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RESEARCH ARTICLE

Is brood parasitism related to host nestling diet and nutrition?

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ABSTRACT

Food and nutrient limitation can have negative effects on survival, fecundity, and lifetime fitness of individuals, which can ultimately limit populations. Changes in trophic dynamics and diet patterns, affected by anthropogenic environmental and landscape change, are poorly understood yet may play an important role in population regulation. We determined diets of Wood Thrushes (*Hylocichla mustelina*), a Neotropical migratory songbird species sensitive to urbanization, and explored how brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) may be related to Wood Thrush nestling diets. Effects of brood parasitism on host nestling diets is an understudied stressor that may help explain observed population declines. We measured carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes of 7 invertebrate food sources (snails, spiders, isopods, earthworms, myriapods, insects, and caterpillars), blood plasma from adult male and female Wood Thrushes and from Wood Thrush nestlings in nests with and without Brown-headed Cowbird nestlings. Wood Thrush diet compositions were largely composed of high calcium (Ca) foods (51–62%, 95% highest density intervals [HDI]), including snails, isopods, and myriapods, as well as spiders (23–33%, 95% HDI). Caterpillars were the least common food item in Wood Thrush diets (0.01–3 %, 95% HDI). Wood Thrush nestling diets in nests without Brown-headed Cowbirds contained greater proportions of Ca-rich foods and spiders compared to the diet of nestlings in parasitized nests. Our data demonstrate that Wood Thrushes preferred Ca- and protein-rich foods, which may have important implications for adult survival and fecundity as well as nestling nutrition and development. Our results suggest that brood parasitism is related to host nestling diet, which could have potentially negative effects on developing nestlings through nutritional stress that may in turn affect survival, fecundity, and ultimately limit population growth.

Keywords: brood parasitism, Brown-headed Cowbird, carbon, *Hylocichla mustelina*, *Molothrus ater*, nitrogen, nutritional stress, stable isotopes, Wood Thrush

¿Está relacionado el parasitismo de nidada con la dieta y la nutrición del hospedero de los polluelos?

RESUMEN

Las limitaciones de alimentos y nutrientes pueden tener efectos negativos en la supervivencia, la fecundidad y la adecuación biológica de los individuos, lo que puede en última instancia limitar a las poblaciones. Los cambios en las dinámicas tróficas y en los patrones de la dieta, afectados por los cambios antropogénicos del ambiente y del paisaje, no están claramente entendidos pero pueden jugar un rol importante en la regulación poblacional. Determinamos la dieta de *Hylocichla mustelina*, una especie de ave canora migrante neotropical sensible a la urbanización, y analizamos como el parasitismo de nidada por parte de *Molothrus ater* puede relacionarse con la dieta de los polluelos de *H. mustelina*. Los efectos del parasitismo de nidada sobre la dieta de los polluelos del hospedero son un factor de estrés poco estudiado que pueden ayudar a explicar los declives poblacionales observados. Medimos los isótopos estables de carbono ($\delta^{13}C$) y nitrógeno ($\delta^{15}N$) de siete fuentes de alimentos de invertebrados (caracoles, arañas, isópodos, lombrices de tierra, miriápodos, insectos y orugas), y el plasma sanguíneo de los machos y las hembras adultas de *H. mustelina* y de los polluelos de *H. mustelina* en nidos con y sin polluelos de *M. ater*. La composición de la dieta de *H. mustelina* estuvo en gran medida compuesta por alimentos con calcio (Ca) (51–62 %, 95% de intervalo de máxima densidad (IMD)), incluyendo caracoles, isópodos y miriápodos, como así también arañas (23–33%, 95% IMD). Las orugas fueron el ítem alimenticio menos común en la dieta de *H. mustelina* (0.01–3 %, 95% IMD). La dieta de los polluelos de *H. mustelina* en los nidos sin *M. ater* presentó mayores proporciones de alimentos ricos en Ca y arañas en comparación con la dieta de los polluelos en los nidos parasitados. Nuestros datos demuestran que los individuos de *H. mustelina* prefirieron alimentos ricos en Ca y proteínas, lo que puede tener implicancias importantes para la supervivencia y la fecundidad de los adultos, así como para la nutrición y el desarrollo de los polluelos. Nuestros resultados sugieren que el parasitismo de nidada está relacionado con la dieta de los polluelos del hospedero, lo que puede tener efectos potencialmente negativos

en los polluelos en desarrollo a través de estrés nutricional que puede, a su vez, afectar la supervivencia, la fecundidad y en última instancia el crecimiento poblacional.

Palabras clave: carbono, estrés nutricional, *Hylocichla mustelina*, isótopos estables, *Molothrus ater*, nitrógeno, parasitismo de nidada.

INTRODUCTION

Diet and nutrition affect lifespan and fecundity of organisms across taxa (Lee et al. 2008, Benstead et al. 2014), which may in turn influence and ultimately limit populations (Lack 1968). Developmental stress resulting from malnutrition during ontogeny (Herring et al. 2011, Will et al. 2014) can negatively affect brain development (Lanet and Maurange 2014) and lead to reduced lifetime fitness for individuals (Maklakov et al. 2008). How ecological change affects trophic dynamics, diets, and populations remain central questions in ecology (Heath et al. 2014).

More than 40% of Neotropical migratory songbird species have declined during the past 50 years (Sauer et al. 2012). Causes of these declines are likely due to a synergy of habitat loss and fragmentation (Burke and Nol 2000), urbanization (Suarez-Rubio et al. 2011), pollution (Condon and Cristol 2009), climate change (Both et al. 2009), and brood parasitism (Brittingham and Temple 1983, Trine 1998). Neotropical migrants are particularly vulnerable to broad-scale changes in the amount, arrangement, and quality of habitat required for breeding, wintering, and migration periods (Sillet and Holmes 2002). Causes of Neotropical migrant population declines have been related to breeding season fitness reductions linked to vegetation cover (Holmes 2011), nest predation (Newell and Kostalos 2007), brood parasitism (Hoover and Brittingham 1993, Lloyd et al. 2005), and food or nutrient availability (Richmond et al. 2011). Changes in trophic interactions among vegetation community composition and structure and food availability have been demonstrated (Hagar et al. 2007), but the mechanisms leading to reduced fecundity remain unclear.

Avian brood parasites such as the Brown-headed Cowbird (*Molothrus ater* [Boddaert, 1783]) have negative effects on host nestling growth, and in some cases nestling survival, due to early hatching and out-competing host nestlings for food resources (Lichtenstein and Sealy 1998, Hauber 2003, Grim 2006). Nestling development influences lifetime fitness by affecting survival probability, length of development time, and adult survival and fertility (Istock 1983). Nestling development in free-living birds can be affected by habitat (Kaiser and Lindell 2007, Richman et al. 2014), food and nutrient availability (Dawson and Bidwell 2005), food quality (Cohen et al. 2014), and brood size (Boonekamp et al. 2014). In captivity, nestling growth rates have been shown to be directly related to food and nutritional quality (Soma et al. 2006), and nutritional stress can negatively affect brain development and subsequent mating success (Nowicki et al. 1998, Peters et al. 2014).

To date, only a few studies have explored the effects of brood parasitism on host nestling diets, even though it may play an important role in population regulation (Brooke and Davies 1989, Grim and Honza 1997). Previous studies (e.g., Brooke and Davies 1989, Grim 2006) have relied on quantifying diets through observing parental food source provisioning as opposed to estimating the assimilated food sources in nestling diets. However, experimental studies that have manipulated parasitism of free-living birds have demonstrated that nestling diet along with cowbird nestling growth rates can be influenced by host clutch size (Kilner et al. 2004), and that hatching asynchrony can give cowbird nestlings a competitive edge in the procurement of food resources from host parents (Hauber 2003). We estimated assimilated food sources in diets of adult and nestling Wood Thrushes (*Hylocichla mustelina* [Gmelin, 1789]), a well-studied Neotropical migratory songbird species, to explore how brood parasitism may be related to nestling diets. Previous research studying interactions between brood parasites and host species have largely focused on coevolution and host suitability (Kilpatrick 2002, Soler 2014), parental provisioning (Hoover and Reetz 2006, Rivers et al. 2014), and overall parasitism rates (Carrie 1999, Stoklosa et al. 2014), and have demonstrated potential negative effects for host species. Although primary dietary constituents of Wood Thrushes have been documented in previous studies (Cooper 1975, Holmes and Robinson 1988), Wood Thrush diets of assimilated foods have not yet been described using more robust techniques to determine important patterns that may help improve our understanding of limiting factors for breeding populations.

In this study, we used stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$, respectively) to estimate Wood Thrush diets and determine if diets differed (1) between sexes and age groups (adults and nestlings), and (2) between Wood Thrush nestlings in nests with and without parasitic Brown-headed Cowbird nestlings while accounting for variation in site differences related to patterns in food availability and brood parasitism occurrence within small urban forest fragments. We predicted that diets of Wood Thrush nestlings would differ in relation to presence or absence of Brown-headed Cowbird parasitism, and specifically, that Wood Thrush nestlings in nests with

Brown-headed Cowbirds would eat fewer high-quality prey items (e.g., snails and spiders), most likely resulting from competition between host and parasitic nestlings for food items provisioned by host parents, as previous studies have suggested.

METHODS

Study Area

The study area was located on the boundary of the Piedmont plateau and Atlantic Coastal Plain physiographic regions (Fenneman and Johnson 1946), which is generally characterized by low rolling hills and clay soils within the White Clay Creek watershed. Sampling sites (21) were randomly located within 18 distinct forest fragments in Newark, Delaware, USA (39°41′1.40″N 75°44′58.77″W; Figure 1). Each site was located along an edge adjacent to nonforest land cover to control for site-level edge effects. Sites ranged in size from 2.1 to 16.3 ha and included Ecology Woods (Bray et al. 1965), where an ongoing 40-year demographic study on breeding Wood Thrush occurs (Figure 1, Table 1). Sites were gridded with 50 × 50 m cells using alpha-numerically marked locations (hereafter points). We randomly selected a subset of 311 points equally distributed among sites from within the set of all alpha-numerically identified points in 21 sites. The secondary forest vegetation community is generally dominated by tree species: tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), red oak (*Quercus rubra*), white oak (*Quercus alba*), pignut hickory (*Carya glabra*), and American beech (*Fagus grandifolia*), and understory shrub species: multiflora rose (*Rosa multiflora*), spicebush (*Lindera benzoin*), green briar (*Smilax rotundifolia*), Japanese honeysuckle (*Lonicera japonica*), southern arrowwood (*Viburnum dentatum*), autumn olive (*Elaegnus umbellat*a), and sweet pepperbush (*Clethra alnifolia*).

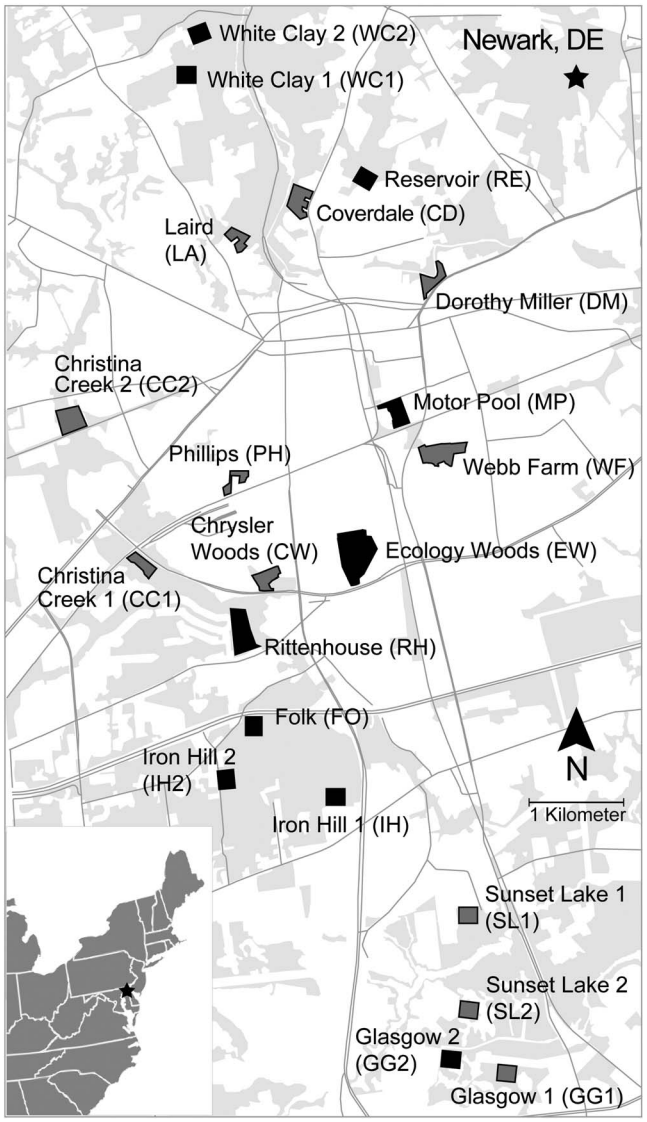

FIGURE 1. Map of 21 forest fragment sites where invertebrate food availability and breeding Wood Thrushes were sampled from May through August 2011–2013 in and near Newark, DE, USA. Forested land cover is indicated by light gray polygons, roads are shown by gray lines, and sites are designated where breeding Wood Thrushes were sampled (black polygons) and did not occur (dark gray polygons).

Food Resource Availability Sampling

Invertebrates were sampled from soil, leaf litter, and understory vegetation to estimate food availability, and we assessed variation within taxa among sites to account for potential effects on Wood Thrush diets.

Soil sampling. We sampled earthworms using electroshocking methods at 63 points consisting of 3 randomly chosen points within each of 21 sites from 26 June to 7 July 2013 using a modified octet design (Weyers et al. 2008). Sampling areas at each point consisted of a 0.22-m^2 area with 8 electrodes (i.e. 30.5 cm, stainless steel spikes) placed 20 cm deep into the soil in an octagonal arrangement (see Weyers et al. 2008 for details). Electrodes for each pair (i.e. positive and negative) were placed 52 cm apart (the diameter of the circular sampling area), and each electrode was placed roughly 20 cm apart along the perimeter of the circle. Each electrode pair was labeled A, B, C, and D and connected to a 12V battery. We measured voltage within the sampling area using a digital voltmeter (Commercial Electronic, model MAS830B, China). We rotated the electrical field within the sampling area following Thielemann (1986) and electrified the spikes in the following 8 sequences: AB, ABC, BC, BCD, CD, ACD, AD, and ABD. The duration of each sequence ranged from 1 to 2.5 min, depending on earthworm emergent activity. For example, when earthworm activity was high, sequence durations were longer. We waited a minimum of a 0.5 min with no

TABLE 1. List of 21 study sites, locations, and areas (ha) in and near Newark, DE, USA.

Site Name	ID	Latitude	Longitude	Site area (ha)	Patch area (ha)
Christina Creek 1	CC1	N39°39′39.01	W75°46′14.82	4.2	50.8
Christina Creek 2	CC2	N39°40′30.67	W75°46′48.91	8.2	12.7
Coverdale	CD	N39°41′47.37	W75°45′5.64	6.2	155.5
Chrysler Woods	CW	N39°39′33.67	W75°45′21.27	4.5	5.5
Dorothy Miller	DM	N39°41′18.01	W75°44′7.76	4.2	68.8
Ecology Woods	EW	N39°39′44.15	W75°44′39.60	16.2	16.6
Folk	FO	N39°38′43.19	W75°45′26.75	5.0	150.1
Glasgow 1	GG1	N39°36′39.99	W75°43′29.84	5.2	75.6
Glasgow 2	GG2	N39°36′47.12	W75°43′54.97	4.7	75.6
Iron Hill 1	IH1	N39°38′19.57	W75°44′46.89	5.2	150.1
Iron Hill 2	IH2	N39°38′19.47	W75°45′33.24	5.1	150.1
Laird	LA	N39°41′31.69	W75°45′32.85	4.5	10.1
Motor Pool	MP	N39°40′33.05	W75°44′21.38	5.1	5.9
Phillips	PH	N39°40′10.80	W75°45′34.74	3.6	4.6
Reservoir	RE	N39°41′55.62	W75°44′36.30	5.0	53.3
Rittenhouse	RH	N39°39′14.80	W75°45′29.70	11.0	50.8
Sunset Lake 1	SL1	N39°37′35.87	W75°43′46.05	4.5	157.9
Sunset Lake 2	SL2	N39°37′4.62	W75°43′48.67	4.6	157.9
White Clay Creek 1	WC1	N39°42′32.14	W75°45′58.16	5.2	163.6
White Clay Creek 2	WC2	N39°42′45.29	W75°45′53.72	5.4	163.6
Webb Farm	WF	N39°40′17.90	W75°44′2.48	8.7	11.1

electrodes on between sequences, allowing partially surfaced earthworms to move out of the soil and to collect earthworms that had already surfaced. We only collected earthworms within the 0.22 m^2 sampling area and disregarded worms surfacing outside the area. All earthworms were identified to family by a single observer using field guides (Edwards 2004).

Leaf litter sampling. Invertebrates were sampled from leaf litter collected on the forest floor from 311 randomly selected points in 21 sites from 17 June 2010 to 5 September 2011. At each sampling location, all leaf litter within 0.5 m^2 was collected and placed in bags. Leaf litter samples were transferred to Berlese funnels (Berlese 1905) outfitted with 25 watt incandescent light bulbs for 3 days to collect invertebrates in jars filled with 80% ethanol. Samples were then hand-sifted using a 4 mm sieve to retrieve any remaining invertebrates. Finally, leaf litter volume was measured (L) for each sample using a graduated plastic bucket. A trained observer identified all invertebrates to family using field guides (Burch 1962, Dindal 1990, Triplehorn and Johnson 2005). These data were pooled by class for estimation of leaf litter invertebrate densities.

Understory branch-clipping. Invertebrates on understory vegetation were sampled from 168 randomly selected points on 4 sampling occasions: 14 June, 27 June, 11 July, and 23 July 2012. A branch-clipping technique was used to sample invertebrates from the 4 dominant native understory vegetation species: American beech, spicebush, red maple; and one dominant nonnative species: multiflora rose (Johnson 2000). Two replicate branch clippings were collected at 2 randomly selected points per sampling period from each of the focal species by placing a branch with 10 or more leaves into a heavy-duty garbage bag, clipping the branch at the base of the trunk, and immediately tying the bag to seal it. Invertebrates were killed using ethyl acetate-soaked cotton balls prior to removal from branches in the laboratory. All invertebrates collected on branches were stored in quart-sized plastic Ziploc bags at −80°C until they were sorted and identified to family by a trained observer using field guides (Triplehorn and Johnson 2005). All leaves from branches were removed and weighed (g) with a Sartorius Acculab electronic balance (Göttingen, Germany) to determine the number of individuals per leaf wet mass (g). Replicate samples were pooled to calculate mean density for each sampling period per site for each of the 4 plant species; means were then summed across plant species to estimate total invertebrate density per site.

Food source preparation. We used a subset of invertebrates from earthworm, leaf litter, and understory vegetation sampling and invertebrates from targeted collections for stable isotope analysis (see Methods). All invertebrates were identified to family and stored frozen at −80°C. All invertebrates were rinsed in deionized water and sonicated for 1 min to remove dirt and debris. Samples were then dried at 60°C for 48 hr or until dry, homogenized, and weighed to approximately 300–400 μg on a Sartorius Cubis microbalance and placed into tin capsules for measurement of stable isotopes of C and N.

Wood Thrush Diet Sampling

Nest monitoring and capture techniques. Active Wood Thrush nests were monitored every 2–3 days

following initial discovery from 1 May to 20 August during the 2011–2013 breeding seasons (Martin and Geupel 1993). During each nest check the numbers of Wood Thrush and Brown-headed Cowbird eggs and nestlings present were recorded. For each nest, the location (UTM coordinates), height (m), plant species, and subsequent estimated distance to nonforest edge using ArcMap 10.1 (ESRI 2011) were recorded. We used a comparative approach to test for differences in host nestling diets between naturally occurring parasitized and nonparasitized nests within our study area. Nests were considered parasitized if at least one Brown-headed Cowbird nestling that could accept food from Wood Thrush host parents was present in the nest. We used logistic regression to test for effects of distance to edge (m), site, and month (i.e. May, June, July) on Brown-headed Cowbird parasitism occurrence and found no effects for distance to edge (z-value = –0.895, $P = 0.371$) for any sites or months (all P-values > 0.998). Adult Wood Thrushes were captured and sampled using mist nets (36-mm mesh size). We estimated nestling age to within ±2 days from time since known hatch date or based on the degree of feather development when hatch date was unknown. We sampled Wood Thrush nestlings that were 6–10 days old by extracting them from nests by hand (Federal Bird Banding permit #: 23475) between 6 May and 15 August 2011–2013. All birds were fitted with aluminum U.S. Geological Service (USGS) bands, and adults were given unique color-band combinations to allow future identification by sight.

Determining diet constituents. Fecal samples of captured birds were collected in paper bags and stored in 95% ethanol to determine prominent Wood Thrush invertebrate food groups to be isolated for stable isotope analysis. Wood Thrush fecal samples ($n = 306$) were visually examined (Burger et al. 1999), and 6 major food groups were identified having the following frequency of occurrence (mean% of total ± SE): Insecta (excluding lepidopterans; 99 ± 0.7%), Arachnida (spiders; 45 ± 2.8%), Myriapoda (millipedes and centipedes; 58 ± 2.8%), Isopoda (wood lice; 13 ± 2.0%), Lepidoptera larvae (caterpillars; 6 ± 1.3%), and Gastropoda (land snails; 3 ± 1.0%). Additionally, earthworms were included as a known food source for Wood Thrushes based on previous studies (Cooper 1975, Holmes and Robinson 1988).

Blood plasma collection. Blood samples were collected via brachial artery puncture using 27 gauge, 1.27 cm syringes in heparinized capillary tubes (75 μL) according to IACUC regulations, under permit #:1129-2012-2. Capillary tubes containing blood were sealed with crito-seal clay and stored immediately on ice in the field. Red blood cells (RBC) were separated from plasma within 2–3 hr of collection by centrifugation for 7 min at 11,700 rpm in a Clay Adams Autocrit Ultra 3 centrifuge (Becton Dickinson, Franklin Lakes, NJ, USA). Capillary tubes were then scored using a fine file, and RBC and plasma were transferred to sterile cryo-vials and stored frozen at –80°C. Plasma samples from each individual were lyophilized (Labconco, Kansas City, MO, USA), and freeze-dried samples were homogenized with a quartz mortar and pestle. Samples were then weighed to ~300-400 μg on a Sartorius Cubis microbalance (Göttingen, Germany) into tin capsules for stable isotope analysis.

Measurement of Carbon And Nitrogen Stable Isotope Ratios

Isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were measured using a Costech Elemental Analyzer (Valencia, California, USA) connected via a Thermo Scientific ConFlow IV to a Thermo Delta V (Bremen, Germany) isotope ratio measuring mass spectrometer located at the Stable Isotope Geochemistry Laboratory at University of Delaware in Newark, Delaware. Stable isotope ratios are reported as δ-values expressed as parts per thousand (‰) derived from:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000,$$

where X is ^{13}C or ^{15}N and R represents the associated $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio; $R_{standard}$ is the isotope ratio of international references for C or N. The $\delta^{13}C$ and $\delta^{15}N$ values of our samples were calibrated against 2 USGS standards (USGS 40 and 41). Values for $\delta^{13}C$ and $\delta^{15}N$ in USGS 40 are –26.39 and –4.57‰, respectively and in USGS 41 are 37.63 and 47.57‰, respectively. Two internal standards (acetanilide and benzoic acid) were used in all runs. Samples and correction standards were run in duplicate or more. All C and N isotope data are reported as $\delta^{13}C$ and $\delta^{15}N$ relative to the Peedee Belemnite (PDB) and atmospheric N_2, respectively, both of which are assumed equal to 0.0‰. The analytical precision of the $\delta^{13}C$ and $\delta^{15}N$ analyses, on the basis of replicate analyses of the internal standards under the same analytical conditions as of the samples, was better than ±0.2‰. For example, acetanilide and USGS 40 yielded standard errors of 0.17 for $\delta^{15}N$ and 0.10 for $\delta^{13}C$, and 0.17 for $\delta^{15}N$ and 0.13 for $\delta^{13}C$, respectively. Carbon half-life ($C_{t1/2}$) for C incorporation to Wood Thrush plasma was estimated to be roughly 1–2 days based on mean body mass of adult and nestling Wood Thrushes (0.5 × adult mass) collected during this study (51 g and 25.5 g, respectively) and with values measured in American Crows (*Corvus brachyrhynchos*; $C_{t1/2}$ 2.9 days; Hobson and Clark 1993) and Yellow-rumped Warblers (*Setophaga coronate*; $C_{t1/2}$ 0.4–0.7 days; Pearson et al. 2003).

Mixing models were run in the "siar" package in R (Parnell et al. 2008) using Markov Chain Monte Carlo simulations with 1,000,000 iterations and a burn-in period of 100,000 iterations (Parnell et al. 2010). These multiple-source, concentration-dependent mixing models incorporate uncertainty in all model parameters (Parnell et al. 2008)

TABLE 3. Invertebrate density mean (SE) for spiders, insects, caterpillars, snails, myriapods, isopods, and earthworms among 10 forest fragment sites (see Table 1 for abbreviations) sampled from April to September 2010–2013 in and near Newark, DE. Invertebrates were sampled and density calculated for soil (individuals m^{-2}), leaf litter (individuals L^{-1} leaf litter), and understory vegetation (individuals g^{-1} leaf mass) sampling substrates. Number of plots is indicated by *n*. Differences among sites for invertebrate groups are shown by superscript lowercase letters.

			Sites		
			EW	FO	GG2
Food source	Sampling substrate	*n*	mean (SE)	mean (SE)	mean (SE)
Spiders	Understory vegetation	111	0.05 (0.02)	0.05 (0.02)	0.12 (0.10)
	Leaf litter	148	0.17 (0.06)	0.13 (0.05)	0.12 (0.05)
Insects	Understory vegetation	115	0.31^{ab} (0.11)	0.12^{ab} (0.05)	0.13^{b} (0.10)
	Leaf litter	163	3.41^{ab} (0.89)	3.28^{ab} (0.58)	9.12^{a} (2.21)
Caterpillars	Understory vegetation	112	0.37 (0.16)	0.13 (0.05)	0.03 (0.01)
Snails	Leaf litter	143	0.19^{c} (0.08)	0.43^{bc} (0.09)	0.12^{c} (0.08)
Myriapods	Leaf litter	148	0.20^{b} (0.08)	0.32^{b} (0.14)	0.17^{b} (0.07)
Isopods	Leaf litter	148	0.29 (0.16)	0.30 (0.13)	0.10 (0.05)
Earthworms	Soil	30	37.88 (12.40)	65.15 (17.47)	1.52 (1.52)

and compute true probability distributions of most-likely solutions. For all model runs, parameters included $\delta^{13}C$ and $\delta^{15}N$ values of blood plasma and the 7 food sources, trophic enrichment factors from Caut et al. (2009) for $\delta^{13}C$ and $\delta^{15}N$ (–0.08‰ and 2.82‰, respectively), and measured C and N concentrations of each food source (this study). An initial model including all 150 Wood Thrushes as one group with vague priors, and a subsequent model with informative priors derived using the siarelicit function in siar, were used to estimate overall contributions to diet. The same procedure was followed for Wood Thrushes broken into 4 groups (adult females, adult males, and nestlings in nests without and with Brown-headed Cowbird parasitism) to asses differences in diets among groups. Sensitivity analyses were conducted by varying trophic enrichment factor values of C from 0 to 2‰, and values of N from 0 to 3‰. All mean relative contributions to diet differed by a maximum of 4.7% for all food sources.

To compare diet patterns among groups, we first randomly sampled 100 iterations from posterior distributions from each Wood Thrush group. We then aggregated food sources a posteriori (i.e. after model runs with all 7 food sources) into Ca-rich prey (i.e. snails, isopods, and myriapods) and insects (i.e. insects and caterpillars) by summing estimated relative proportions of each food source within each iteration of the posterior distributions (Phillips et al. 2014). Due to the compositional nature of these data (i.e. proportions constrained to the summation to 1), posterior distributions were transformed to centered Logratios (Aitchison et al. 2000) with the "compositions" R package (van den Boogaart et al. 2013) before using a nested analysis of variance (ANOVA) design to test for differences among Wood Thrush groups nested within the following food source categories: Ca-rich foods, spiders, earthworms, and insects (i.e. insects and caterpillars combined).

Software R v3.1.2 (R Development Core Team 2014) was used for all statistical tests. All data were assessed for departures from normality using Shapiro-Wilk tests, examination of quantile-quantile plots, and visual evaluation of homoscedasticity. In all instances where assumptions of normality were violated, nonparametric tests were used (Zar 2010).

RESULTS

Food Resource Availability

We sampled 12,419 invertebrates and identified specimens to family that comprised earthworms in soil ($n = 484$), invertebrates in leaf litter ($n = 11{,}395$), and arthropods in understory vegetation ($n = 540$; see Appendix Table 2). We used nonparametric Kruskal-Wallis rank sum tests (Siegel and Castellan 1988) in the "pgirmess" R package (Giraudoux 2014) and found differences in invertebrate density among food source groups in leaf litter ($\chi^2 = 402.3$, $df = 5$, $P < 0.001$) and in understory vegetation ($\chi^2 = 33.03$, $df = 9$, $P < 0.001$; Table 3). For leaf litter, insect density (5.39 ± 0.60 individuals L^{-1}) was greater than all other invertebrate groups, and insect density ($\chi^2 = 19.22$, $df = 9$, $P < 0.05$), snail density ($\chi^2 = 75.84$, $df = 9$, $P < 0.001$), and myriapod density differed among sites ($\chi^2 = 33.22$, $df = 9$, $P < 0.001$; Table 3). In understory vegetation, densities of both caterpillars (0.36 ± 0.06 individuals g^{-1}) and insects (0.23 ± 0.03 individuals g^{-1}) were greater than spiders (0.08 ± 0.02 individuals g^{-1}), and only insect density (individuals g^{-1} leaves) differed among sites ($\chi^2 = 28.98$, $df = 9$, $P < 0.001$; Table 3).

Stable Isotopic Composition of Carbon and Nitrogen

Analysis of food sources. We sampled 215 invertebrates comprising 25 families and 7 classes from leaf litter,

TABLE 3. Extended.

Sites						
IH1	IH2	MP	RE	RH	WC1	WC2
mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)
0.11 (0.04)	0.05 (0.02)	0.03 (0.02)	0.05 (0.02)	0.09 (0.07)	0.19 (0.16)	0.10 (0.05)
0.44 (0.22)	0.09 (0.03)	0.24 (0.14)	0.35 (0.13)	0.03 (0.02)	0.07 (0.03)	0.13 (0.07)
0.21^{ab} (0.09)	0.10^{ab} (0.03)	0.10^{ab} (0.05)	0.33^{ab} (0.11)	0.47^{ab} (0.16)	0.53^{a} (0.12)	0.25^{ab} (0.08)
5.18^{ab} (2.0)	6.81^{ab} (1.58)	8.72^{ab} (4.56)	6.24^{ab} (1.30)	1.81^{b} (0.50)	3.92^{ab} (0.71)	5.94^{ab} (1.57)
0.15 (0.05)	0.09 (0.04)	0.80 (0.24)	0.54 (0.19)	1.01 (0.33)	0.49 (0.20)	0.53 (0.31)
2.25^{ab} (0.59)	0.19^{c} (0.06)	0.15^{c} (0.08)	1.07^{abc} (0.35)	0.42^{bc} (0.13)	1.31^{abc} (0.33)	4.38^{a} (0.71)
0.47^{ab} (0.20)	0.17^{b} (0.08)	0.16^{b} (0.09)	1.26^{ab} (0.49)	0.36^{b} (0.16)	0.62^{ab} (0.28)	6.74^{a} (2.90)
0.19 (0.18)	0.10 (0.03)	0.26 (0.12)	0.22 (0.09)	0.14 (0.04)	0.09 (0.04)	0.94 (0.62)
13.64 (9.46)	74.24 (24.38)	206.06 (123.6)	15.15 (12.95)	145.45 (91.06)	25.76 (6.60)	148.48 (49.12)

understory vegetation, and soil samples for stable isotope analysis (Table 4). Overall, mean food source $\delta^{13}C$ and $\delta^{15}N$ values were –25.5 ± 0.21‰ and 0.38 ± 0.18‰, respectively. We found $\delta^{13}C$ differed among food sources ($F = 63.8$, df = 6, $P < 0.001$), and was greatest in snails (–22.2 ± 0.47‰), followed by isopods (–23.7 ± 0.20‰) and myriapods (–24.0 ± 0.23‰), earthworms (–25.5 ± 0.17‰), spiders (–25.9 ± 0.16‰), insects (–27.2 ± 0.29‰), and caterpillars (–30.4 ± 0.28‰; Figure 2). We found $\delta^{15}N$ differed among food sources ($F = 24.96$, df = 6, $P < 0.001$), and was greatest in spiders (2.84 ± 0.29‰), followed by snails (1.40 ± 0.35‰), isopods (0.65 ± 0.28‰), earthworms (0.63 ± 0.49‰), insects (–0.04 ± 0.39‰), myriapods (–1.51 ± 0.54‰), and caterpillars (–2.37 ± 0.18‰; Figure 2).

Analysis of blood plasma. We used data from 117 captured and sampled Wood Thrushes: 37 adult females,

TABLE 4. Invertebrates (total individuals) sampled from 1 May to 15 August 2011–2013 from sites in and near Newark, DE, USA, for stable isotope analysis. Numbers of invertebrates are shown (*n*) and are grouped by food source, class, order, and family.

Food source	Class	Order	Family	*n*
Insects (18)	Insecta	Coleoptera	Staphylinidae	1
			Carabidae	1
			Curculionidae	1
		Hymenoptera	Formicidae	6
		Hemiptera	Flatidae	1
			Pentatomidae	1
			Reduviidae	1
		Orthoptera	Gryllidae	2
			Tettigoniidae	1
		Diptera	Muscidae	3
Snails (35)	Gastropoda		Polygyridae	2
			Zonitidae	33
Caterpillars (35)	Insecta	Lepidoptera	Arctiidae	2
			Notodontidae	3
			Papillionidae	5
			Pieridae	3
			Geometridae	22
Isopods (38)	Malacostraca	Isopoda	Oniscidae	37
			Armadillidiidae	1
Myriapods (20)	Chilopoda		Julidae	2
		Geophilomorpha		2
			Parajulidae	13
			Xystodesmidae	3
Spiders (35)	Arachnida	Aranae		31
		Opiliones		4
Earthworms (34)	Clitelatta	Haplotaxida	Lumbricidae	27
	Oligochaeta	Megadrilacea	Megascolecidae	7

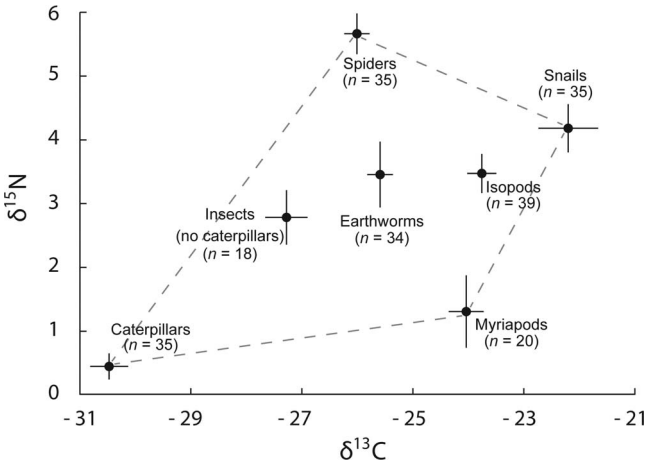

FIGURE 2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (mean ± SE) for 7 Wood Thrush food sources (labeled) sampled from 1 May to 31 August 2011–2013 in and near Newark, DE, USA.

36 adult males, and 44 nestlings (33 without and 11 with Brown-headed Cowbirds). Wood Thrush nestlings were sampled from 20 nests, of which 30% were parasitized. Wood Thrush nestling clutch sizes ranged between 1 and 4 with a mean of 3.0 ± 0.86 (SD). To control for potential bias due to variation in parasite:host nestling ratios, we included only nests with one Brown-headed Cowbird nestling in our analyses, resulting in Brown-headed Cowbird nestling to Wood Thrush nestling ratios that ranged from 0 to 0.5. Overall, mean Wood Thrush blood plasma $\delta^{13}C$ and $\delta^{15}N$ values were –24.8 ± 0.09‰ and 4.42 ± 0.14‰, respectively. We used ANOVA in the "stats" R package (R Core Development Team 2014) and found a difference among years in plasma $\delta^{15}N$ ($F = 7.5$, df $= 2$, $P < 0.001$), but not for plasma $\delta^{13}C$ ($F = 2.0$, df $= 2$, $P = 0.15$; Figure 3A). Tukey's post hoc tests revealed that mean plasma $\delta^{15}N$ was greater in 2012 (5.00 ± 0.23‰) than in 2013 (4.16 ± 0.22‰, $P < 0.01$) and 2011 (3.97 ± 0.23‰, $P < 0.01$; Figure 3A). We found no differences among sites for plasma $\delta^{13}C$ ($F = 0.87$, df $= 9$, $P = 0.55$) or plasma $\delta^{15}N$ ($F = 1.78$, df $= 9$, $P = 0.08$). We found that plasma $\delta^{13}C$ differed between breeding season periods coarsely defined as "early" (1 May–30 June) and "late" (1 July–31 August; $F = 8.26$, df $= 1$, $P < 0.01$), but found no such differences for $\delta^{15}N$ ($F = 0.02$, df $= 1$, $P = 0.89$; Figure 3B). Mean plasma $\delta^{13}C$ was greater earlier (–24.5 ± 0.08‰) than later (–25.2 ± 0.15‰) in the breeding season (Figure 3B). Wood Thrush blood plasma differed among the 4 groups for $\delta^{13}C$ ($F = 27.6$, df $= 3$, $P < 0.001$) and for $\delta^{15}N$ ($F = 50.5$, df $= 3$, $P < 0.001$). Tukey's post hoc tests

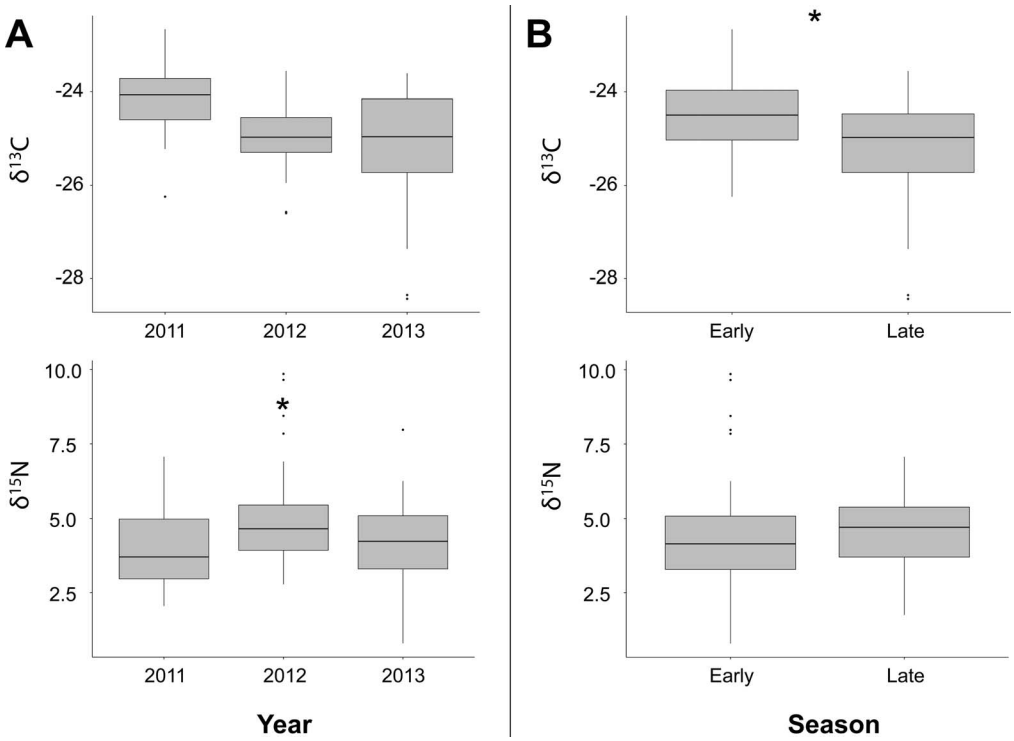

FIGURE 3. Boxplots comparing carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for blood plasma (**A**) among years, and (**B**) between early and late season for all Wood Thrushes sampled from 1 May to 31 August 2011–2013 in and near Newark, DE, USA. Asterisks indicate significant differences ($P < 0.05$). Gray boxes, whiskers, and dots indicate inter-quartile ranges, 95% CIs, and outliers, respectively.

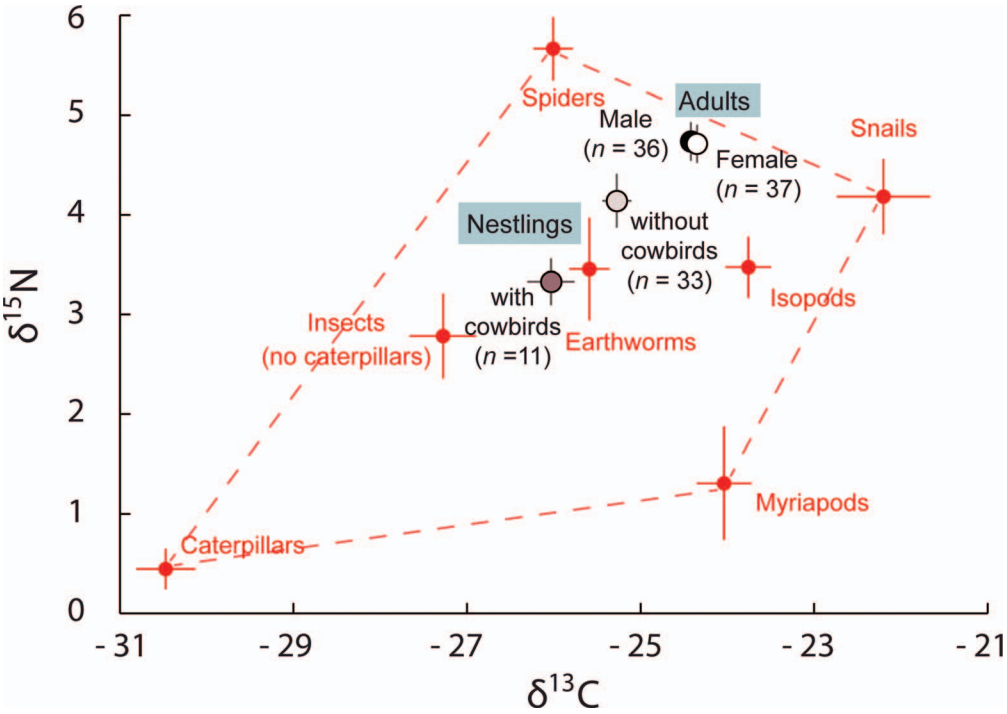

FIGURE 4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (mean ± SE) for blood plasma from adult males (black) and females (white), and nestlings without Brown-headed Cowbirds (light gray) and with Brown-headed Cowbirds (dark gray) from Wood Thrushes sampled from 1 May to 31 August 2011–2013 in and near Newark, DE, USA.

showed that plasma $\delta^{13}C$ for adult males (–24.4 ± 0.11‰) and females (–24.4 ± 0.12‰) was similar ($P = 0.99$), and both were greater than nestlings with ($P < 0.01$) and without ($P < 0.001$) Brown-headed Cowbirds (Figure 4). Wood Thrush nestlings without Brown-headed Cowbirds (–25.3 ± 0.17‰) had greater plasma $\delta^{13}C$ than nestlings with Brown-headed Cowbirds (–26.0 ± 0.28‰, $P < 0.05$; Figure 4). Post hoc tests also showed that Wood Thrush plasma $\delta^{15}N$ values for adult males and females (4.70 ± 0.23‰ and 4.72 ± 0.25‰, respectively) were greater than nestlings with (4.14 ± 0.27‰, $P < 0.05$) and without (3.34 ± 0.27‰, $P < 0.001$) Brown-headed Cowbirds (Figure 4). However, Tukey's post hoc test showed that plasma $\delta^{15}N$ for Wood Thrush nestlings with and without Brown-headed Cowbirds was similar ($P = 0.21$; Figure 4).

Comparison of Wood Thrush diets among groups. Wood Thrushes ate differing relative proportions among food sources; here we report ranges as upper and lower bounds of 95% highest density intervals (HDI). Bayesian mixing model estimates of relative proportions of food sources to diet (95% HDI) consisted of snails (0.22–0.36), spiders (0.25–0.35), isopods (0.11–0.25), earthworms (0.04–0.15), myriapods (0.03–0.13), insects (0.01–0.07), and caterpillars (0.0003–0.03; Figure 5).

We used a nested ANOVA approach on centered Logratio transformed data (Aitchison et al. 2000) in the stats R package (R Core Development Team 2014), and found that Wood Thrush groups nested within a posteriori aggregated food sources differed ($F = 521$, df = 12, $P < 0.001$). We subsequently used Tukey's post-hoc tests ($P < 0.05$) to determine group differences (95% HDI), and found that Wood Thrush nestlings in nests without Brown-headed Cowbirds ate more Ca-rich foods (0.36–0.55) and spiders (0.16–0.35) compared to nestlings in nests with Brown-headed Cowbirds (0.28–0.50, 0.15–0.31, respectively; Table 5). Nestlings in nests without Brown-headed Cowbirds ate fewer insects (0.07–0.21) than nestlings in nests with Brown-headed Cowbirds (0.15–0.32; Table 5). Adult male and female Wood Thrushes ate similar amounts of all food sources (Table 5).

Food availability and resource use. We compared relative diet contributions of 7 food sources and normalized means of overall food source availability data by multiplying both by the total number of birds sampled and independently testing each Wood Thrush group using Fisher's exact test of independence (Fisher 1935) on a 2×7 matrix (Patefield 1981). We subsequently computed Bonferroni's z statistics and confidence intervals to determine significance and effect sizes for how each food source was used by each Wood Thrush group (e.g., significantly less than or greater than expected) in relation to its availability (Neu et al. 1974). We found that food resource use of all Wood Thrushes combined was independent of available food resources (Fisher's exact

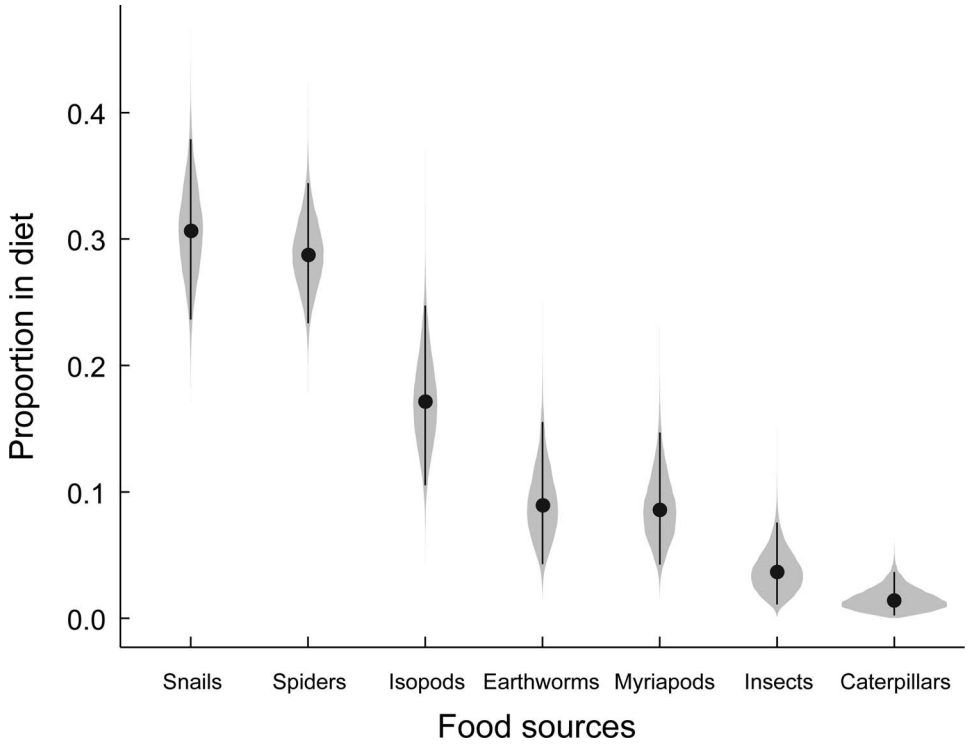

FIGURE 5. Violin plots of posterior distributions showing overall relative contributions of 7 invertebrate food sources to Wood Thrush diets from birds sampled from 1 May to 31 August 2011–2013 in Newark, DE, USA. Dark black circles and lines indicate medians and 95% highest density intervals (HDI) of posterior distributions, respectively.

TABLE 5. Descriptive statistics of Wood Thrush relative contributions of food sources to diet for adult females and males, and nestlings from nests with and without Brown-headed Cowbird parasitism based on estimated posterior distributions from Bayesian mixing models. For each Wood Thrush group within each of 4 food sources we show relative contributions to diet 95% highest density intervals (HDI), geometric mean (SD), and centered Logratio mean (SD) values. Tukey's HSD post-hoc test results are indicated by superscript uppercase letters on Logratio means.

	Adult		Nestling	
Food source	Female	Male	Without Brown-headed Cowbirds	With Brown-headed Cowbirds
Ca-rich				
95% HDI	0.58–0.69	0.58–0.68	0.36–0.55	0.30–0.51
Geometric mean (SD)	0.64 (0.03)	0.63 (0.03)	0.45 (0.05)	0.41 (0.06)
Centered Logratio mean (SD)	1.62 (0.13)^{A}	1.61 (0.14)^{A}	0.74 (0.14)^{B}	0.57 (0.19)^{C}
Spiders				
95% HDI	0.22–0.33	0.22–0.34	0.16–0.34	0.12–0.28
Geometric mean (SD)	0.28 (0.03)	0.28 (0.03)	0.25 (0.05)	0.20 (0.04)
Centered Logratio mean (SD)	0.78 (0.16)^{B}	0.80 (0.18)^{B}	0.12 (0.20)^{D}	−0.14 (0.21)^{E}
Earthworms				
95% HDI	0.02–0.09	0.02–0.09	0.06–0.25	0.06–0.24
Geometric mean (SD)	0.05 (0.02)	0.05 (0.02)	0.15 (0.05)	0.15 (0.05)
Centered Logratio mean (SD)	−0.90 (0.32)^{G}	−0.86 (0.31)^{G}	−0.40 (0.30)^{F}	−0.48 (0.28)^{F}
Insects				
95% HDI	0.01–0.05	0.01–0.06	0.07–0.21	0.15–0.33
Geometric mean (SD)	0.03 (0.01)	0.03 (0.01)	0.14 (0.04)	0.24 (0.05)
Centered Logratio mean (SD)	−1.49 (0.31)^{H}	−1.54 (0.32)^{H}	−0.45 (0.22)^{F}	0.04 (0.19)^{DE}

*Superscript letters A–H indicate significant differences ($P < 0.01$) among centered Logratio transformed means of relative contributions of food sources to Wood Thrush diets.

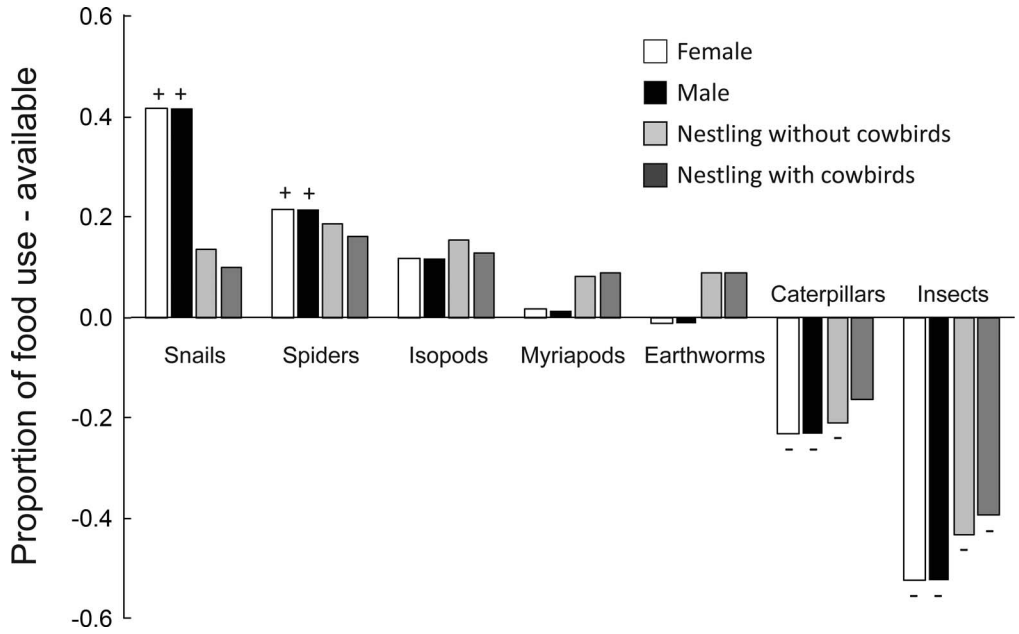

FIGURE 6. Proportion of food resources used by adult females (white), males (black), nestlings without Brown-headed Cowbirds (light gray), and nestlings with Brown-headed Cowbirds (dark gray) minus proportion of available food resources. Signs above or below bars represent Bonferroni *z* statistic test results indicating that Wood Thrushes ate food sources more (+) or less (–) frequently than expected based on availability of food resources. Bars with no signs indicate food use at expected frequencies based on food availability.

test; $P < 0.001$). Multiple pairwise comparisons with Bonferroni corrected *P*-values indicated that observed food source use compared to expected was significantly greater for spiders, earthworms, isopods, myriapods, and snails compared to insects and caterpillars ($P < 0.01$, all cases; Figure 6). Fisher's exact test results showed that food resource use by adult males ($P < 0.001$) and females ($P < 0.001$) was independent of food source availability, and subsequent pairwise tests showed that spiders, isopods, and snails were used significantly more than insects ($P < 0.01$, all cases) and caterpillars ($P < 0.05$, all cases; Figure 6). Wood Thrush nestlings without Brown-headed Cowbirds ate food sources independent of availability (Fisher's exact test; $P < 0.001$), and pairwise tests indicated that spiders, isopods, and snails were used significantly more than insects ($P < 0.05$, all cases; Figure 6). We found that Wood Thrush nestlings with Brown-headed Cowbirds consumed food sources independent of food availability ($P < 0.05$), but no pairwise differences were found. All Wood Thrushes combined ate 7 times the snails, 4 times the spiders, and 17 times the isopods than were available with a greater frequency than was expected, and ate 1/14 the available insects and 1/17 the available caterpillars at less than expected frequencies (Figure 6). Nestlings without Brown-headed Cowbirds ate snails, spiders, and isopods at expected frequencies and ate 1/5 the available insects and 1/8 the available caterpillars less frequently than expected (Figure 6). Nestlings with Brown-headed Cowbirds ate snails, spiders, isopods, and caterpillars at expected frequencies and ate 1/3 the available insects at less than expected frequency (Figure 6). Both adult female and male Wood Thrushes ate 12 times the available snails and 4 times the available spiders more frequently than expected and ate 1/20 the available caterpillars and insects at less than expected frequency (Figure 6). All Wood Thrush groups ate earthworms and myriapods at expected frequencies (Figure 6).

DISCUSSION

Here we show that Wood Thrush nestlings in nests with Brown-headed Cowbirds were fed a lower proportion of snails, isopods, and spiders compared to Wood Thrush nestlings in the absence of Brown-headed Cowbirds. These results support our predictions that Brown-headed Cowbird nestlings may outcompete host nestlings for high-quality food provisioned by host parents. Snails, isopods, and myriapods are all rich in Ca (Steel 1993, Hotopp 2002) and spiders are high in protein (Ramsay and Houston 2003) and taurine, an amino acid that may enhance brain development (Arnold et al. 2007); all are high-quality foods for nestlings that help fulfill specific nutritional requirements for optimal growth and development (Weathers 1996, Gebhardt-Heinrich and Richner 1998, Klasing 1998). Based on daily food requirements for a 25-g nestling (Nagy et al. 1999), we used our determined diets (i.e. means and 95% confidence

intervals [Cis]) and mean Ca content (mg) for food sources (this study) and estimated that the daily Ca intake (mg day^{-1}) for Wood Thrush nestlings parasitized by Brown-headed Cowbirds would be reduced by 9–18% day^{-1} compared to Wood Thrush nestlings in nests without Brown-headed Cowbirds. For nestlings in parasitized nests, this corresponds to a reduction in percent dietary Ca from 8% down to 2%. Reductions of both Ca- and protein-rich food sources in diets of nestlings with Brown-headed Cowbirds suggest that Brown-headed Cowbirds may be outcompeting host nestlings for nutrient-rich food sources, which may have negative effects on nestling development and subsequent adult fitness.

Wood Thrushes ate and assimilated more snails and spiders and fewer insects compared to previous studies (Weaver 1949, Cooper 1975, Holmes and Robinson 1988). Weaver (1949) examined stomach contents and found 11% contained caterpillars, 8% spiders, 6% insects, and 38% was of plant origins. Holmes and Robinson (1988) examined regurgitated food from Wood Thrushes and found 68% insects, 12% caterpillars, and 10% myriapods and snails combined. Cooper (1975), using ligatures, found that Wood Thrush nestling diets were composed of 60% insects, 16% caterpillars, 8% myriapods, 7% spiders, 6% earthworms, 2% isopods, and no snails. In contrast to all other Wood Thrush diet analyses published to date, we estimated greater percentages of spiders, snails, and isopods in the diet. Differences among studies of Wood Thrush diets are certainly due to different methodologies used. Traditional methods for determining diets (e.g., analysis of stomach contents and fecal samples) tend to be biased because food sources have differing detection probabilities due to factors like fragility, size, and digestibility (Votier et al. 2003). For example, although we estimated high levels of snails in the diet (~30%) using stable isotopes, only 3% of all fecal samples contained identifiable snails. Differing diet patterns could also be affected by the extent of the sampling area and variation in available food at a given time. Weaver (1949) sampled Wood Thrushes from a broad geographic range within the U.S. and southern Canada, Holmes and Robinson (1988) sampled Wood Thrushes from Hubbard Brook experimental forest (New Hampshire), and Cooper (1975) sampled diets of nestling Wood Thrushes at the University of Delaware Ecology Woods.

Reduced available Ca for breeding birds has been used to explain population declines (Graveland 1990, Reynolds and Perrins 2010), especially in northeastern North America where high levels of acid deposition has occurred over the past several decades (Hames et al. 2002, Menz and Seip 2004). Reductions in Ca availability in soils and Ca-rich prey (e.g., snails, isopods, and myriapods) can limit both egg production and nestling development, thereby limiting populations (Graveland and Drent 1997, Reynolds 2001, Pabian and Brittingham 2011). Specifically, Ca availability can limit nestling skeletal mineralization rates (Klasing 1998) and nestling growth rates (Poulin and Brigham 2001, Dawson and Bidwell 2005).

Calcium also plays a critical role in brain development through Ca-mediated signaling (Rosenberg and Spitzer 2011), and the detrimental effects of nutritional stress during development have been widely demonstrated (Eeva et al. 2003, Long et al. 2009, Lanet and Maurange 2014). Ecological changes that affect food or nutrient availability can cause nutritional stress in free-living birds (Davis et al. 2005, Kitaysky et al. 2006, Herring et al. 2011), and experimental tests have demonstrated how nestling nutritional stress negatively affects growth, brain development, and song learning in captive birds (Nowicki et al. 2002, Spencer et al. 2004, MacDonald et al. 2006). In light of evidence supporting the nutritional stress hypothesis and recent development of experiments to test it, it logically follows that future studies should seek to link developmental nutrition to other life history attributes such as survival, lifespan, and fitness. Boonekamp et al. (2014) found that telomere loss due to experimentally manipulated developmental stress in free-living nestling Jackdaws (*Corvus monedula*) reduced post-fledgling survival and recruitment. We propose that this framework would be ideally suited for studying how ecological interactions resulting from environmental and landscape change (e.g., brood parasitism) can lead to nutritional stress, that can in turn negatively affect survival, fecundity, and potentially limit population growth.

The causes of the observed range-wide declines in Wood Thrush populations remain unclear (Faaborg 2014). Several studies have suggested that these population declines may be due to multiple interacting factors including fragmentation and human development (Phillips et al. 2005, Tittler et al. 2006), food limitation (Martin 1995), acid rain-induced Ca limitation (Hames et al. 2002), and cowbird parasitism (Brittingham and Temple 1983, Trine 1998, Etterson et al. 2014). Our results demonstrate how brood parasitism can affect host nestling diets, effectively reduce Ca- and protein-intake, and potentially lead to suboptimal diets and nutritional stress for Wood Thrush nestlings. Additionally, Wood Thrushes breeding in small urban forest fragments preferred snails, spiders, and isopods, in contrast to what was available. This information further supports the importance of Ca- and protein-rich food sources for breeding Wood Thrushes to accommodate nutritional requirements for egg production and nestling provisioning. Our mixing models account for invertebrate food sources, but we are aware that other foods contribute to the diet, such as seeds, fruits, and small vertebrates (Cooper 1975, Holmes and Robinson 1988, this study). However, given Ca and protein limitations for breeding adults and developing nestlings (Weathers 1996,

Klasing 1998), we believe that these data represent critical aspects of Wood Thrush diets.

Future studies should directly estimate cowbird nestling diets along with host nestlings using stable isotopes to further test the hypothesis that differences in observed diets are due to cowbirds outcompeting host nestlings for Ca- and protein-rich food items. Linking data of assimilated diets with parental provisioning rates, nestling hatch order, growth rates, and begging behavior would also provide novel insight into brood parasite-host interactions. Investigating further details of cowbird nestling development following studies like Hargitai et al. (2012) could also help our understanding of host–parasite nestling interactions in relation to food and nutrient allocation. More studies on effects of brood parasitism on nestling diet could also measure passively deposited corticosterone in nestling feathers to quantify the degree of nutritional stress due to brood parasitism on host nestlings. In this way, potential carry-over effects of parasitism into subsequent years should be investigated for both host adults (Mark and Rubenstein 2013) and nestlings. Additionally, deliberate examination of how ecological interactions among Ca and food availability and parasitism rates affect diets of host nestlings, perhaps through simultaneous manipulation of brood parasite populations and methods described in this study, would be beneficial.

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APPENDIX

APPENDIX TABLE 2. Invertebrate groups (total individuals), class, and family collected in soil, leaf litter, understory vegetation, from 10 forest sites where nesting Wood Thrush occurred from May to September 2010–2013 in and near Newark, DE, USA.

Invertebrate group	Class	Family	Soil	Leaf Litter	Understory
Earthworms (484)	Clitelatta	Lumbricidae	219	—	—
	Oligochaeta	Megascolecidae	265	—	—
Snails (661)	Gastropoda	Discidae	—	1	—
		Gastrodontidae	—	398	—
		Haplotrematidae	—	24	—
		Helicodiscidae	—	70	—
		Polygyridae	—	11	—
		Pristilomatidae	—	10	—
		Strobilopsidae	—	14	—
		Subulinidae	—	1	—
		Succineidae	—	16	—
		Vertiginidae	—	3	—
		Zonitidae	—	113	—
Spiders (1853)	Arachnida	Araneae	—	126	108
		Chernetidae	—	308	—
		Ixodidae	—	1,277	—
		Opiliones	—	4	—
		Trogulidae	—	—	30
Isopods (158)	Crustacea	Isopoda	—	157	1
Insects (8688)	Insecta	Acerentomidae	—	8	—
		Anobiidae	—	0	1
		Anthribidae	—	1	—
		Aphelinidae	—	1	—
		Aphididae	—	9	46
		Apidae	—	1	—
		Aradidae	—	1	—
		Bibionidae	—	35	—
		Blattellidae	—	13	—
		Blattidae	—	1	—
		Braconidae	—	6	1
		Brentidae	—	3	—
		Caeciliusidae	—	1	—

APPENDIX Continued.

Invertebrate group	Class	Family	Soil	Leaf Litter	Understory
		Campodeidae	—	9	—
		Cantharidae	—	11	9
		Carabidae	—	27	2
		Cecidomyiidae	—	32	—
		Ceraphronidae	—	3	—
		Chironomidae	—	2	—
		Chrysomelidae	—	7	4
		Cicadellidae	—	1	41
		Cleridae	—	1	—
		Coreidae	—	1	1
		Cryptophagidae	—	1	—
		Curculionidae	—	52	23
		Cydnidae	—	3	—
		Diapriidae	—	22	—
		Elateridae	—	16	9
		Empididae	—	11	1
		Encyrtidae	—	1	—
		Entomobryidae	—	838	—
		Epipsocidae	—	26	—
		Eulophidae	—	1	—
		Eurytomidae	—	1	—
		Flatidae	—	0	129
		Formicidae	—	1,064	29
		Gryllidae	—	8	65
		Heleomyzidae	—	4	—
		Histeridae	—	1	—
		Hypogastruridae	—	111	—
		Ichneumonidae	—	5	—
		Isotomidae	—	2,035	—
		Lampyridae	—	4	5
		Lathridiidae	—	2	—
		Lycidae	—	1	—
		Lygaeidae	—	52	1
		Megaspilidae	—	1	—
		Melandryidae	—	2	—
		Meloidae	—	2	1
		Melyridae	—	1	—
		Miridae	—	3	3
		Mordellidae	—	0	3
		Mutillidae	—	1	—
		Mycetophilidae	—	2	1
		Mymaridae	—	1	—
		Nitidulidae	—	42	1
		Noteridae	—	1	—
		Oestridae	—	2	—
		Onychiuridae	—	1,065	—
		Pentatomidae	—	7	5
		Phlaeothripidae	—	118	—
		Phoridae	—	15	1
		Platygastridae	—	10	—
		Pselaphidae	—	12	—
		Psychodidae	—	3	—
		Pteromalidae	—	2	—
		Pteromalidae	—	2	—
		Ptiliidae	—	1	—
		Ptilodactylidae	—	4	—
		Reduviidae	—	0	12
		Rhinotermitidae	—	15	—
		Rhyparochromidae	—	1	—
		Scarabaeidae	—	15	—

APPENDIX Continued.

Invertebrate group	Class	Family	Soil	Leaf Litter	Understory
		Scelionidae	—	1	—
		Sciaridae	—	56	3
		Scirtidae	—	4	—
		Scydmaenidae	—	2	—
		Sminthuridae	—	582	—
		Staphylinidae	—	152	—
		Stratiomyiidae	—	3	—
		Tachinidae	—	1	—
		Tenebrionidae	—	49	1
		Therevidae	—	1	—
		Thripidae	—	157	—
		Tipulidae	—	1	—
		Tomoceridae	—	1,520	—
Caterpillars (52)	Lepidoptera		—	40	—
		Crambidae	—	1	—
		Gelechiidae	—	1	—
		Geometridae	—	2	3
		Noctuidae	—	2	—
		Oecophoridae	—	1	—
		Pyralidae	—	2	—
Millepedes and Centipedies (523)	Myriapoda	Geophilomorpha	—	30	—
		Julidae	—	39	—
		Lithobiomorpha	—	21	—
		Parajulidae	—	338	—
		Polydesmidae	—	1	—
		Symphyla	—	8	—
		Xystodesmidae	—	86	—
All invertebreates (12,419)			484	11,395	540