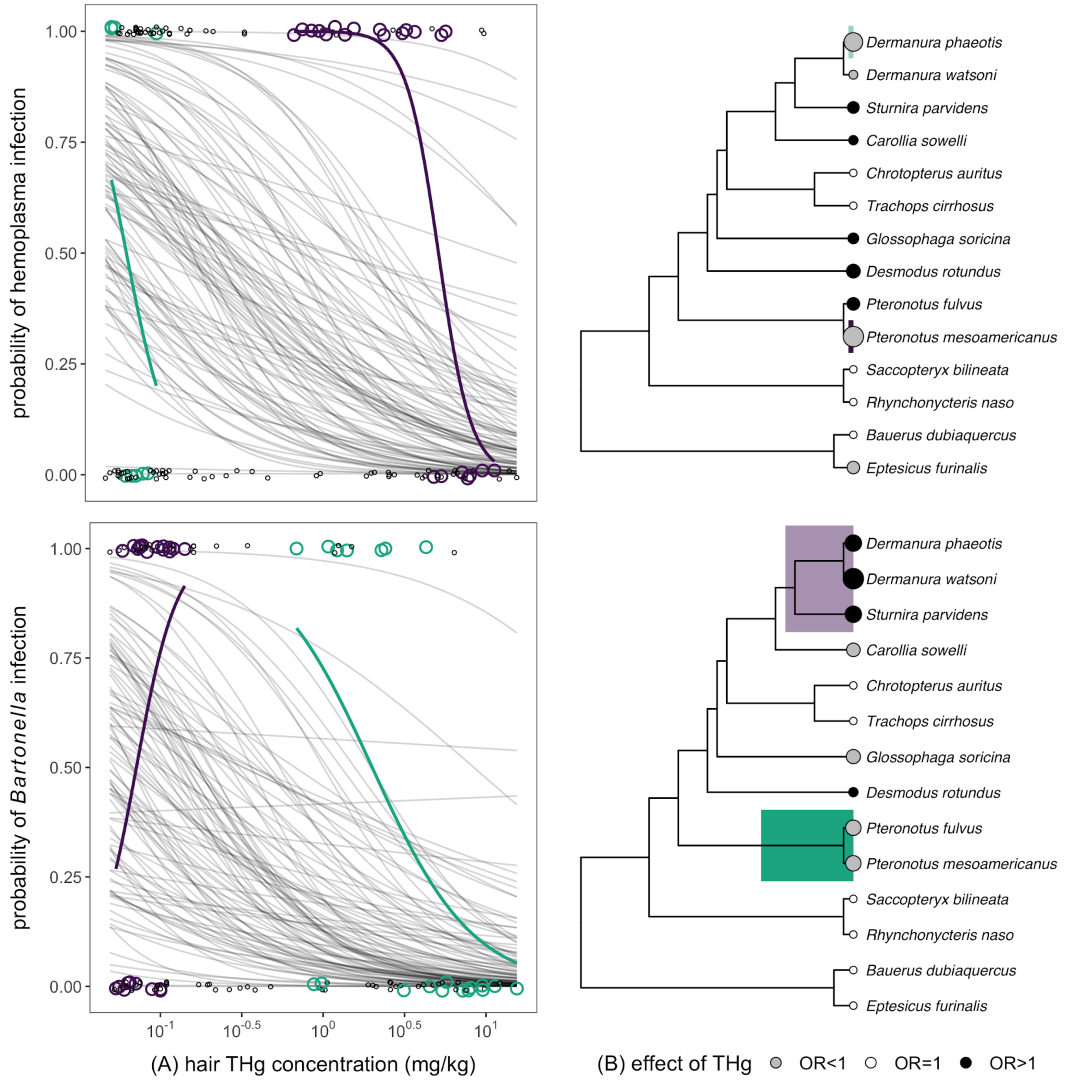


Figure 3. Associations between fur THg and bacterial infection (A) across the Belize Neotropical bat community and (B) on a per-species basis. Points in A indicate individual bats, and thin lines show 100 random draws from the posterior distribution of the phylogenetic GLMMs. Points in B indicate bat species, are scaled by the absolute log odds, and are colored by the direction of the relationship between THg and infection: null effects (i.e., OR=1, white), protective effects of THg (i.e., OR<1, grey), and mercury as a risk factor (i.e., OR>1, black). Data are shown for hemoplasmas (top) and *Bartonella* (bottom). Color indicates bat clades identified through phylogenetic factorization of log odds ratios, with lines indicating clade-specific GLM fits.



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