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Mercury Concentrations in Bicknell's Thrush and Other Insectivorous Passerines in Montane Forests of Northeastern North America

CHRISTOPHER C. RIMMER,[1,*] KENT P. MCFARLAND,[1] DAVID C. EVERS,[2] ERIC K. MILLER,[3] YVES AUBRY,[4] DANIEL BUSBY[5] AND ROBERT J. TAYLOR[6]
[1]*Vermont Institute of Natural Science, 2723 Church Hill Road, Woodstock, VT, 05091,*
[2]*BioDiversity Research Institute, 19 Flaggy Meadow Road, Gorham ME, 04038*
[3]*Ecosystems Research Group, Ltd., P.O. Box 1227 Norwich, VT 05055*
[4]*Canadian Wildlife Service, Environment Canada, 1141Route de l'Église, P.O. Box 10100, Sainte-Foy, PQ Canada G1V 4H5*
[5]*Canadian Wildlife Service, Environment Canada, P.O. Box 6227 Sackville, NB Canada E4L 1G6*
[6]*Trace Element Research Laboratory, Texas A & M University, VMA Building, Room 107, Highway 60, College Station, TX, 77843–4458*

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Abstract. Anthropogenic input of mercury (Hg) into the environment has elevated risk to fish and wildlife, particularly in northeastern North America. Investigations into the transfer and fate of Hg have focused on inhabitants of freshwater aquatic ecosystems, as these are the habitats at greatest risk for methylmercury (MeHg) biomagnification. Deviating from such an approach, we documented MeHg availability in a terrestrial montane ecosystem using a suite of insectivorous passerines. Intensive and extensive sampling of Bicknell's thrush (*Catharus bicknelli*) indicated significant heterogeneity in MeHg availability across 21 mountaintops in northeastern North America. Southern parts of the breeding range tended to be at greater risk than northern parts. Mean blood Hg concentrations for Bicknell's thrush at 21 distinct breeding sites ranged from 0.08 to 0.38 ug/g (ww) and at seven Greater Antillean wintering sites ranged from 0.03 to 0.42 ug/g (ww). Overall concentrations were significantly greater in wintering than in breeding areas. Mercury exposure profiles for four passerine species on Mt. Mansfield, Vermont indicated greatest MeHg uptake in Bicknell's thrush and yellow-rumped warbler (*Dendroica coronata*) and lowest in blackpoll warbler *(Dendroica striata)* and white-throated sparrow *(Zonotrichia albicollis)*. The MeHg and total Hg ratio in blood in these four species was nearly 1:1. There was no correlation between blood and feather Hg concentrations in breeding Bicknell's thrush, in part because of apparent retention of winter Hg body burdens, within-season variation of MeHg availability, and confounding factors such as influences from age. Adult thrushes had significantly higher concentrations of feather Hg than did young-of-the-year. Although individual patterns of inter-year feather Hg concentrations were disordered, some individuals exhibited bioaccumulation of MeHg. Female blood Hg concentrations were significantly lower than males', in part because females have additional depurating mechanisms through eggs. Older male Bicknell's thrushes that breed in New England are therefore likely at greatest risk. Mechanisms for Hg methylation in montane areas without standing water are not yet fully understood. However, recent studies indicate that

*To whom correspondence should be addressed:
Tel.: +802-457-1053 ext. 120; Fax: +802-457-1053;
E-mail: crimmer@vinsweb.org

MeHg is present in forest tree leaves and leaf detritus; saturated soils and other moist microhabitats may also contribute to MeHg availability. Our finding of a correlation between regional litterfall Hg flux patterns and Bicknell's thrush blood Hg concentrations demonstrates on-site availability of MeHg. Further investigations into MeHg availability in montane environments are recommended to assess risk to insectivorous passerines, particularly the Bicknell's thrush.

Keywords: Songbirds; Catharus bicknelli; Nearctic-neotropical migratory birds; methylmercury

Introduction

It is well established that elevated levels of atmospheric mercury (Hg) deposition and methylmercury (MeHg) bioavailability in the northeastern United States influence wildlife populations. Investigations have focused on multiple trophic levels of freshwater aquatic ecosystems (Evers et al., 2004; Bank et al., 2005; Chen et al., 2005; Kamman et al., 2005; Pennuto et al., 2005), where converted MeHg biomagnifies through the aquatic foodweb, from phytoplankton and zooplankton to invertebrates, amphibians, fish, and piscivorous vertebrates. Particular emphasis has been on higher trophic piscivorous wildlife, which are most at risk from mercury's ability to bioaccumulate and biomagnify (Thompson, 1996; USEPA, 1997; Evers et al., 2005).

Little is known about MeHg availability or toxicity in passerine birds, especially those species not associated with aquatic systems (Thompson, 1996; Wolfe and Norman, 1998; Wiener et al., 2003). Further, exceedingly few data exist on MeHg burdens in migratory passerine birds, which are potentially exposed to varying environmental levels of Hg during their breeding, migration, and wintering periods. Birds are an important taxon for sampling because they are well-established bioindicators of MeHg availability (Burger, 1993; Furness and Greenwood, 1993; Bowerman et al., 2002; Mason et al., 2005), they are relatively easily sampled, and commonly used matrices reflect $>95\%$ of the total body burden of Hg (Evers et al., 2005). Among passerines, obligate insectivorous species are most likely to be at risk from Hg toxicity, although established impact thresholds are only now being developed at the individual level (G. Heinz, pers. com.) and no published studies have investigated population level risk.

While pathways for Hg uptake and bioaccumulation in terrestrial ecosystems are not well understood, recent research has shown that Hg deposition varies by a factor of three at both regional and local scales due to proximity of emissions sources, climatic effects, and variations in surface characteristics that influence dry deposition (Miller et al., 2005; VanArsdale et al., 2005). Mercury loading is significantly (2–5×) higher in montane areas of the Northeast than in surrounding low elevation areas (Lawson, 1999; Miller et al., 2005). Orographically enhanced precipitation and interception of acidic, pollutant-laden cloud water contribute to increased Hg deposition in high elevation ecosystems. However, the possible toxic effects of such deposition on montane biota are largely unknown. Numerous studies have demonstrated that MeHg is present in both live and recently senesced forest foliage in proportions of approximately 1% of the total Hg content (e.g. Lee et al., 2000; Schwesig and Matzner, 2000; St. Louis et al., 2001; Ericksen et al., 2003; see earlier studies reviewed by Grigal, 2002). It is not clear at this time if this MeHg is methylated within the leaf or if it represents direct deposition of atmospheric gas-phase MeHg. Evergreen species have both higher total Hg concentrations and higher proportions of MeHg than deciduous species. Using their model of Hg accumulation in leaves, Miller et al. (2005) estimated that MeHg made available to terrestrial food webs by forest foliage ranges from 5 to 135 ng m^{-2} y^{-1} in northeastern North American forests. Baseline data on total Hg levels and ratios of MeHg:Hg in wildlife from terrestrial habitats are needed to address this issue.

In this paper, we present data on Hg concentrations in terrestrial passerine birds of montane forests in the northeastern United States and adjacent Canada. We focus on the Bicknell's thrush *(Catharus bicknelli)*, a 25–30 g passerine that breeds from southern Quebec and the Maritime provinces south through New York and New England, where it is

restricted to coniferous forest typically above 900 m (Ouellet, 1993; Atwood et al., 1996; Rimmer et al., 2001). It winters in the Greater Antilles from sea level to > 2000 m, chiefly in mesic and wet broadleaf forest (Rimmer et al., 2001). Due to its small global population, estimated at < 50,000 individuals (Rimmer et al., 2001), its geographically restricted breeding range, and its dwindling winter habitat, Bicknell's Thrush is considered among the Nearctic-Neotropical migrant species of highest conservation priority in the Northeast (Pashley et al., 2000; Rosenberg and Wells, 2000). Its specialization on high elevation fir-dominated forests suggests that it might be an appropriate bioindicator of MeHg bioavailability in these habitats.

Study area and methods

Field sampling

We sampled passerines in montane forests at two spatial scales, intensive (sites with ≥ 10 samples) and extensive (sites with < 10 samples). We sampled 28 sites overall (Fig. 1). Of these, 21 were on breeding areas and included two sites in Maine (ME), five sites in New Brunswick (NB), two sites in New Hampshire (NH), one site in New York (NY), one site in Nova Scotia (NS), three sites in Quebec (PQ), and seven sites in Vermont (VT). We sampled an additional seven sites within the wintering range of Bicknell's thrush. These included two sites in Cuba, four sites in the Dominican Republic (DR), and one site in Haiti.

Intensive sampling was conducted on two US peaks, Mt. Mansfield (hereafter "Mansfield") in north-central Vermont and Stratton Mountain (hereafter "Stratton") in southwestern Vermont. Both are sites of long-term demographic research on montane forest bird populations. We collected Hg samples on Mansfield during June and July of 2000–2003, and on Stratton in late May to July 2001–2003. Vegetation at these and other breeding sites (see below) is dominated by balsam fir *(Abies balsamea)*, with scattered red spruce *(Picea rubra)*, heart-leafed paper birch *(Betula papyrifera* var. *cordifolia)* and mountain ash *(Sorbus americana)*. This vegetation is stunted by chronic exposure to high winds and heavy winter ice loads, and it is extremely dense. Canopy heights on the Mansfield study site average 1–4 m (mean 2.2 m) and stem densities average 8274/ha (Rimmer and McFarland, 2000); these are typical characteristics of montane fir forests in the northeastern US and Canada.

On Stratton, we sampled Hg levels only in Bicknell's thrush, while on Mansfield, we sampled this and three additional breeding passerines: blackpoll warbler (*Dendroica striata*), yellow-rumped warbler (*Dendroica coronota coronota*), and white-throated sparrow (*Zonotrichia albicollis*). Bicknell's thrush and blackpoll warbler are near-obligate breeding residents of montane forests in the Northeast (Hunt and Eliason, 1999; Rimmer et al., 2001), while yellow-rumped warbler and white-throated sparrow breed at high densities in these forests, but are also common in a variety of low elevation forested habitats throughout the Northeast (Falls and Kopachena, 1994; Hunt and Flaspohler, 1998). All four species are primarily insectivorous during the breeding season with Bicknell's thrush and white-throated sparrow foraging mainly on or close to the ground, blackpoll warblers mainly gleaning foliage, and yellow-rumped warblers capturing insect prey both by foliage gleaning and fly-catching. Bicknell's thrush and blackpoll warbler are long-distance migrants to the Greater Antilles and northern South America, respectively, while yellow-rumped warbler and white-throated sparrow are short- to medium-distance migrants, wintering primarily in the southeastern US. These four species thus represent a diverse array of habitat specialization, foraging guilds, and migration strategies.

We conducted additional intensive sampling of Bicknell's thrush during 2003 at three montane sites in Canada: two in southern Quebec and one on Cape Breton Island, NS. Mont Gosford (hereafter "Gosford"), adjacent to the Maine border, is dominated by 35-year old balsam fir stands, many of which were thinned in the 1980s and 1990s for timber production. Mine Madeleine (hereafter "Gaspé") is located on the Gaspé Peninsula, 475 km northeast of Quebec City and adjacent to the Gaspèsie National Conservation Park. This mountainous study area is characterized by steep rocky slopes covered with dense balsam fir forest interspersed with white birch, balsam poplar *(Populus balsamifera)*, and alder *(Alnus* spp.*)* stands. Cape North is located on the extreme

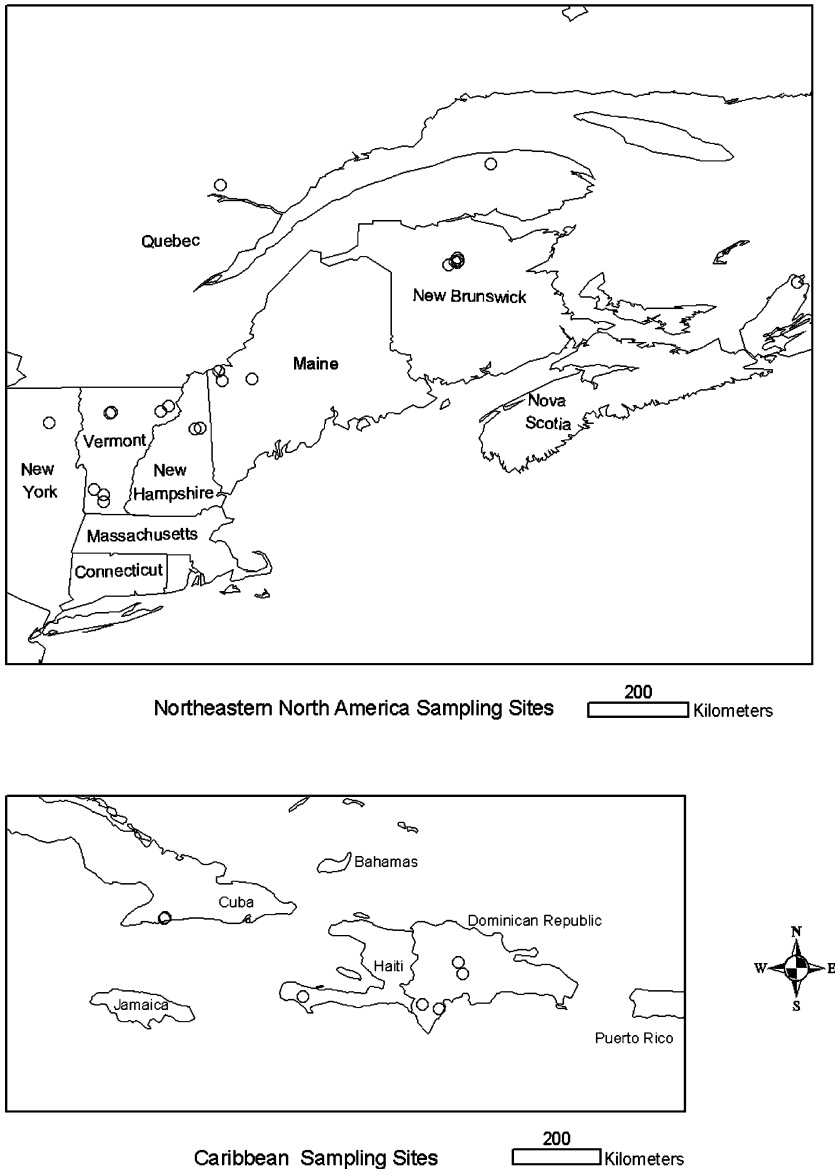

Figure 1. Distribution of sampling locations for the Bicknell's thrush.

northern tip of Cape Breton Island, covering an extensive plateau that projects into the Cabot Strait. The dense habitat at this site consists primarily of balsam fir, paper birch and mountain ash, ranging from 2 to 5 m in height. The forests at Gaspé and Cape North contain many dead standing trees and are stunted due to heavy winter snow cover, ice loading, and chronically harsh winds.

Our extensive sampling included only Bicknell's thrush and was conducted during 2000–2004 at 10 additional peaks in the northeastern US, six additional sites in eastern Canada, and seven sites on the species' Greater Antillean wintering range (Table 1). Preferred winter habitats of this species are mesic to wet broadleaf forests with a dense understory, mainly at high elevations (Rimmer et al., 2001). At all sampling sites in North America and the Caribbean, birds were captured in nylon mist nets (12×2.6 m, 36-mm mesh), either passively or using vocal playbacks as lures. Each

Table 1. Montane forest sites sampled for Bicknell's thrush blood and feather Hg levels, 2000–2004

Site name	State/ Province	Geographic cluster[a]	Lat-long	Elevation (s) Sampled (m)	Feather Hg (ug/g, fw) Mean ± SD (*n*)[b]	Blood Hg (ug/g, ww) Mean ± SD (*n*)
Canada						
Cape North (Cape Breton Island)	NS	8	46°53′ N, 60°31′ W	344–426		0.13 ± 0.03 (12)
Mt. DesBarres	NB	5	47°19′ N, 66°35′ W	668–683		0.13 ± 0.05 (2)
Fisher Ridge	NB	5	47°15′ N, 66°38′ W	654		0.08 (1)
Gaspé Peninsula	PQ	2	49°00′ N, 66°00′ W	1040	0.37 ± 0.2 (18)	0.09 ± 0.02 (21)
Mt. Gosford	PQ	9	45°18′ N, 70°52′ W	1192	0.64 ± 0.23 (24)	0.11 ± 0.04 (26)
Mt. Mitchell	NB	5	47°16′ N, 66°34′ W	688		0.15 (1)
Mt. Nalaisk	NB	5	47°12′ N, 66°45′ W	621		0.12 ± 0.04 (2)
Mt. Valin	PQ	7	48°37′ N, 70°50′ W	860	0.46 ± 0.18 (6)	0.08 ± 0.14 (5)
Unnamed Mtn. near Mt. Mitchell	NB	5	47°14′ N, 66°35′ W	645–664		0.11 ± 0.01 (3)
United States						
Avery Peak	ME	9	45°09′ N, 70°16′ W	900–990	0.29 ± 0.09 (4)	0.27 ± 0.28 (6)
Burke Mtn.	VT	6	44°34′ N, 71°54′ W	930		0.18 ± 0.05 (4)
Carter Notch	NH		44°16′ N, 71°12′ W	1025	0.48 (1)	
East Mtn.	VT	6	44°40′ N, 71°46′ W	1010–1030		0.15 ± 0.08 (5)
Equinox Mtn.	VT	3	43°10′ N, 73°06′ W	1122		0.09 (1)
Mt. Mansfield	VT	4	44°32′ N, 72°49′ W	990–1175	0.70 ± 0.23 (34)	0.10 ± 0.04 (56)
Mt. Snow	VT	3	42°57′ N, 72°55′ W	1025		0.141 (1)
Spruce Peak	VT	4	44°33′ N, 72°47′ W	1000	0.75 ± 0.45 (2)	0.06 ± 0.01 (3)
Stratton Mtn.	VT	3	43°05′ N, 72°55′ W	1065–1200	0.81 ± 0.36 (12)	0.12 ± 0.04 (45)
Mt. Washington	NH	1	44°15′ N, 71°17′ W	1350	0.91 (1)	0.09 (1)
W. Kennebago Mtn.	ME	9	45°07′ N, 70°48′ W	1060		0.38 (1)
Whiteface Mtn.	NY	4	44°22′ N, 73°54′ W	1275–1330	1.21 ± 0.39 (5)	0.08 ± 0.004 (5)
Hispaniola						
Pueblo Viejo	DR	n/a	18°12′ N, 71°32′ W	1400		0.34 ± 0.14 (21)
Cienaga de Manabao	DR	n/a	19°04′ N, 70°47′ W	900		0.03 (1)
Valle Nuevo	DR	n/a	18°50′ N, 70°42′ W	1935		0.10 ± 0.05 (2)
El Cachote	DR	n/a	18°06′ N, 71°11′ W	1190–1240		0.13 ± 0.05 (5)
Plaine Boeuf	Haiti	n/a	18°21′ N, 73°59′ W	1824–1901		0.28 ± 0.57 (8)
Cuba						
Pico Cuba	Cuba	n/a	19°58′ N, 76°51′ W	1426–1800		0.42 ± 0.28 (3)
Pico Suecia	Cuba	n/a	19°59′ N, 76°49′ W	1763		0.21 (1)

[a]Geographic clusters of North American sites reflect spatial proximity (see Fig. 1), which is useful for comparing an abiotic compartment (models of litterfall Hg flux) (Miller et al., 2005) and a biotic compartment (thrush blood Hg) (Fig. 6): 1 = White Mts. (NH); 2 = Gaspé (PQ); 3 = southern VT; 4 = northern Green Mts. (VT) and Adirondack Mt. (NY); 5 = northern NB; 6 = northeastern VT; 7 = northern PQ; 8 = NS; and 9 = northwest ME and southern PQ.
[b]Includes all adult age and sex classes. Individuals sampled in more than one year are counted separately for each year, while only the first sample is included for birds sampled more than twice in a single year.

individual was banded, aged, sexed, measured, and weighed. A 30–50 µl blood sample from the subcutaneous ulnar (brachial) vein was collected in a heparinized capillary tube, refrigerated in a vaccutainer in the field, and frozen within 12–48 h. Samples were frozen until contamination analyses were conducted. We collected both fifth secondary wing feathers from most birds by clipping the calamus close to its insertion point; these were stored in glassine envelopes prior to Hg analyses.

Laboratory analyses

Analysis of tissue samples from 2000 was conducted at the Environmental Chemistry Laboratory of the Sawyer Research Center, Orono, Maine, while all 2001–2003 samples from the US, Dominican Republic, and Haiti were analyzed at Texas A & M Trace Element Research Laboratory (TERL), College Station, Texas. Analysis of Canadian and Cuban samples was performed at

Table 2. Mercury concentrations and blood MeHg:Hg ratios in four species of montane forest breeding birds (adults only) sampled in 2000 and 2001 on Mt. Mansfield, VT. Data presented as arithmetic mean ± SD in ug/g (ww)

Species[a]	Total blood Hg (*n*)	Blood MeHg:Hg ratio (*n*)	Total feather Hg (*n*)
BITH	0.094 ± 0.47 (43)	0.983 ± 0.254 (39)	0.699 ± 0.25 (38)
BLPW	0.055 ± 0.017 (10)	0.895 ± 0.21 (12)	0.397 ± 0.237 (5)
YRWA	0.091 ± 0.055 (13)	0.959 ± 0.189 (15)	1.099 ± 1.119 (4)
WTSP	0.062 ± 0.026 (12)	1.091 ± 0.372 (14)	0.502 (1)

[a]BITH = Bicknell's thrush; BLPW = blackpoll warbler; YRWA = yellow-rumped warbler; WTSP = white-throated sparrow.

the National Wildlife Research Centre of Environment Canada, Ottawa, Ontario.

Blood samples were expressed from sealed capillary tubes and diluted with 2 ml of double deionized water, then homogenized and aliquoted into total Hg and MeHg fractions. Samples were prepared for total Hg according to TERL SOP-ST16, with volumes reduced to accommodate the small volumes available. This method incorporated digestion with nitric acid, sulfuric acid, potassium permanganate, and potassium persulfate. Digest solutions were reduced with hydroxylamine hydrochloride to eliminate excess MnO_2. Samples were prepared for MeHg analysis according to TERL SOP-9712, again with volumes reduced to accommodate sample size limitations. In this method, MeHg was extracted from an acid bromide sample into an organic solvent and prepared for analysis by a permanganate digestion. Feathers were analyzed only for total Hg; using the same digestion process and reagents as were used for blood samples.

Prior to 2003, total Hg and MeHg were both analyzed by element-specific cold vapor atomic absorption using an LDC Mercury Monitor equipped with a 30 cm path cell (SOP-9024). Samples were quantified based on peak height compared with external calibration standards. Quality assurance samples accompanying sample batches included method blanks, laboratory control samples (LCS), certified reference materials (NRCC DOLT-2), matrix spike samples, and duplicate samples. All analytes are reported in units of parts per million (ppm or ug/g), on a wet weight (ww) basis for blood and a fresh weight (fw) basis for feathers. Detection limits were dependent upon sample weights and dilution factors but averaged approximately 0.009 ug/g for both total Hg and MeHg and 0.04 ug/g for total Hg in feathers.

In 2003 and 2004, blood and feather samples were analyzed for total Hg according to TERL SOP-0301. This method utilized a Milestone DMA 80 to combust blood and feather samples in nickel boats in an oxygen-rich atmosphere. Combustion products were passed through a heated catalyst to complete oxidation and then through a gold column which trapped Hg. Upon completion of combustion, the gold trap was heated and the Hg released for analysis by atomic absorption. Some blood samples were analyzed for moisture content prior to Hg analysis. Moisture loss was determined via freeze drying blood samples in aluminum cups, and the cups were then placed in the DMA 80s nickel boats in order to determine Hg content.

Statistical analyses

We examined all data for normality. Non-normal data were log-transformed prior to analyses. Because samples from Canada were collected only in 2003, we examined blood and feather Hg data from Mansfield and Stratton for effects of year; there were no year effects or interactions of year with other variables (ANOVA for year: $F_{2,67} = 1.86$, $p = 0.164$). We thus combined data across years for all North American sites. Statistical analyses were performed on SYSTAT 10.2 (SYSTAT, 2002). Data are presented as arithmetic means and standard deviations (SD).

For population-level analyses of blood Hg levels, we used only the first sample obtained from each individual in each year, although we treated samples from individual thrushes obtained in multiple years independently. This avoided potential problems of within-year autocorrelation, as blood samples reflect short-term dietary Hg uptake (Evers et al., 2005) and thus cannot be considered independent within the same season.

Further, because individuals sampled in both June and July within a single year invariably showed significantly higher blood Hg concentrations in June (see below), we excluded all July samples in our population-level analyses. For feather Hg analyses from individuals that provided samples in multiple years, we used only those samples obtained in the first year. Feathers reflect chronic Hg body burdens (Burger, 1993), such that between-year samples can not be treated independently. We examined differences in blood and feather Hg samples from the five intensive breeding sites using ANOVA with sex, age, sample site, and their interactions as independent variables.

To correlate Bicknell's thrush Hg levels at Mansfield and Stratton with those of regional atmospherically-deposited Hg, we calculated average values for the aggregate presumed breeding home ranges of sampled birds from modeled data (Miller et al., 2005). We selected deposition data for two of eight available habitat classes within this sampling area on each mountain, balsam fir-red spruce-white birch and balsam fir-red spruce, as Bicknell's thrush is most closely associated with these two montane forest types (Rimmer et al., 2001). We considered total deposition rates as well as three different Hg deposition modes (wet, reactive gaseous, and litterfall) that might reflect different degrees of bioavailability of atmospherically-borne Hg to Bicknell's thrush (Miller et al., 2005). Mercury deposited with litterfall is thought to represent primarily elemental mercury vapor that has been assimilated by leaves. Reactive gaseous mercury is $HgCl_2$ that deposits to the surface of leaves.

Results

MeHg: total Hg ratio

The mean ratio of total blood Hg to blood MeHg was close to 1:1 in each of the four species sampled on Mansfield (Table 2). This ratio did not significantly differ among the four species ($\chi^2 = 3.344$, $df = 3$, $p = 0.342$).

Species patterns of Hg levels

Mean blood Hg concentrations were significantly different among the four species sampled on Mansfield (ANOVA: $F_{3,56} = 4.35$, $p = 0.008$; Table 2). Overall mean blood Hg concentrations were highest in Bicknell's thrush, and these were significantly higher than levels of blackpoll warbler and white-throated sparrow (*post-hoc* pairwise comparisons with Bonferroni adjustment: $p = 0.028$ for blackpoll warbler, $p = 0.046$ for white-throated sparrow). Excluding one yellow-rumped warbler with aberrantly high feather Hg of 2.62 ug/g, mean feather Hg concentrations were highest in Bicknell's thrush, but small samples sizes for the three other species limit comparisons (Table 2). Excluding this one yellow-rumped warbler outlier, Bicknell's thrush demonstrated the greatest overall variability in both blood and feather Hg concentrations.

Geographic patterns in Hg levels of Bicknell's thrush

Among the five intensively-sampled sites, blood Hg concentrations differed significantly (ANOVA: $F_{4,92} = 3.66$, $p = 0.02$), being highest at the two most geographically disparate sites, Cape North and Stratton, and lowest at Gaspé (Table 1). There was no significant interaction of either age or sex and site. Although small sample sizes precluded statistical testing of geographic trends among all 21 breeding sites, within New England, blood Hg levels were markedly higher in northeastern Vermont (Burke and East mountains) and Maine than elsewhere in Vermont or in New York (Table 1). Canada lacked a clear pattern, although Quebec samples tended to exhibit lower blood Hg concentrations than in New Brunswick and Nova Scotia.

Our initial comparison of feather Hg concentrations among the four sites that yielded feather samples showed significant between-site differences ($F_{3,76} = 8.37$, $p < 0.001$), but also a significant interaction between age and sampling site ($F_{3,76} = 11.86$, $p < 0.001$). This interaction likely resulted from our unequal samples of age-sex cohorts among sites, with the two Quebec sites strongly skewed by males >2 years old. We therefore pooled feather Hg data from all sites for demographic analyses (below), but were unable to test for differences among sites. Qualitatively, feather Hg concentrations at the four sites showed a similar trend to that of blood, being highest at Stratton and lowest at Gaspé (Table 1). Unlike

blood, however, feather Hg data from all sampling sites increased along an East–West gradient, with levels highest in New York and lowest in Maine and Canada (Table 1).

Blood Hg concentrations of Bicknell's Thrush from breeding areas in North America (Cape North, Gaspé, Gosford, Mansfield, and Stratton) and wintering areas in the Greater Antilles (Dominican Republic and Haiti) were compared using an ANOVA with sample site nested within season. Significant effects were found between season ($F_{1,182} = 149.55$, $p < 0.00001$) and site(season) ($F_{5,182} = 4.96$, $p = 0.00028$). Blood Hg concentrations in wintering birds were generally 2–3 times higher than in birds sampled on their breeding sites. Although small sample sizes limit statistical comparisons among wintering sites, birds from more western locations (Cuba, Haiti, and western Sierra de Bahoruco [Pueblo Viejo]) tended to have higher blood Hg concentrations than birds further east in the Dominican Republic (eastern Sierra de Bahoruco [El Cachote] and Cordillera Central [Valle Nuevo and Cienaga de Manabao]; Table 1).

Bicknell's thrush Hg levels and regional deposition patterns

The significantly higher Hg blood concentrations of thrushes on Stratton versus Mansfield paralleled modeled deposition patterns at the two sites. In the two forest types used by Bicknell's thrush at each site, deposition was consistently higher at Stratton for the three deposition modes we examined (Table 3). Both absolute and relative differences were higher for total Hg deposition than for the other three Hg deposition modes.

Bicknell's thrush demographic Hg profile

Among the five intensively-sampled North American sites, male Bicknell's thrushes had a significantly higher mean blood Hg concentration (0.11 ug/g ± 0.05; SD range 0.04–0.29) than females (0.09 ug/g ± 0.04; SD range 0.02–0.23) (ANOVA: $F_{1,92} = 4.9$, $p = 0.04$). Mean feather Hg concentrations did not differ significantly between males and females (ANOVA: $F_{1,84} = 0$, $p = 0.96$). The relationship between blood and feather Hg concentrations for Bicknell's thrushes from which we obtained both samples in a given year was only weakly positive and not significant (Fig. 2).

Mean feather Hg concentrations of ≥ 2-year old (after second-year [ASY]) Bicknell's thrushes were significantly higher overall than those of yearling (second-year [SY]) birds (ANOVA: $F_{1,84} = 16.63$, $p < 0.0001$), although this was not the case at Gaspé (Table 4). However, among ASY individuals of precisely known age at Mansfield and Stratton, based on multi-year banding histories, no relationship existed between feather Hg concentrations and age. Similarly, no consistent trend was evident among the 20 individuals from which we obtained feathers in multiple years (Fig. 3). Of these birds, from which we obtained samples 1–3 years apart, nine had increased feather Hg concentrations between first and last captures, while the concentrations of 11 individuals decreased. The overall population mean rate of Hg accumulation was −0.01 ug/g ± 0.51 SD (range −0.81 to 1.55). Males ($n = 13$) accumulated feather Hg at an overall mean rate of −0.13 ug/g ± 0.37 (range −0.81 to 0.44), while the mean overall accumulation rate of females ($n = 7$)

Table 3. Modeled atmospheric Hg deposition for Stratton and Mansfield. Data presented as $\mu g/m^2/yr$ (extracted from maps described in Miller et al., 2005)

Deposition mode	Fir-spruce-birch zone		Fir-spruce zone	
	Mansfield	Stratton	Mansfield	Stratton
Reactive gaseous Hg	10.8	12.9	10.8	12.6
Litterfall Hg	13.8	13.9	15.4	15.6
Wet (rain + cloud)	9.3	12.9	13.5	20.7
Total Hg[a]	35.2	42.4	41.2	51.5

[a]Includes dry particulate deposition.

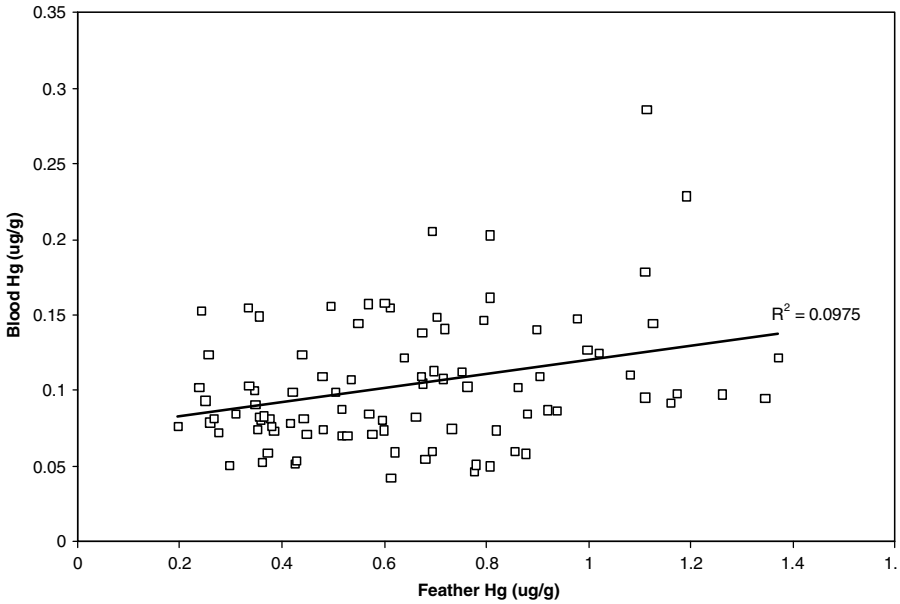

Figure 2. Relationship between blood (ug/g, ww) and feather Hg (ug/g, fw) concentrations in Bicknell's thrushes on Mt. Mansfield and Stratton Mtn., Vermont.

Table 4. Mean feather Hg levels (ug/g, fw) ± SD (*n*) by age class in Bicknell's thrush

Age class[a]	Stratton	Mansfield	Gosford	Gaspé
SY	0.322 ± 0.041 (3)	0.485 ± 0.12 (11)	0.49 ± 0.129 (6)	0.463 ± 0.297 (7)
ASY	0.974 ± 0.231 (9)	0.796 ± 0.193 (23)	0.687 ± 0.236 (18)	0.309 ± 0.079 (11)

[a]SY = second-year (yearling); ASY = after second-year (≥ 2 years old).

was 0.22 ug/g ± 0.68 SD (range −0.56 to 1.55). Of thrushes examined in consecutive years, representing 26 accumulation-years, the mean annual accumulation rate was −0.03 ug/g ± 0.48 SD (range = −0.94 to 0.87). Of 13 males representing 23 accumulation-years, 12 of those years showed an increase, and the mean annual accumulation rate in males was −0.04 ug/g ± 0.51 SD. Of five recaptured females representing six accumulation-years, Hg feather levels increased in four years, and the mean annual accumulation rate for females was 0.02 ± 0.36 ug/g.

Mean blood Hg concentrations of individual Bicknell's thrushes examined on Mansfield and Stratton in multiple years did not show a clear pattern (Fig. 4). We used only those birds sampled during June in each year to limit within-season variability (see below). Of the 16 individuals that provided data in at least two years, representing 20 between-year changes, blood Hg concentrations increased between 11 successive-year captures and declined between nine. Of four birds examined in three consecutive years, none showed a consistent trend over all three years. Mean blood Hg concentrations of males (n = 10) increased 0.004 ug/g + 0.06 SD between successive years, while those of females (n = 3) declined 0.05 ug/g + 0.09 SD.

To examine within-season variability in Hg blood concentrations, we sampled 13 Bicknell's thrushes at three- to four-week intervals during a single breeding season. Every bird showed a decrease in Hg blood concentration between its first and subsequent capture. The mean Hg blood concentration of first captures was 0.14 ug/g ± 0.05 SD, while later-captured birds had mean levels of 0.09 ug/g ± 0.03 SD. This difference was

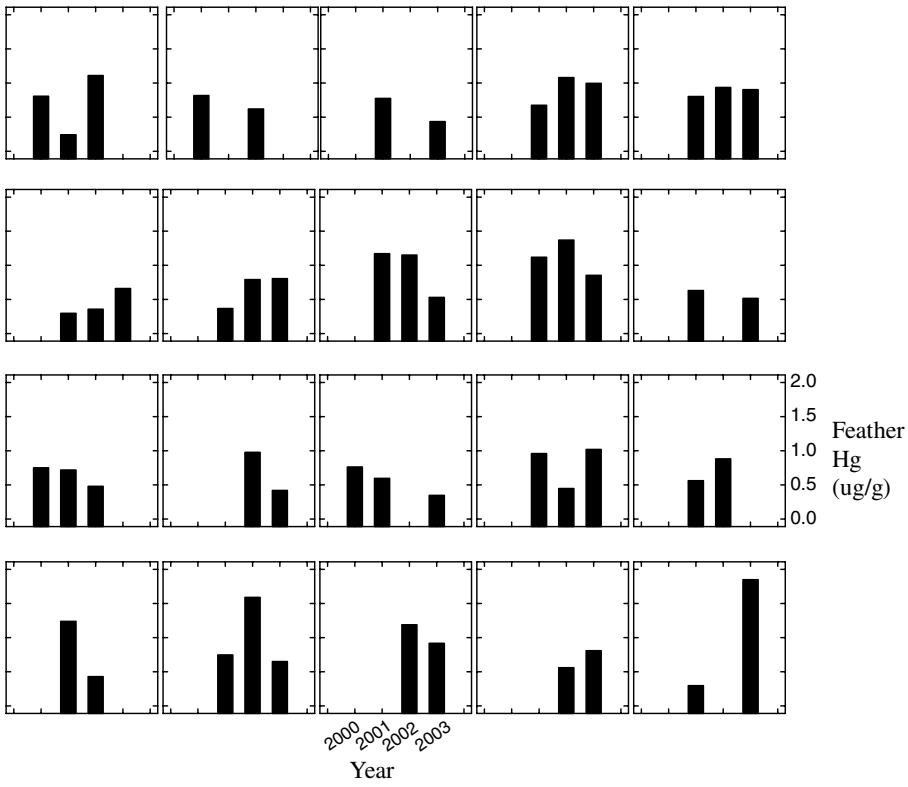

Figure 3. Feather Hg concentrations (ug/g, fw) of Bicknell's thrushes examined in multiple years on Mt. Mansfield and Stratton Mtn., Vermont.

significant (paired t-test: $t = 4.41$, $df = 12$, $p < 0.001$). The mean change in Hg blood concentrations between first and subsequent samples was −0.05 ug/g ± 0.04 SD. A less pronounced seasonal decline in Hg blood concentrations of Bicknell's thrush on Mansfield and Stratton is reflected by population-level data, which show weakly negative relationships between blood Hg concentrations and date on both mountains (Fig. 5).

Discussion

The data presented here for Bicknell's thrush are the most comprehensive and detailed yet available for a strictly terrestrial, insectivorous passerine. The Hg concentrations in this and the other three montane forest species are relatively low compared to those documented in other free-ranging North American birds. However, nearly all species examined to date are associated with aquatic-based systems and are at the top of piscivorous or aquatic insectivorous trophic webs (Thompson, 1996; Evers et al., 2005). Bicknell's thrushes inhabit conifer-dominated forests and are not closely tied to aquatic habitats at any phase of their annual cycle. Methylation dynamics and MeHg availability in terrestrial systems are not well understood, but our results indicate that a mechanism for biotic uptake of MeHg exists in montane forests.

Total Hg and MeHg relationships in blood

All four species sampled on Mansfield exhibited MeHg:Hg ratios of nearly 1:1 (Table 2). Such a ratio in blood is well-established in piscivorous birds (Scheuhammer, 1991; Thompson, 1996; Evers et al., 1998; Fournier et al., 2002), however, it is less well known for insectivorous passerines. The high proportion (90–100%) of MeHg in blood from our suite of montane insectivorous passerines

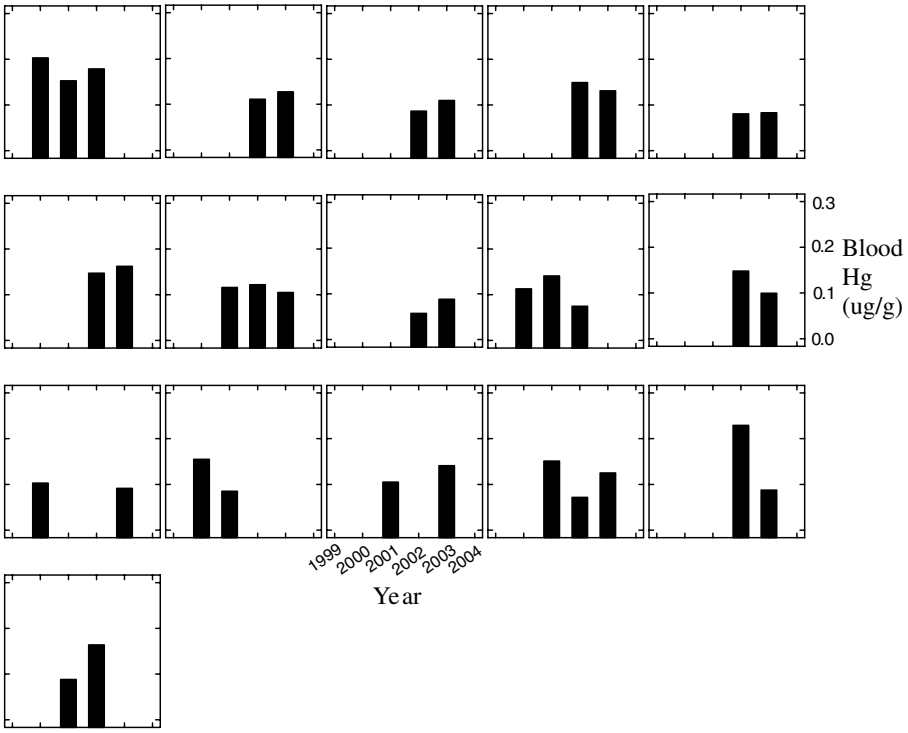

Figure 4. Blood Hg concentrations (ug/g, ww) of Bicknell's thrushes examined during June in multiple years on Mt. Mansfield and Stratton Mtn., Vermont.

was expected, even though there are species-specific differences in how MeHg is absorbed into the blood (Monteiro and Furness, 2001). Unlike fish, which form the dietary basis for piscivorous birds and generally have whole body content >85% MeHg (Wiener and Spry, 1996), insects generally have far less MeHg content (average ~65%; Pennuto et al., 2005), but exhibit a broad range with lowest levels in detritivores (20–25%) and highest levels in predatory insects like dragonflies (95%) (Tremblay et al., 1996; Tremblay and Lucotte, 1997). However, the transfer of more limited MeHg concentrations in insect prey to insectivorous birds does not appear to be significantly different than in piscivorous birds. Both Gerrard and St. Louis (2001) and Wolfe and Norman (1998) found high MeHg:Hg ratios in the tissues of various insectivorous passerines. Our analysis indicates that even insectivorous birds dependent on terrestrial food-webs are susceptible to MeHg availability and bioaccumulation.

Comparisons of Hg exposure during the breeding season

Blood Hg concentrations of four montane breeding birds at Mansfield fell into two general groups: higher exposure (pooled mean, 0.09 ug/g) in Bicknell's thrush and yellow-rumped warbler and lower exposure in blackpoll warbler and white-throated sparrow (pooled mean, 0.06 ug/g). Compared to other sampling sites in northeastern North America, Bicknell's thrush blood Hg concentrations were 34% lower at Mansfield than elsewhere (unweighted, arithmetic mean = 0.14 ± 0.08 SD, n = 18 sampling locations). Because there are few studies documenting insectivorous passerine Hg exposure (Bishop et al., 1995; Wolfe and Norman, 1998; Gerrard and St. Louis, 2001; Reynolds et al., 2001; Adair et al., 2003) and because none of the existing studies sampled blood for Hg analysis, few comparisons are available. Two exceptions are from northeastern North America. Shriver et al. (2002) sampled and

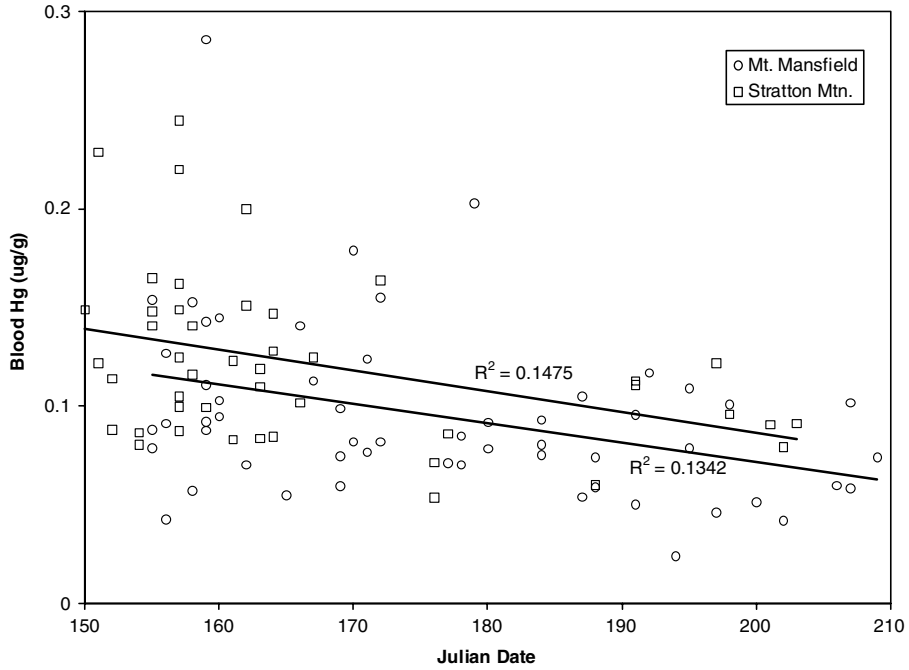

Figure. 5. Relationship of blood Hg concentrations (ug/g, ww) in Bicknell's thrush by Julian date (150 = 31 May, 180 = 30 June, 210 = 30 July) on Mt. Mansfield and Stratton Mtn., Vermont. Mt. Mansfield = lowerline, Stratton Mtn. = upperline.

analyzed the blood Hg concentrations of saltmarsh and Nelson's sharp-tailed sparrows (*Ammodramus caudacutus* and *A. nelsoni*, respectively) at five Maine estuaries and found relatively high Hg levels. Mean concentrations for the saltmarsh sharp-tailed sparrow (0.69 ug/g) were significantly higher than for the closely related Nelson's sharp-tailed sparrow (0.41 ug/g), and both were higher than the mean concentrations found in Bicknell's thrush from 21 distinct breeding sites (Table 1). Blood Hg concentrations in 10 insectivorous passerines associated with riverine habitats on the Sudbury River, Massachusetts varied from 0.04 ug/g in the yellow warbler (*Dendroica petechia*) to 0.92 ug/g in the northern waterthrush (*Seiurus noveboracensis*) (Evers et al., 2005). In that study, adult mean Hg blood concentrations were lower than those of Bicknell's thrush for three of the 10 species (barn swallow [*Hirundo rustica*], gray catbird [*Dumetella carolinensis*], and yellow warbler).

The causes of intra-site differences in the blood Hg concentrations of insectivorous passerines likely parallel patterns found in piscivorous birds. Evers et al. (2005) identified differences among species within the same habitat as primarily related to trophic level. Biomagnification of MeHg in aquatic systems is largely dictated by the diversity and density of the planktivorous community (Chen et al., 2005). An analogous community of terrestrially-based microorganisms is likely present in montane habitats, as passerine blood Hg concentrations average only one order of magnitude less than concentrations in small piscivores such as the belted kingfisher (*Ceryle alycon*) (Evers et al., 2005). The trophic level of MeHg in the diet of a Bicknell's thrush is likely higher than in a blackpoll warbler because thrushes are larger-bodied and feed on larger arthropods (Hunt and Eliason, 1999; Rimmer et al., 2001) that tend to be more predaceous and have higher levels of MeHg than smaller arthropods (Tremblay and Lucotte, 1997). While Bicknell's thrush and blackpoll warbler follow the regression model by Evers et al. (2005) that predicts $>70\%$ of the variation in passerine blood Hg levels as a function of body weight, the yellow-rumped warbler and white-throated sparrow deviate from this model. The white-throated sparrow has a lower component of insects in its breeding season diet (Falls and Kopachena, 1994), and this may contribute to

lower blood and feather Hg concentrations than those in thrushes and even smaller species such as warblers. The relatively high and variable mean Hg concentrations in yellow-rumped warbler blood may be an artifact of small sample size, a more varied diet, and preference toward black flies (*Simulus* spp.), which have an aquatic larval phase that is likely more exposed to MeHg availability than terrestrial insects.

Geographic patterns in Bicknell's thrush

The lack of a clear geographic pattern in Hg levels of Bicknell's thrush by individual mountain is not surprising, given the heterogeneity of Hg deposition across northeastern North America (Miller et al., 2005; VanArsdale et al., 2005). However, the overall trend of higher Hg blood and feather concentrations in thrushes in the southern part of the species' breeding range and lower concentrations in northern areas implies a linkage between atmospherically-deposited Hg and MeHg availability. This is reinforced by the strong correlation of deposition and thrush blood data on Stratton and Mansfield. Higher modeled deposition data from Stratton reflect a plume of atmospheric-borne Hg from the southwestern part of the study area (Miller et al., 2005), which decreases northward and eastward. The significantly higher blood and feather Hg concentrations of Bicknell's thrushes on Stratton versus Mansfield further suggest linkages with regional MeHg availability.

The markedly higher mean blood Hg concentrations of thrushes in the Greater Antilles versus the northeastern North America sampling sites is counter to expected lower levels. Sampling of birds in marine (Burger and Gochfeld, 1991) and estuarine (Burger et al., 1992) environments in Puerto Rico in the late 1980s found relatively low body burdens of Hg. Significant local or regional industrial sources of Hg are unknown for the Greater Antilles. Because the global pool of Hg is increasing (UNEP, 2003), isolated islands and other areas disconnected from local and regional emission sources may be increasingly important for long-term monitoring (Mason et al., 2005). Until biogeochemical processes can be quantified in the breeding and wintering habitats of Bicknell's thrush, determining differences in MeHg availability between the two areas will remain problematic.

Interpreting blood-feather Hg relationships

We used two matrices, blood and feathers, to better understand spatiotemporal pathways of Hg exposure and potential effects on Bicknell's thrush. The lack of a correlation between blood and feather Hg concentrations and the disordered patterns in repeated measurements of feather Hg among individual birds demonstrate the dynamic complexity of MeHg availability for the Bicknell's thrush. Although adult Bicknell's thrushes undergo a complete remigial molt in August in their breeding areas (Rimmer et al., 2001), blood Hg concentrations measured in June and July are not predictive of August feather Hg levels (albeit, representing MeHg depuration 12 months prior). Confounding factors contributing to a decoupling of the two tissues are (1) within-summer changes in MeHg availability, (2) annual differences in Hg deposition and potentially in MeHg availability, (3) dietary changes within-summer and among years, (4) depuration of MeHg in eggs, (5) gender and (6) age differences in MeHg uptake, and (7) MeHg bioaccumulation.

Atmospheric deposition of Hg is not consistent within or between years (VanArsdale et al., 2005). The relationship of available inorganic Hg and associated methylation is also inconsistent and often non-linear, and is therefore difficult to predict even in well-studied freshwater aquatic systems (Wiener et al., 2003). Prey availability may be the most important driving factor in MeHg availability in montane systems. Precipitation events and sudden temperature drops can rapidly alter the composition of the montane forest insect community (Rimmer and McFarland, unpubl. data), which may subsequently affect trophic level representation of MeHg. Because predaceous insects generally have significantly higher MeHg levels than non-predaceous insects (Tremblay et al., 1996), rapid change in trophic structure and therefore MeHg availability is likely. Variations in the relative abundance of folivores and detritivores further complicate patterns of MeHg availability.

Eggs provide a short-term pathway of MeHg sequestration (Thompson, 1996). Depending on the success of initial nesting attempts, female Bicknell's thrushes may produce up to three clutches in a single breeding season (Rimmer et al., 2001). Because a rapid equilibrium between dietary

uptake of MeHg and blood MeHg is typical (Kambamandi-Dimou et al., 1991) and because egg MeHg primarily reflects blood MeHg levels (Evers et al., 2003), the influence of egg MeHg depuration on blood-feather decoupling of Hg levels is likely not a driving factor. However, loss of Hg through eggs may at least partly contribute to gender differences in Hg levels of Bicknell's Thrush, particularly because the species exhibits no significant sexual dimorphism in body mass or bill size (important metrics for dimorphism) (Rimmer et al., 2001) that might account for niche partitioning of prey.

Age responses to MeHg availability are well quantified with this study. One-year-old (SY) thrushes had significantly lower feather Hg concentrations than adults (ASY) at both intensively sampled Vermont sites and one of two Quebec sites (Table 1). Other studies have documented similarly significant differences in Hg body burdens between unfledged young and adult birds (Thompson, 1996), including passerines (Evers et al., 2005). However, differences in Hg levels among age classes of adult passerines have not previously been described. In our study, some known-age adult thrushes exhibited a significant increase in feather Hg concentrations with increasing age, while other individuals did not. Feather Hg concentrations were highly variable among individual birds examined in multiple years, likely reflecting the variable dynamics of MeHg availability in wintering and breeding areas. Because feathers provide one of the most effective pathways of MeHg depuration (70–93% of the body burden; Burger, 1993), it appears that the elimination of Hg through feathers is greater in some years than others.

Linking blood Hg levels with litterfall Hg deposition

Greater exposure to MeHg availability in wintering versus breeding areas likely contributes to body burdens of Hg in spring arrivals that exceed those of late-summer residents. The parallel decline of blood Hg levels in Bicknell's thrush during the breeding season on both Mansfield and Stratton suggests that much of the Hg blood and feather concentrations represent dietary uptake in wintering areas. The half-life of MeHg in the blood of non-molting adults is 40–60 days in Cory's shearwater (*Calonectris diomedea*) (Monteiro and Furness, 2001) and 84 days in mallards (*Anas platyrhynchos*) (Heinz and Hoffman, 2004). The retention of MeHg in the blood of Bicknell's thrush during its two to four week spring migration is therefore a potentially important contributor to blood Hg concentrations documented in the earlier part of the breeding season. Such a geographically disjunct influence on blood Hg levels of spring arrivals assumes that MeHg availability is static over the breeding season. In freshwater aquatic systems, MeHg availability increases throughout the summer as the sulphur-reducing bacteria responsible for methylation show a positive correlation with water temperature; however, the mechanisms that drive methylation in montane environments without standing water are poorly known (Wiener et al., 2003).

While these mechanisms remain uncertain (atmospheric deposition or bio-methylation), it appears that autotrophs make significant amounts of MeHg directly available to the terrestrial food web. Assuming a constant ratio of MeHg:Hg in leaves, the model for total Hg accumulation presented by Miller et al. (2005) suggests that MeHg made available via the leaf pathway would be lowest in spring and would increase five-fold (day 20 through day 140) during the growing season as leaves assimilate mercury from the atmosphere. Average MeHg concentrations might range from 0.02 (0.11) to 0.12 (0.54) ng/g in first-year evergreen leaves. Food webs deriving energy from the detrital leaf layer representing the previous year's leaf crop can be expected to be exposed to MeHg concentrations >0.5 ng/g. In Germany, Schwesig and Matzner (2000) measured MeHg concentrations in the Oi layer of soils of approximately 0.8–1.0 ng/g, in forests where fresh leaf litter concentrations ranged from 0.07 to 1.49 ng/g.

The availability of MeHg based on this process may partly explain the link with metrics related to atmospheric deposition. Miller et al. (2005) established deposition and concentration patterns of leaf, litterfall, precipitation (wet and dry), and particulate Hg. Regional comparisons of these patterns and nine geographic clusters of mean blood Hg concentrations of Bicknell's

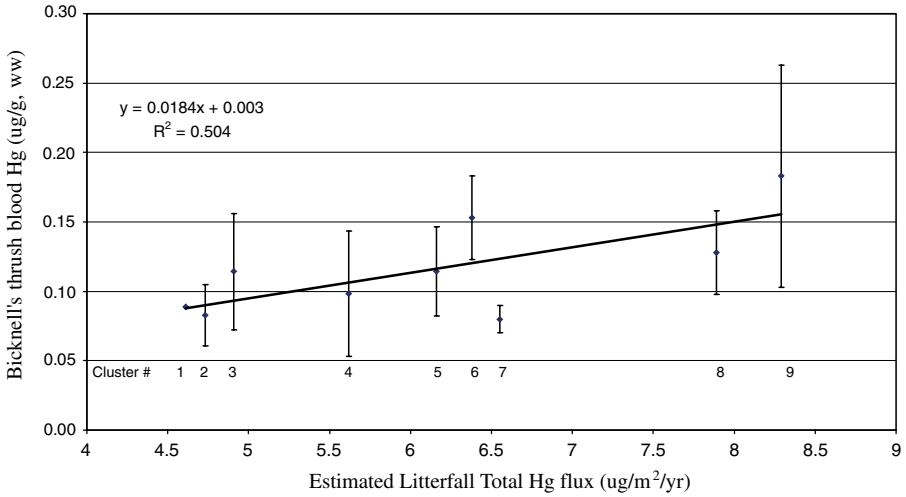

Figure 6. Relationship between modeled litterfall Hg flux (ug/m^2/yr) and the geometric mean +/− SE of Bicknell's thrush blood Hg concentrations (ug/g, ww). Clusters represent geographical grouping of thrush blood Hg samples from 21 different mountains.

thrush (see Table 1 for how sampling sites were grouped) demonstrated a significant correlation with litterfall Hg deposition ($r^2 = 0.49$, $p < 0.05$) (Fig. 6).

Conservation of Bicknell's thrush and the montane bird community

Biogeochemical factors that dictate MeHg availability in terrestrial montane habitats of northeastern North American and in the Greater Antilles are poorly known and warrant further investigation. The issue is of particular concern because the Bicknell's thrush is the most highly ranked Nearctic-Neotropical migrant passerine for conservation priority in the northeastern US (Pashley et al., 2000), where it is restricted to high elevation forests for breeding. Unlike migratory piscivorous birds, such as the common loon (*Gavia immer*), that breed on freshwater lakes and winter in marine systems, where MeHg availability is three times lower (Evers et al., 1998), the Bicknell's thrush is exposed to significantly higher Hg levels on its wintering grounds. Our finding of elevated MeHg availability in the Greater Antilles is unexpected based on previous avian Hg studies in subtropical areas (Burger and Gochfeld, 1991; Burger et al., 1992), and it heightens conservation concerns for the Bicknell's Thrush, which is also exposed to elevated Hg levels in its montane forest breeding areas. Such chronic exposure to Hg throughout its annual cycle, in combination with potential synergistic impacts from calcium deficiencies in areas of northeastern North America (Hames et al., 2002), might exert population level impacts in Bicknell's Thrush. Effects-based research to elucidate the relationship of MeHg burdens to demographics and reproductive success in this and other insectivorous migratory passerines is needed.

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