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Mercury bioaccumulation and trophic transfer in the terrestrial food web of a montane forest

Christopher C. Rimmer · Eric K. Miller ·
Kent P. McFarland · Robert J. Taylor ·
Steven D. Faccio

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Abstract We investigated mercury (Hg) concentrations in a terrestrial food web in high elevation forests in Vermont. Hg concentrations increased from autotrophic organisms to herbivores < detritivores < omnivores < carnivores. Within the carnivores studied, raptors had higher blood Hg concentrations than their songbird prey. The Hg concentration in the blood of the focal study species, Bicknell's thrush (*Catharus bicknelli*), varied over the course of the summer in response to a diet shift related to changing availability of arthropod prey. The Bicknell's thrush food web is more detrital-based (with higher Hg concentrations) in early summer and more foliage-based (with lower Hg concentrations) during late summer. There were significant year effects in different ecosystem compartments indicating a possible connection between atmospheric Hg deposition, detrital-layer Hg concentrations, arthropod Hg concentrations, and passerine blood Hg concentrations.

Keywords Mercury bioaccumulation · Food web · *Catharus bicknelli* · Montane forests

C. C. Rimmer (✉) · K. P. McFarland · S. D. Faccio
Vermont Center for Ecostudies, P.O. Box 420, Norwich,
VT 05055, USA
e-mail: crimmer@vtecostudies.org

E. K. Miller
Ecosystems Research Group, Ltd., P.O. Box 1227, Norwich,
VT 05055, USA

R. J. Taylor
Trace Element Research Laboratory, Department of Veterinary
Integrative Biosciences, Texas A&M University, College
Station, TX 77843-4458, USA

Introduction

Methylmercury (MeHg), the bioavailable form of mercury (Hg), is a neurotoxin with well-documented, adverse impacts on natural systems and wildlife populations. Most investigations on MeHg bioaccumulation and biomagnification have focused on freshwater aquatic ecosystems, where conditions promoting methylation are common and Hg concentrations in upper trophic level consumers may be high (e.g., Bank et al. 2005, 2007; Chen et al. 2005; Evers et al. 2005; Yates et al. 2005). Research has increasingly demonstrated that MeHg impairs reproductive performance, lifetime productivity, growth and development, behavior, motor skills, and survivorship in aquatic birds and other wildlife (Wolfe et al. 1998; Evers et al. 2004, 2008; Scheuhammer et al. 2007; Bennett et al. 2009). Further, Hg toxicity may suppress immunocompetency (Hawley et al. 2009), disrupt endocrine responses to stress (Franceschini et al. 2009; Wada et al. 2009), and interact with other contaminants to exert potentially adverse effects (Bergeron et al. 2009a). Despite the recent documentation of elevated Hg exposure in terrestrial biota (summary in Driscoll et al. 2007a), relatively little is known about pathways for Hg uptake and transfer in upland ecosystems, or about Hg risk thresholds for terrestrial organisms.

Trophic transfer of Hg in a strictly terrestrial food web has not been documented, although Cristol et al. (2008) reported MeHg biomagnification in biota from a terrestrial habitat adjacent to a Hg-contaminated river in Virginia. Total Hg concentrations increased in known avian prey items (Orthoptera [grasshoppers] → Lepidoptera [moths or caterpillars] → Aranea [spiders]) to passerine birds. Nearly 50% of the Hg in spiders, which comprised 20–30% of diet in three focal songbird species, was in the form of bioavailable MeHg. Twelve of 13 avian species sampled had significantly higher blood Hg concentrations at the contaminated site than at uncontaminated reference sites. Cristol et al. (2008) concluded that aquatic Hg moved into and through the terrestrial food web, where avian consumption of predatory invertebrates increased the food chain length and caused MeHg to biomagnify.

In montane areas of northeastern North America, anthropogenic Hg deposition from atmospheric sources is 2–5 times higher than in surrounding low elevation areas (Miller et al. 2005). Although mechanisms that drive methylation in montane forests are poorly understood, Hg has recently been documented to bioaccumulate in montane fauna of the Northeast (Bank et al. 2005; Rimmer et al. 2005; Evers and Duron 2008). In particular, Bicknell's thrush (*Catharus bicknelli*), a Nearctic-Neotropical migratory songbird, has been shown to exhibit elevated Hg blood and feather concentrations among all age and sex classes across its breeding range (Rimmer et al. 2005). This rare, range-restricted habitat specialist of montane forests is an avian species of high continental conservation concern (Rimmer et al. 2001; Rich et al. 2004). As a higher trophic level consumer, primarily of arthropods, Bicknell's thrush is a potentially valuable bioindicator of montane forest ecosystem health. Understanding of Hg burdens in this species and in trophic compartments of its food web could contribute to species-specific and ecosystem-based conservation planning.

To elucidate trophic transfer of Hg in montane forests, we sampled leaf litter and biota at a long-term study site in the northeastern U.S. Our goals were to examine Hg concentrations and their variability among compartments of a terrestrial food chain during the montane summer.

Study area and methods

Field sampling

As part of long-term demographic research on montane forest bird populations in the northeastern U.S., we investigated the bioaccumulation and trophic transfer of Hg on Stratton Mountain (43°05′N, 72°55′W) in southern Vermont. From late May through late July in 2004–2007, we sampled discrete compartments in the terrestrial food web, using an established study site between 1,075 and 1,180 m elevation. To reflect a range of trophic levels, we sampled leaf litter, foliage, folivorous and carnivorous arthropods, a terrestrial salamander, an insectivorous passerine bird, and two carnivorous raptors. Birds were sampled across our entire mountaintop study area of ~50 ha, while we sampled salamanders over a much smaller area of ~3 ha. We collected leaf litter, foliage and arthropod samples at two sites 50 m apart at 1,100 m elevation. One site was situated on the northwest-facing edge of a 30-m wide ski slope, the second 50 m to the west in mature, closed-canopy forest dominated by balsam fir (*Abies balsamea*).

Avian sampling was conducted on a near-daily basis throughout the entire sampling period in each summer, typically between dawn and mid-morning and from late afternoon through dusk, weather permitting. Sampling of litter and other biota was conducted opportunistically in dry and relatively warm weather, both to maximize logistic efficiency and to take advantage of peak activity patterns of exothermic arthropods. Because inclement weather is frequent at high elevations, we were unable to sample litter, foliage and arthropods as frequently as planned.

Care was taken to minimize cross contamination of samples, especially those that required manual handling (e.g., litter and foliage). We generally used latex gloves during sampling, and we cleaned sampling utensils with distilled water or 5% nitric acid. All samples were frozen within 2 h of collection and maintained frozen until analysis.

Leaf litter

At both sampling sites, we collected leaf litter and organic soil samples of ~250 cm^3 to a depth of 5–10 cm, using a small hand trowel that was wiped cleaned and rinsed with nitric acid and distilled water between individual sampling events. Care was taken not to include any portion of the underlying inorganic soil horizon. We collected three samples per site on 21 July 2004, 6 June 2006, and 15 June 2007; on 13 July 2007, we collected one sample at each site. Each sample was double-bagged in Ziploc® bags.

Foliage

We sampled whole leaves of three dominant deciduous tree species (paper birch [*Betula papyrifera* var. *cordifolia*], American mountain-ash [*Sorbus americana*], and pin cherry [*Prunus pennsylvanica*]) and needles from the dominant conifer (balsam fir), generally following methods outlined by Rea et al. (2002). Using hand pruners (wiped and cleaned with distilled water between each individual sampling event), we snipped the distal 20–30 cm of branch tips between 2 and 3 m height on mid- and upper-canopy trees. On deciduous species, this yielded samples of 8–12 leaves, while coniferous branch tips generally contained 6–10 branchlets. We sampled and homogenized for analysis the previous 2–3 years of growth of fir needles on each branch, with the exception of three 2007 samples for which we separately clipped and analyzed needles grown in 2005, 2006 and 2007. For each species, we collected three replicates at both sampling sites on five dates: 21 July 2004, 8 and 28 June 2005, and 15 June and 13 July 2007. All foliage samples were transferred immediately upon collection to Ziploc® plastic bags, double-bagged inside a second Ziploc® bag.

Arthropods

We sampled terrestrial and arboreal arthropods at both sites on six dates: 21 July 2004, 8 and 28 June 2005, 11 July 2006, and 15 June and 13 July 2007. We collected ground-dwelling arthropods (as well as a single sample of small gastropods) primarily through visual searches and probing of the top leaf litter layer. Individuals were collected either with plastic forceps or an aspirator, then transferred immediately to sterile plastic vials. For flying and arboreal arthropods, we used sweep nets, shook understory branches onto plastic protective sheets, or collected foliage-dwelling individuals with forceps or directly into storage vials. For small and medium-sized arthropods, we typically combined multiple individuals of a distinct taxon (e.g., ants, spiders, Opiliones [harvestmen]) into single storage vials. Prior to analysis, we identified each sample, whether consisting of a single or multiple individuals, to the lowest possible taxonomic level (usually order), using several references that included Borror and White (1970), Borror et al. (1981), and on-line sources such as BugGuide.Net (Iowa State University 2009). Due to the very small masses of many individual arthropods (below detection limits for Hg determination), we created composites of identifiable taxon for laboratory analyses. For all taxa for which we collected an adequate number of individuals for analysis, we archived at least one frozen reference sample.

Red-backed salamander

On 26 June 2006, we conducted active searches for red-backed salamanders (*Plethodon cinereus*) in forested habitat on Stratton Mountain by turning over objects (logs, rocks, etc.) under which salamanders often hide. All salamanders were captured by hand at 1,000–1,110 m elevation, placed in a moistened plastic bag, and measured (snout-to-vent, and total length). A tissue sample was collected from each individual by clipping a small (~5 mm) portion of their tail tip using surgical scissors. Tail clipping is a non-destructive sampling method because salamanders readily regenerate tails (Stebbins and Cohen 1995); in some populations 50–80% of individuals show signs of tail regeneration (Maiorana 1977). Hg concentrations in salamander tail tips have been shown to provide a strong positive correlation with whole body Hg burdens (Bergeron et al. 2009a). Salamanders were then immediately released at their point of capture. All samples were immediately stored in Whirl-pak® sample bags, which were sealed in Ziploc® bags.

Birds

Using standard arrays of 6 and 12-m, 36-mm mesh nylon mist nets throughout our study site, we captured individuals of our focal avian species, Bicknell's thrush, using both passive and vocal broadcast elicitation methods. In the course of this netting, we incidentally captured individuals of two raptorial species, sharp-shinned hawk (*Accipiter striatus*) and northern saw-whet owl (*Aegolius acadicus*). Sharp-shinned hawks are predators on small passerines, and are known to regularly depredate Bicknell's thrush (Rimmer et al. 2001). Northern saw-whet owls primarily feed on small rodents, but they occasionally take passerine birds, including *Catharus* thrushes (Rasmussen et al. 2008) and are thus potential predators of Bicknell's Thrush. All captured birds were banded with uniquely numbered U.S. Fish and Wildlife Service aluminum leg bands, aged and sexed according to standard criteria (Pyle 1997; Collier and Wallace 1989), and weighed prior to release. A series of morphometric measurements was also taken. From each individual of these three species, we collected 30–50 μl of blood in a 75 μl heparinized capillary tube by puncturing the cutaneous ulnar (brachial) vein with a 27.5 gauge needle. Capillary tubes were sealed on both ends with Crito-seal or Critocaps® and placed in a labeled glass 7 cc vacutainer. We sampled blood from all individuals upon their initial captures in each year, and we subsequently collected blood samples from individuals captured 1 week or more after collection of their previous sample.

Laboratory analyses

All samples were analyzed at the Texas A&M University Trace Element Research Laboratory (TERL). Upon arrival at TERL, frozen samples were assigned unique laboratory identification numbers. Samples other than blood were transferred to labeled, tared polyethylene Ziploc® bags, weighed, and lyophilized using a Labconco Freezone 12L freeze dryer. Moisture content was determined by weight loss following freeze drying. Dry samples were prepared for analysis by powdering tissue in either a Spex 6800 cryogenic grinding mill or a Retsch ZM 200 ultra centrifugal mill. Homogenized samples were stored in Ziploc® bags until analyzed.

Hg concentrations were determined by a combustion/trapping/atomic absorption technique (U.S. EPA 1998). Aliquots of sample were carefully weighed to the nearest 0.0001 or 0.00001 g, transferred to precombusted nickel boats, and analyzed using a Milestone DMA 80 Hg analyzer. Samples were heated in a tube furnace at 850°C under a stream of oxygen, and combustion products were passed through a catalyst, then through a gold-coated sand column where Hg atoms were trapped. Following thermal desorption, the oxygen gas stream carried Hg vapor through two atomic absorption cells that quantified Hg over the range 0.001–0.700 μg.

Instrument calibration utilized certified reference materials as standards. Laboratory quality control samples included a method blank, certified reference materials, a duplicate sample, and a spiked sample with each batch of 20 or fewer samples.

We measured only total Hg in each compartment, rather than bioavailable MeHg, due primarily to cost constraints associated with MeHg assays and a limited budget. Although the ratio of MeHg to total Hg may vary temporally and spatially within and among taxa (Cristol et al. 2008; Evers and Duron 2008), total Hg concentrations are commonly used to indicate exposure and as a proxy for MeHg toxicity. In passerine birds of montane forests, MeHg constitutes nearly 100% of total Hg (Rimmer et al. 2005). Results from TERL were provided in units of parts per million (ppm or μg/g) as wet weight (ww) for avian blood and dry weight (dw) for other compartments. To facilitate comparability among compartments, we converted avian blood Hg concentrations from wet to dry weight, using a conversion factor based on known moisture content (74.8 ± 2.3%) of 47 Bicknell's thrush blood samples.

Statistical analyses

We examined all Hg data for normality. Non-normal data were log-transformed prior to analysis. Descriptive statistics, linear regressions and ANOVA analyses were calculated with JMP 6.03 (SAS Institute 2009). We also used General Linear Models (GLMs) in SYSTAT 12 (Systat Software 2008) to examine within-season and between-year effects in Hg data for each sampled compartment, using different combinations of potential interactions as terms in the model.

Our previous work reported that blood Hg concentrations of both individual birds and the sampled population significantly declined during the breeding season (Rimmer et al. 2005). We therefore modeled blood Hg concentrations for all thrushes sampled in more than 1 year using a GLM, in which the interaction between year (2004–2007) and date were used as terms in the model. Because the interaction was significant ($F_{3,98} = 5.126$, $P = 0.002$), we examined each year separately and found 2004 to be significantly different from 2005 to 2007. A GLM excluding 2004 was not significant for the year term ($F_{2,72} = 0.141$, $P = 0.869$). We then examined blood Hg in a GLM using sex, age (second-year and after second-year), date, and an interaction between sex and date as terms, with data pooled for 2005–2007 and repeated for 2004 alone. We included the sex-date interaction because females can depurate Hg through egg laying (e.g., Thompson 1996; Monteiro and Furness 2001; Evers et al. 2005), which occurs primarily during the middle 2 weeks in June (Rimmer et al. 2001).

There were significant and clear discontinuities in the overall declining trend of Bicknell's thrush blood Hg during the season, with blood concentrations rising rapidly from day 143 (23 May) through day 158 and falling fairly rapidly from day 160 through day 165 (14 June). This period was followed by a steady and slower rate of decline through day 206 (25 July). For the purposes of statistical analysis, the period prior to day 165 was classified as "Early" and day 165 and afterward as "Late" season. A one-sided *t*-test was used to evaluate differences in blood Hg concentrations between Early and Late season.

Classification of invertebrate foraging guilds

We classified arthropod samples in three broad foraging guilds (Detrital, Canopy, Varied) according to the base of their known or suspected trophic web. Detrital arthropods included detritivorous organisms living primarily in the bark of dead and downed trees, as well as in leaf litter and upper soil layers. Canopy dwellers included herbivorous taxa inhabiting most structural forest layers from the forest floor to the uppermost tree canopy. We considered varied arthropods to be those that are primarily carnivorous and feed on either Canopy or Detrital organisms.

We further classified arthropods within each broad guild (primarily by order) as Carnivorous, Omnivorous, Herbivorous-Detrital, Herbivorous-Canopy, and Varied. Carnivores included arachnids (spiders and harvestmen) and blood-sucking Diptera (flies). Herbivorous-Detrital included organisms that feed on plants and fungi in the detrital layer, while the Herbivorous-Canopy class included organisms that feed on above-ground plant structures (generally live plants). The Varied class captured organisms such as some Diptera that are typically considered omnivorous. For ants, our personal observations suggested that early season foraging occurs primarily in the detrital layer (i.e., Herbivorous-Detrital), while late season ants were more often seen foraging in the canopy (i.e., Herbivorous-Canopy). For other Hymenoptera (e.g., wasps, bees, sawflies), our field observations and literature searches suggested that all were Herbivorous-Canopy foragers.

Finally, we classified arthropods as early- or late-season based on the dates on which they were sampled in each year (1–27 June = early, 28 June–21 July = late). Although little information exists on the dietary composition of Bicknell's thrush during its breeding period, the species is reported to be a "versatile" feeder in both microhabitat and behavior (Rimmer et al. 2001). Under the assumption that thrushes are opportunistic foragers, taking available prey in proportion to their abundance and ease of capture, we further assumed that our opportunistic sampling constituted a first-order proxy for foraging success, and that the within- and between-year composition of our arthropod samples reflected the prey items available to Bicknell's thrush. We therefore lumped all orders in our analyses of date and year effects on Hg concentrations, rather than comparing individual orders, which were subject to small sample sizes, high variance and disparities in total biomass or species composition among sampling events. This sample compositing should reflect Hg bioavailability in food items accessible to Bicknell's thrush.

Results

Overall, Hg concentrations showed a generally increasing trend by trophic level (Fig. 1, "Appendix"). Leaf litter detritus deviated markedly from this pattern, with total Hg concentrations elevated above those in any biotic compartment except sharp-shinned hawk, the top trophic level consumer in our samples (Fig. 1, "Appendix"). Mean litter Hg concentrations differed among years ($F_{2,15} = 6.46$, $P = 0.01$), but not sampling location ($F_{1,15} = 0.02$, $P = 0.88$), and were significantly higher in 2006 than in 2004 and 2007, which did not significantly differ. We did not detect within-year differences in leaf litter Hg concentrations. We documented a relatively high mean concentration of 0.323 µg/g ± 0.09 SD on 6 June 2006, but no significant difference in mean concentrations between samples collected on 13 June and 15 July 2007 (0.228 ± 0.102 SD [$n = 6$] and 0.292 ± 0.031 SD [$n = 2$], respectively; $t = 0–1.836$, $df = 5.954$, $P = 0.12$).

Hg concentrations in balsam fir branches with aggregated needle samples (2–3 years of growth) were greater than those in the three deciduous tree species, both individually and combined (Fig. 1, "Appendix"). Single-year needle samples consistently increased in Hg content with age at an annual rate of 0.0142 µg/g ($r^2 = 0.94$, $P < 0.0001$). Seasonally, deciduous leaves had significantly increasing Hg concentrations with date ($F_{1,50} = 4.92$, $P = 0.03$), accumulating 0.00001 µg/g per day during the growing season. Aggregated fir needles showed no between-year or within-season temporal trend, but Hg tissue concentrations were significantly greater in fir branches sampled in the forest interior than on the ski area edge ($F_{1,17} = 2.69$, $P = 0.001$).

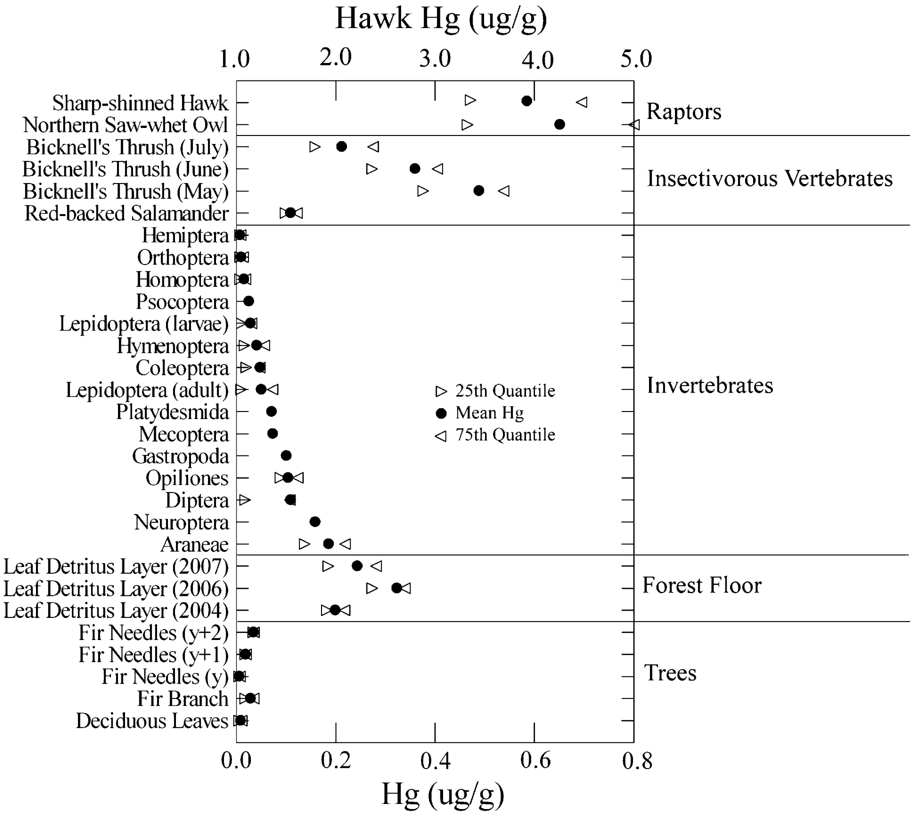
Hg concentrations in arthropods ranged widely but were lowest in herbivorous insects, highest in predatory taxa (spiders, Neuroptera [lacewings], and harvestmen; Fig. 1, "Appendix"). The single gastropod sample had relatively high Hg burdens, while the Diptera sample was elevated in part by an outlier value of 0.982 µg/g in a single bloodsucking tabanid (deer fly). Among the three broad foraging guilds, Detrital and Varied arthropods had significantly higher Hg concentrations than Canopy foragers (ANOVA: $F_{2,173} = 10.42$, $P < 0.0001$), but were not significantly different from each other. Carnivorous, Omnivorous and Herbivorous-Detrital foraging classes had significantly higher Hg concentrations than Varied or Herbivorous-Canopy arthropods (ANOVA: $F_{4,171} = 32.8$, $P < 0.001$). Although not significantly different, Hg in Carnivorous arthropods was higher than in Omnivorous foragers, which in turn had higher Hg concentrations than Herbivorous-Detrital arthropods.

We found no significant year effect in Hg concentrations within any of the six arthropod orders that yielded sufficient sample sizes for analysis among years (Araneae, Opiliones, Coleoptera, Diptera, Hymenoptera, and Lepidoptera [larvae]). However, combining all arthropods from each sampling event yielded a significant effect of year, with 2004 significantly lower than 2005–2007 (Tukey–Kramer HSD $P = 0.05$, ANOVA $P = 0.06$). This year effect is interpreted as a combination of differences in Hg concentrations and differences in orders represented in the samples from each year. Due to the opportunistic nature of the sampling, the different representation of orders probably represents different availability of food items between 2004 and 2005–2007. No within-season effects of date were found for individual orders or all arthropods combined in 2005 or 2007, the 2 years in which early- and late-season sampling was conducted.

Among the three foraging guilds, we found a significant temporal shift in the proportions of arthropods sampled, from Detrital (63% of total) dominant in early season samples to a more even distribution between Detrital (36%), Varied (33%), and Canopy (32%) foragers in late season samples ($\chi^2 = 15.16$, $df = 2$, $P = 0.0005$). Similarly, foraging subclasses showed a shift between early and late season samples, with Carnivorous (19% early, 14% late) and Herbivorous-Detrital arthropods (7% early, 5% late) declining in proportional abundance and Herbivorous-Canopy invertebrates (6% early, 16% late) increasing ($\chi^2 = 1.99$, $df = 4$, $P = 0.018$).

Available prey item biomass also shifted from early to late season, in parallel with changes in arthropod prey abundance. Detrital food web-based organisms comprised 60% of biomass in early season samples and only 25% of sampled biomass in the late season. Canopy food web-based organisms increased from 19% of sampled biomass in the early season to 46% of biomass in late season samples. Carnivorous organisms comprised a large share of biomass (41%) in early season samples and a much smaller share (21%) in the late season. Herbivores increased from 18% of sampled biomass in the early season to 45% in late season samples.

Fig. 1 Mean, 25th, and 75th percentile Hg concentrations (dry weight) for leaf detritus and biota sampled on Stratton Mountain, Vermont in 2004–2007. The *x*-axis for sharp-shinned hawk is different than for the other biotic compartments, because of the species' disproportionately higher blood Hg concentrations. Avian blood Hg concentrations were converted from wet weight (see "Methods") to facilitate comparisons among compartments



Among vertebrates, Hg burdens in red-backed salamander tails were comparable to whole-body Hg concentrations in several invertebrate groups on which they reportedly prey, including harvestmen, gastropods, and dipterans (Fig. 1; "Appendix"). For the 162 blood samples from adult Bicknell's thrushes, a marked year effect was evident, with Hg concentrations in 2004 (0.071 ± 0.006 μg/g) significantly lower than in 2005–2007 (0.093 ± 0.004 μg/g; ANOVA $P = 0.0002$, Tukey–Kramer HSD $P = 0.05$), which did not differ. Bicknell's thrush blood Hg concentrations showed no effects of sex or age classes in 2004 or 2005–2007 (Table 1), nor any interaction between sex and date. However, for the sample population, blood Hg concentrations showed a significantly decreasing linear trend with date across all years ($r^2 = 0.36$, $P < 0.0001$, $n = 150$). Although statistically significant as a linear trend over the season, the temporal pattern of Blood Hg concentration was actually a rapid increase followed by a rapid decrease, followed by a more steady decline through the end of the season (Fig. 2). Early season (prior to day 165) blood concentrations were significantly different from late season concentrations ($P < 0.00001$, one-sided *t*-test). Blood Hg concentrations in the two predatory bird species, northern saw-whet owl and sharp-shinned hawk, were elevated above those of Bicknell's thrush, markedly so in the latter species (Fig. 1, "Appendix").

Discussion

Although specific trophic relationships within the montane forest food web are not well documented, the Hg concentrations we report here appear to reflect transfer of Hg from lower to higher trophic levels with a resulting increase in Hg burden. While Hg concentrations within each compartment or biotic group did not invariably accord with known or suspected patterns of trophic transfer, the general progression was consistent with expectations: food web base (foliage < litter), herbivorous arthropods < detritivorous arthropods < predatory arthropods < insectivorous vertebrates < carnivorous vertebrates (Fig. 1, "Appendix"). The congruence of year effects in leaf litter, arthropods and Bicknell's thrush blood further suggests the existence of dietary linkages across trophic compartments at this montane forest site.

Foliage and leaf litter

Our results are consistent with those of other studies that reported greater leaf litter detritus Hg concentrations relative to those in live foliage (e.g., up to 60% greater), due to the accumulation of Hg over time, and the concentration of Hg relative to elements that leach and are respired or translocated out of foliage during senescence and decomposition (Lindberg 1996; Rea et al. 1996, 2002; Tyler

Table 1 Hg concentrations by year in age and sex classes of Bicknell's thrush on Stratton Mountain, Vermont, 2004–2007

Age–sex class	2004	2005	2006	2007
SY[a] male	0.051 (1)	0.08 ± 0.019 (8)	0.09 ± 0.046 (15)	0.099 ± 0.041 (11)
SY female	0.105 (1)	0.091 ± 0.046 (8)	0.083 ± 0.042 (2)	0.063 ± 0.025 (3)
ASY[b] male	0.07 ± 0.038 (23)	0.088 ± 0.022 (13)	0.091 ± 0.03 (17)	0.12 ± 0.05 (19)
ASY female	0.065 ± 0.031 (9)	0.111 ± 0.101 (9)	0.075 ± 0.031 (4)	0.089 ± 0.029 (10)
All males	0.069 ± 0.038 (24)	0.085 ± 0.021 (21)	0.091 ± 0.37 (32)	0.112 ± 0.048 (30)
All females	0.064 ± 0.034 (11)	0.101 ± 0.078 (17)	0.078 ± 0.031 (6)	0.082 ± 0.029 (13)
All SY birds	0.078 ± 0.038 (2)	0.085 ± 0.035 (16)	0.089 ± 0.044 (17)	0.102 ± 0.041 (20)
All ASY birds	0.069 ± 0.036 (32)	0.098 ± 0.066 (22)	0.088 ± 0.03 (21)	0.11 ± 0.044 (32)

Data presented as arithmetic mean ± SD (*n*) in µg/g (wet weight)

[a] SY = second-year (≤1 year old)

[b] ASY = after second-year (≥2 years old)

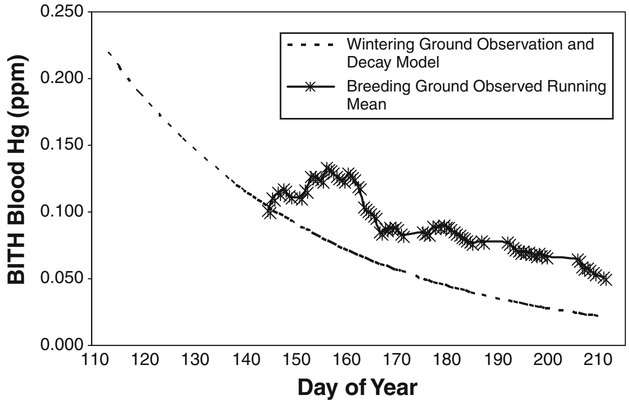


Fig. 2 Exponential decay model of the dissipation of wintering ground Hg burden and observed blood Hg concentrations (wet weight) on the breeding grounds in Bicknell's thrush. Due to the fluctuations in number of birds captured and sampled daily, the observed blood concentrations are presented as 10 day moving averages

2005). Hg foliar concentrations in the three deciduous species on Stratton were slightly higher than those reported from five hardwoods species at mid-elevations in north-central Vermont (Rea et al. 2002). Aggregated balsam fir needle Hg concentrations were higher than those of deciduous leaves; current-year needle Hg concentrations were almost identical, while those of 2 and 3 year old needles progressively increased and were higher than deciduous leaf Hg concentrations. This was an expected result, because our aggregated fir needle samples were composed of 3 years of growth, and thus accumulated Hg sequestration, while deciduous leaves reflected Hg uptake only since the occurrence of leaf-out 0.5–1.5 months prior to sampling (Grigal 2003).

Softwood-dominated leaf litter detritus at Stratton Mountain had relatively high total Hg concentrations compared to those of most biotic compartments. This was not unexpected, as leaf litter has lost much of its original mass via decomposition while retaining most of its original Hg content in addition to binding additional Hg deposited via rain, snow, and canopy throughfall (Grigal 2003). Furthermore, the proportion of total Hg as bioavailable MeHg (%MeHg) must be considered in examining the trophic relationship between detritus and consumers within the food web. MeHg is the form of Hg most readily assimilated by consumer organisms, and %MeHg is known to increase with increasing trophic level complexity. MeHg represents only ~1–2% of total Hg in forest detritus (Hall and St Louis 2004) and foliage (Erickson et al. 2003), while it constitutes ~25–60% of total Hg in terrestrial arthropods (Cristol et al. 2008; Evers and Duron 2008), 46–60% in terrestrial amphibians (Bergeron et al. 2009b), and nearly 100% in Bicknell's thrush (Rimmer et al. 2005). Litter Hg concentrations reflect deposition, retention and release, but these mechanisms and their relationship to bioavailability of MeHg in montane forest litter need further investigation. Demers et al. (2007) found that Hg accumulated in both hardwood and softwood litter during the growing season. Hall and St Louis (2004) also reported that both MeHg and total Hg concentrations in softwood-dominated litterfall of Canadian boreal forests increased over time (800 days). We did not detect an increase in litter Hg concentrations over a much shorter early summer sampling interval (28 days) in this study.

Arthropods

Although few published data exist on Hg concentrations of terrestrial arthropods, our data are consistent with those of others in which primary consumers (herbivores and detritivores) show lower Hg concentrations than secondary consumers (predatory species). Zheng et al. (2008) studied three arthropods in a Hg-contaminated grassland of China and found Hg concentrations of 0.043 and 0.037 µg/g in two primary consumers (*Locusta* sp. and *Acrida* sp.) and "higher" (no value given) Hg concentrations in a secondary consumer, *Paraten-odera sinensis*. Cristol et al. (2008) sampled orthopterans, lepidopterans, and spiders in Virginia upland habitats adjacent to Hg-contaminated rivers and at uncontaminated reference sites. Mean Hg concentrations of all three orders were "negligible" at reference sites, and lower than concentrations we obtained on Stratton Mountain, while Hg concentrations at contaminated sites were dramatically higher (spiders = 1.24 ± 1.47 μg/g, lepidopterans = 0.38 ± 2.08 μg/g, orthopterans = 0.31 ± 1.22 μg/g; Cristol et al. (2008)). In the Catskill region of New York, preliminary data, based on small sample sizes, suggested spiders have Hg concentrations 2–3 times higher than those of other arthropods (Evers and Duron 2008). Although published data are scant for terrestrial invertebrates, %MeHg generally increases at successive trophic levels within invertebrate food webs (Cristol et al. 2008), as shown in aquatic systems (e.g., Tremblay et al. 1996; Mason et al. 2000; Haines et al. 2003).

Red-backed salamander

Although the diet of red-backed salamanders in montane forests is not well known, Burton (1976) found that the species preyed primarily on mites, spiders, snails, and numerous insect families at elevations of 450–750 m in northern hardwood forests at the Hubbard Brook Experimental Forest in New Hampshire. The relatively high concentrations of Hg in our salamander samples suggest that they feed at a high trophic level within the invertebrate community, or that their preferred prey accumulate relatively high amounts of Hg due to micro-habitat preferences, soil strata, or other variables. Red-backed salamanders live and forage in moist soils, often near stream edges where total sediment Hg and MeHg concentrations are highest (Morel et al. 1998). Although our sampling effort was limited, we found salamanders only along stream edges on our study site. Since they rarely move away from these moist micro-habitats, their prey may consist of a disproportionate number of invertebrates found only along stream edges. Consistent with documented declines in this species' abundance with increasing elevation in the Hubbard Brook watershed (Burton and Likens 1975), salamander densities in the montane forest appear to be quite low, possibly due to predominantly shallow, acidic soils. These soils have been shown to disrupt sodium balance in red-backed salamanders, which are rarely found on soils with a pH ≤ 3.7 (Frisbie and Wyman 1991). At an uncontaminated riverine site in Virginia, Bergeron et al. (2009a) documented mean red-backed salamander Hg concentrations very similar to those on Stratton Mountain, suggesting similar dietary patterns and trophic transfer of Hg.

Birds

Blood Hg concentrations in Bicknell's thrush (breeding season ww mean = 0.088 μg/g ± 0.003 SD; converted dw mean = 0.348 μg/g ± 0.012 SD) were lower than previously reported in this species on Stratton Mountain (0.12 μg/g ± 0.04 SD ww; Rimmer et al. 2005). There was an initial increase in blood Hg concentration from 0.1 to 0.13 μg/g during the first 2 weeks on the breeding ground (days 143–158, Fig. 2). Blood Hg concentrations then declined rapidly from days 160–165 after which a more steady but slower rate of decline persisted through the last samples on day 206 (Fig. 2).

As a long-distance migrant, Bicknell's thrush spends 7–8 months per year away from its northeastern U.S. breeding sites (Rimmer et al. 2001). Previous research has shown that blood Hg concentrations of thrushes sampled in January and February on their Caribbean wintering grounds averaged 2–3 times higher than in birds sampled on breeding sites (Rimmer et al. 2005). We constructed an exponential decay model to estimate the carry-over effects of Hg burdens obtained on the wintering grounds on Hg concentrations during the breeding season. Although there is no published information on the half-life of MeHg, total Hg or other elements in passerine blood, MeHg turnover data exist for non-molting adults of three primarily aquatic birds. The half-life of blood MeHg is 31.5–63 days for great skua (*Catharacta skua*; Bearhop et al. 2000), 40–60 days for Cory's shearwater (*Calonectris diomedea*; Monteiro and Furness 2001), and 74 days for mallard (*Anas platyrynchos*; Heinz and Hoffman 2004). Because Bicknell's thrushes are much smaller than these three species, with higher basal metabolism and presumably lower absolute rates of Hg ingestion, we conservatively estimate 30 days as a probable half-life of MeHg in Bicknell's thrush blood. Further, the increased metabolic demands of migration likely accelerate loss of Hg obtained in winter habitats during transit from wintering to breeding grounds. Although the species' precise spring departure and arrival dates are not known, nearly all individuals depart their Hispaniolan wintering sites for northward migration before 1 May and arrive at Vermont breeding sites before 1 June (CCR and KPM unpublished data). Using estimated parameters of blood Hg at the time of wintering ground departure equal to 2.5 times the average breeding ground concentration (Rimmer et al. 2005), a 30 day migration period, and a 30 day half-life, an exponential decay model successfully predicted the initial breeding-ground blood Hg observations (0.101 μg/g, $n = 4$ on day 143; Fig. 2).

Although data on dietary composition of this species are sparse, owing to the difficulty of direct observation and sampling known food items, our data strongly suggest that a seasonal shift in diet accounts for the initial increase in

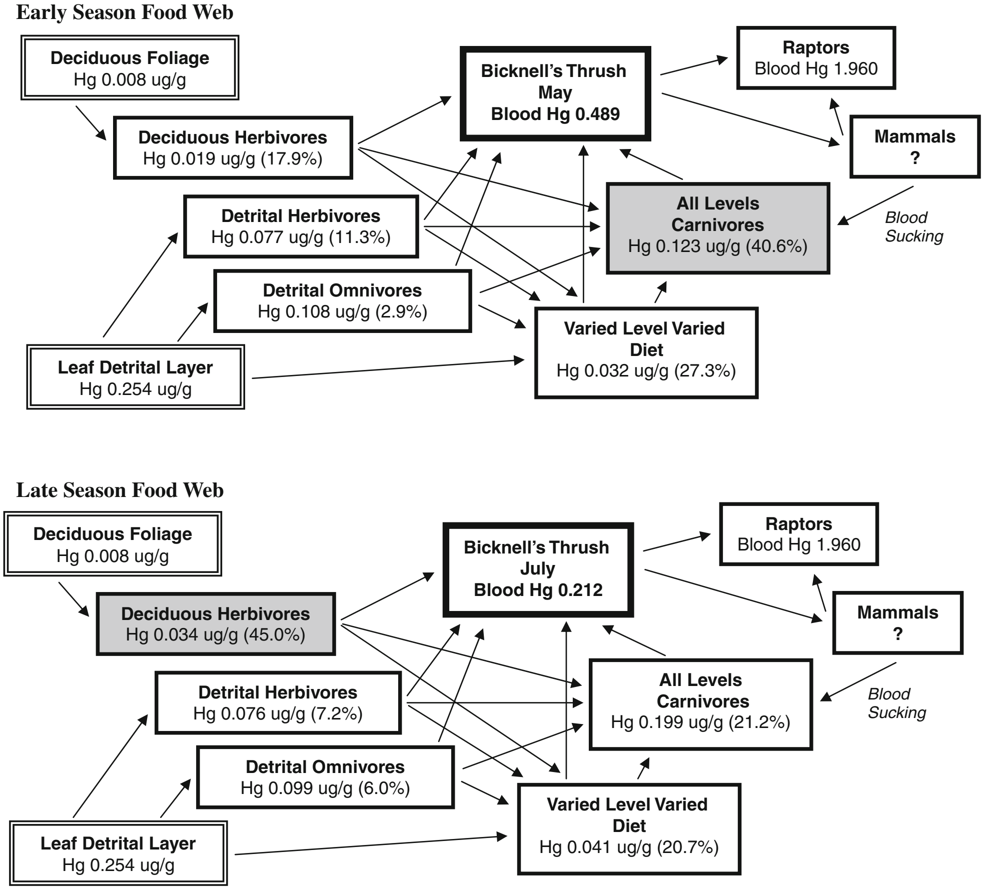


Fig. 3 Shifts in food web structure from early to late summer in a montane forest ecosystem. The relative biomass of different arthropod feeding guilds (as percents in parentheses) and each compartment's mean Hg concentration (dry weight) are indicated. A detrital-based food web dominates the early season, while a canopy-based food web increases in importance during the late summer season. Bicknell's thrush (heavy border) is the focal species in this study. *Shaded boxes* represent the largest contributions by mass (and abundance—see text) to the diet of Bicknell's thrush in a given period of its breeding season. Thrush and raptor blood Hg concentrations were converted from wet weight (see "Methods") to facilitate comparisons among compartments

May and subsequent decline of Hg blood concentrations during June and July (Fig. 3). There was a significant difference ($P < 0.00001$, 1-sided t-test) between Early and Late season blood Hg concentrations in Bicknell's thrush. Birds return to their breeding grounds during the very early stages of leaf-out, prior to the emergence of most folivorous arthropods. At this time, spiders are relatively numerous and we suspect that this group constitutes a significant portion of the species' diet. As a primarily ground-foraging species, Bicknell's thrush likely feed disproportionately on spiders, harvestmen, and ants early in the growing season. Snails may also be taken by females to supplement calcium mobilization for egg production. As new coniferous and deciduous foliage emerges during June, Bicknell's thrush likely shift to a higher proportion of folivorous arthropods, such as larval ledpidopterans, hymenopterans (sawflies and ichneumons), and hemipterans. The change in food item availability and lower Hg burdens in late-season potential prey items likely account for the drop in thrush blood concentrations between early and late summer on the breeding grounds (Figs. 2 and 3). Data are limited on within-season changes in MeHg concentrations and %MeHg among terrestrial biota, but Mason et al. (2000) found few differences over three sampling periods (October, April, and July) among predatory and non-predatory aquatic invertebrates. Our interpretations of Hg concentrations among the compartments we sampled assume that %MeHg did not differ significantly between early- and late-season samples. Further research is needed to determine this.

Arthropod data corroborate an apparent seasonal diet shift by Bicknell's thrush along the Hg concentration spectrum of potential prey items (Fig. 3). As measured by both relative abundance and biomass, Carnivorous and Herbivorous-Detrital arthropods (those highest in Hg) were the dominant potential prey items early in the season and decreased in late season samples. Conversely, lower trophic level arthropods (mostly canopy herbivores with lower Hg concentrations) increased in relative abundance and biomass over the summer, dominating the potential late season prey availability.

Independently-collected sweep net data from June and July of 2000 and 2001 at 1,065–1,200 m elevation on Stratton Mountain further corroborate our results in documenting a seasonal shift in montane forest arthropod abundance. For two of the most commonly encountered taxa in sweep net samples, spiders and holometabolous larvae, relative abundance as measured by both percentage of total samples and mean mass per sample showed opposite trends between early June and mid-July (A. Strong, University of Vermont unpublished data). Spiders markedly declined as a percentage of total arthropods sampled (34–14%), while the mean mass per sample decreased less sharply (0.38–0.28 g) through the period. In contrast, both the percentage and mean mass of larvae per sample dramatically increased over the 7 week sampling period in both years (percentage: 4–25%; biomass: 0.26–2.51 g).

The Hg concentration in Bicknell's thrush blood at the end of the breeding season is 1.6 times the concentration of residual wintering-ground Hg burden predicted by the exponential decay model. This suggests that Hg in the breeding ground diet provides a significant component of the total Hg burden of birds during the breeding season. Still, Hg burdens carried from the wintering grounds may be substantial. Further study is warranted into sources of Hg in the winter diet of Bicknell's thrush, changes in avian blood Hg concentrations through the wintering period, turnover of Hg and MeHg in blood, and comparison of Hg burdens in migrant species with those in taxonomically and ecologically similar, co-occurring resident passerines.

The two predatory bird species, sharp-shinned hawk and northern saw-whet owl, had elevated blood Hg from Bicknell's thrush and red-backed salamanders (Fig. 1, "Appendix"). Reflecting its exclusive diet of small songbirds, including Bicknell's thrush, sharp-shinned hawk blood Hg was expected to be higher, and was likely accounted for by trophic biomagnification. The order of magnitude increase above Bicknell's thrush was greater than expected; however, variance was large. Northern saw-whet owls had blood Hg concentrations that likely reflected this species' dietary specialization on small mammals (e.g., red-backed voles [*Clethrionyms gapperi*]), most of which feed on seeds and vegetation. In contrast to Bicknell's thrush, one individual sharp-shinned hawk captured on 5 June and again on 13 July 2006 had nearly identical blood Hg on the two dates, 0.967 and 0.975 ppm, respectively. Hawks are unlikely to switch prey items within a summer, and this finding reinforces the likelihood that seasonal declines in thrush blood Hg signal a dietary shift from carnivorous to herbivorous arthropods.

Year effects in Hg concentrations

Significantly lower Hg concentrations in three sampled compartments (detritus, arthropods, Bicknell's thrush) during 2004 versus 2005–2007 provide compelling evidence for dietary linkages and trophic transfer in the terrestrial montane forest community. Bioavailability of Hg, as reflected through uptake by Bicknell's thrush, has been shown to correlate to modeled atmospheric deposition patterns (Rimmer et al. 2005). Our results further corroborate this link, in that Hg deposition data from nearby Underhill, Vermont were relatively lower from 1999 to 2003 (mean 9.3 $\mu g/m^2$/year) and relatively higher from 2004 to 2007 (mean 11.6 $\mu g/m^2$/year) (E. Miller, manuscript in preparation). As early season prey items are dependent on the detrital-based food web, there is likely a time lag between deposition changes and changes in Hg burdens of the detrital-based food web. This shift from a lower to higher mercury deposition regime could have accounted for the lower Hg concentrations on Stratton Mountain in 2004 and relatively higher concentrations from 2005 to 2007.

Summary and conclusions

Overall, Hg concentrations suggest a pattern of biomagnification at successive trophic levels in the montane forest food web (Fig. 1, "Appendix"). Within-season changes in Bicknell's thrush blood Hg concentrations were consistent with a diet switch from more Hg-rich detrital-based prey abundant in the early summer food web to prey relatively lower in Hg content that were more abundant in the foliage-based food web of mid to late summer. The significant and consistent year effect among the trophic compartments of litter, arthropods and thrush blood strongly suggests that avian dietary differences are reflected in blood Hg concentrations. Although our lack of MeHg data for all trophic compartments (except Bicknell's thrush) limits ideal comparisons across the food web, other published studies support our contention that total Hg concentrations are a valid proxy for MeHg burdens in the compartments we sampled. We believe our results provide strong evidence that Hg and MeHg bioaccumulate and biomagnify in the montane forest biotic community.

High-elevation forest biota of the northeastern U.S. could serve as useful biomonitors of temporal and spatial Hg changes in terrestrial food webs resulting from current and proposed controls on Hg emissions. Scientists and policy makers are developing a long-term Hg monitoring framework (Mason et al. 2005; Driscoll et al. 2007b), which, while focused on aquatic systems and biota, should incorporate a terrestrial component. The montane coniferous forests inhabited by breeding Bicknell's thrush are vulnerable to both elevated Hg deposition (Miller et al. 2005) and climatic warming (Rodenhouse et al. 2008). Impacts to these geographically restricted habitats could have profound effects on their unique assemblage of flora and fauna, as well on aesthetic and recreational opportunities for millions of people in the northeastern U.S. A baseline of Hg data currently exists for Bicknell's thrush, and we believe the species is a valuable bioindicator for continued monitoring of Hg contamination in terrestrial food webs. Although toxicity thresholds for free-living vertebrate wildlife are not well-established, the Hg concentrations we report are substantially below those known to cause lethal or sub-lethal effects in other vertebrate species (e.g., Scheuhammer et al. 2007 review; Brasso and Cristol 2008; Evers et al. 2008; Hawley et al. 2009). However, sub-lethal fitness impacts can be difficult to detect, and we suggest that effects-based investigations should be conducted to examine the ecological significance of MeHg bioavailability in montane forest biota.

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Appendix

See Table 2.

Table 2 Means, standard deviations, and ranges of Hg concentrations (μg/g) in leaf litter and biotic compartments sampled on Stratton Mountain, Vermont in June and July of 2004–2007

Compartment	Mean	SD	Range	*n*
Leaf litter (all years)	0.254	0.091	0.141–0.492	20
Leaf litter (2004)	0.199	0.04	0.141–0.259	6
Leaf litter (2006)	0.323	0.09	0.254–0.492	6
Leaf litter (2007)	0.217	0.058	0.149–0.314	7
Deciduous leaves (all species)	0.009	0.004	0.003–0.02	44
Paper birch	0.007	0.003	0.002–0.13	25
Mountain ash	0.009	0.005	0.005–0.22	26
Pin cherry	0.007	0.003	0.003–0.01	6
Balsam fir branches	0.029	0.014	0.009–0.058	22
Balsam fir needles (new)	0.006	0.001	0.005–0.008	4
Balsam fir needles (1 year)	0.019	0.002	0.018–0.021	4
Balsam fir needles (2 year)	0.035	0.02	0.034–0.037	3
Araneae (spiders)	0.173	0.081	0.02–0.334	19
Coleoptera (beetles)	0.048	0.067	0.004–0.391	36
Diptera (flies)	0.11	0.17	0.002–0.984	50
Gastropoda (snails)	0.101			1
Hemiptera (true bugs)	0.008	0.002	0.006–0.009	2
Heteroptera (assassin bugs)	0.016	0.17	0.004–0.04	4
Hymenoptera (ants, wasps, sawflies)	0.04	0.033	0.004–0.12	20
Lepidoptera (adult)	0.05	0.07	0.006–0.13	3
Lepidoptera (larvae)	0.29	0.28	0.007–0.108	13
Mecoptera (scorpionflies)	0.074			1
Neuroptera (lacewings)	0.159			1
Opiliones (harvestmen)	0.105	0.029	0.056–0.142	7
Orthoptera (grasshoppers)	0.01	0.005	0.003–0.014	4
Platydesmida (millipede)	0.071			1
Psocoptera (barkflies)	0.026			1
Red-backed salamander	0.11	0.02	0.085–0.131	4
Bicknell's thrush (early June 2004)	0.091	0.04	0.051–0.199	13
Bicknell's thrush (late June 2004)	0.063	0.022	0.035–0.107	12
Bicknell's thrush (early July 2004)	0.072	0.028	0.055–0.105	3
Bicknell's thrush (late July 2004)	0.033	0.012	0.014–0.046	6
Bicknell's thrush (May 2005–2007)	0.123	0.047	0.05–0.267	35
Bicknell's thrush (early June 2005–2007)	0.106	0.055	0.046–0.378	38
Bicknell's thrush (late June 2005–2007)	0.083	0.022	0.046–0.132	30
Bicknell's thrush (early July 2005–2007)	0.065	0.014	0.046–0.095	25
Northern saw-whet owl	0.164	0.059	0.107–0.251	6
Sharp-shinned hawk	0.989	0.501	0.393–1.62	4

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