WOOD THRUSH DIET, GENETICS, AND POPULATION ECOLOGY

by

Zachary S. Ladin

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology

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Zachary S. Ladin

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EPIGRAPH

To a bird,
A bird beholden
to aeons of ancient forests,
and traditions tirelessly passed on
from mother to nestling,
from sire to son.

To a bird,
A bird unassuming
and unbeknown
that dire times
are arrived.

To a bird,
A bird singing perfect multiphony,
suchness manifests.

Here, I humbly offer a morsel emerging
on pages, numbers and words.
So that we may continue to count your multitudes,
and hear forests rejoice
at the return of once hatchlings
now themselves,
passing eternal secrets on
from mother to nestling,
from sire to son.

A lad in the woods

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I want to share my gratitude for the many people, and serendipitous events that have collectively contributed to the achievement of this goal, a major milestone in my life and career. Thank you from the depths of my being. First, I acknowledge the unconditional love and support of my parents and their parents, who have not only encouraged me to dream big from the beginning, but who have personally inspired me to pursue greatness, and at all costs, to follow my heart. To Maeve and Bill Foley, who fostered a young boy's disproportionate obsession with birds at an early age, and started me on this avian-inspired journey. I fondly thank my first mentor, friend, and birder-extraordinaire, Bill McEneaney, for showing me the limitless sky, and the feathered wonders that gather there. I humbly thank Dr. Scott McWilliams, who has been an exemplary role model, mentor, and friend throughout my academic journey. I thank Dr. Larry Englander for helping feed my imagination and passion. I am indebted to all the faculty and students here within the department who have helped nurture my curiosity, and who have given me the tools and the gumption to approach the important challenges that the world today faces. I acknowledge Dr. Roland Roth, and his valuable contributions to the study of wood thrushes, and am honored to have helped continue this important long-term research. I am grateful for the involvement of Dr. Jan Baetens and his expertise in ecological modeling. I offer special thanks to

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ABSTRACT

Rapid anthropogenic environmental and landscape change broadly influences

ecosystems, communities, and populations. This research is focused on the response

of the wood thrush (*Hylocichla mustelina*), a forest-breeding songbird, to effects of

urbanization, habitat loss, and fragmentation. I tested hypotheses dealing with food

resource use, genetic structure, and metapopulation dynamics associated with

potentially limiting factors for breeding wood thrushes that have been suggested to be

contributing to observed range-wide population declines over the past 50 years. These

findings can improve our understanding of how limiting factors may be related to

wood thrush population declines within urbanized and fragmented landscapes. This

work is unique in that it builds upon an ongoing long-term study of wood thrushes in

and near Newark, Delaware, USA, and provides new insight into their breeding

ecology. Using stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes, I demonstrated that

wood thrush diets contained higher proportions of calcium-rich snails than was

previously described. I also found that avian brood parasitism by the brown-headed

cowbird (*Molothrus ater*) is related to nestling diet, which may lead to negative effects

on nestling development. I used five microsatellite markers to explore the effect of

forest fragmentation on fine-scale genetic structure of wood thrushes. Despite

relatively low levels of genetic differentiation among sites, I found patterns of genetic

flow that were not well explained by inter-site distances (m). Like many songbird

species, wood thrushes are socially monogamous, however paternity analysis of wood

thrush nestlings revealed that 29 % of offspring were the result of extra-pair mating events. These findings suggest that wood thrush are potentially engaging in inter-site forays during the breeding season, or may be shifting breeding locations annually. Wood thrushes with nests closer to non-forested edges, male wood thrushes with longer wing chord (mm), and males with lower body mass (g) had a higher probability of having offspring through extra-pair matings. Finally, I modeled the metapopulation dynamics of wood thrushes within the study area by integrating several empirically-based approaches to test wood thrush population responses to conservation actions. I found that the probability of wood thrush site occupancy, survival, fecundity, and recruitment could be increased over the next 30 years by reducing the proportion of impervious surface within 500 m buffers around forest sites, and by removing brown-headed cowbirds from wood thrush breeding areas. However, only when these two conservation strategies were applied simultaneously, did simulated wood thrush populations attain positive annual growth rates. In summary, my findings suggest that cowbird parasitism is related to wood thrush nestling diet, and in general, wood thrushes do not appear to be calcium limited. Wood thrushes in and near Newark, Delaware are not experiencing loss of genetic diversity due to habitat fragmentation, and could benefit from reductions of impervious surface on the landscape and brown-headed cowbird parasitism rates. Collectively, my findings provide important new information that can help guide conservation strategies for wood thrushes breeding in

the mid-Atlantic United States, a region where observed rates of breeding population declines are at their greatest.

Chapter 1

IS BROOD PARASITISM RELATED TO HOST NESTLING DIET AND NUTRITION?

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. I 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. The effects of brood parasitism on host nestling diets are an understudied stressor that may help explain observed population declines. I measured carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes of seven 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 or without cowbird nestlings. Wood thrush diet compositions were largely comprised 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 cowbirds contained greater proportions of Ca-rich foods and spiders compared to the diet of nestlings in parasitized nests. These 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. These 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.

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 can 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).

Over 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, Leimgruber and Renner 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 (Sillett 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, Dugger and Starkey 2007), but the mechanisms leading to reduced fecundity remain unclear.

Avian brood parasites, such as the brown-headed cowbird (*Molothrus ater*) (Boddaert, 1783) (hereafter cowbird), 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 life-

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time 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 are 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). I 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 been 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. Herein, I 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 cowbird nestlings, while accounting for variation in site differences related to patterns in food availability and brood parasitism occurrence within small urban forest fragments. I predicted that diets of wood thrush nestlings would differ in relation to presence or absence of cowbird parasitism, and specifically, that wood thrush nestlings in nests with 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 that 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 and near Newark, Delaware, USA (39°41'1N 75°44'58W) (Fig. 1.1). Each site was located along an edge adjacent to non-forest land cover to control for site-level edge effects. Sites ranged in size from 2.1 ha to 16.3 ha, and included Ecology Woods (Bray et al. 1965) where an ongoing 40-year demographic study on breeding wood thrushes occurs (Fig. 1.1, Table 1.1). Sites were gridded with 50 m × 50 m cells using alpha-numerically marked locations (hereafter points). I 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*).

Food resource availability sampling

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

Soil sampling

I sampled earthworms using electroshocking methods at 63 points consisting of 3 randomly chosen points within each of 21 sites from 26 June – 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 through placement of 8 electrodes (i.e., 30.5 cm, stainless steel spikes) in an octagonal arrangement, which were placed 20 cm deep into the soil (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. I measured voltage within the sampling area using a digital voltmeter (Commercial Electronic, model MAS830B, China). I rotated the electrical field within the sampling area following Thielemann (1986). I electrified the spikes in the following eight sequences: AB, ABC, BC, BCD, CD, ACD, AD, and ABD. The duration of each sequence ranged from 1 to 2.5 minutes depending on earthworm emergent activity. For example, when earthworm activity was high, sequence durations were longer. I waited a minimum of a 0.5 min with no electrodes on in between sequences allowing partially surfaced earthworms to move out of the soil and to collect earthworms that had already surfaced.

I 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 – 5 September 2011. At each sampling location all leaf litter within 0.5 m^2 was collected and placed the litter in bags. Leaf litter samples were transferred to Berlese funnels (Berlese 1905) outfitted with 25-watt incandescent light bulbs for 3 days that collected 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 in Liters (L) was measured for each sample using 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 then pooled by class to estimate leaf litter invertebrate densities.

Understory branch-clipping

Invertebrates on understory vegetation were sampled from 168 randomly selected points on four 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 (*Fagus grandifolia*), Spicebush (*Lindera benzoin*), Red Maple (*Acer rubrum*), and one dominant nonnative species: Multiflora Rose *(Rosa multiflora)* (Johnson 2000). Two replicate branch clippings were collected at two 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 sealing the bag by tying. 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 four plant species, and then means were summed across plant species to estimate total invertebrate density per site.

Food source preparation

I used a subset of invertebrates from earthworm, leaf litter, and understory vegetation sampling and invertebrates from targeted collections for stable isotope analysis (see below for 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 hours or until dry, homogenized, and weighed to ca. 300–400 μg on a Sartorius Cubis microbalance and placed into tin capsules for measurement of stable isotopes of carbon and nitrogen.

Wood thrush sampling

Nest monitoring and capture techniques

Active wood thrush nests were monitored every 2–3 days following initial discovery from 1 May – 20 August during the 2011–2013 breeding seasons (Martin and Geupel 1993). During each nest check the numbers of wood thrush and cowbird eggs and nestlings present were recorded. For each nest, the location (UTM coordinates), height (m), plant species, and subsequently estimated distance to non-forest edge using ArcMap 10.1 (ESRI 2011), were recorded. I used a comparative approach to test for differences in host nestling diets between naturally occurring parasitized and non-parasitized nests within the study area. Nests were considered parasitized if at least one cowbird nestling that could accept food from wood thrush host parents was present in the nest. I used logistic regression to test for effects of distance to edge (m), site, and month (i.e., May, June, July) on 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). I 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. I 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 – 15 August 2011–2013. All birds were fitted with aluminum US Geological Service 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 six 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) in accordance with University of Delaware Institutional Animal Care and Use Committee (IACUC) regulations, under permit #:1129-2012-2 (Appendix A). 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 minutes 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, Missouri, USA), and

freeze-dried samples were homogenized with a quartz mortar and pestle. Samples were then
weighed to ca. 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 δ^{13}C and δ^{15}N were measured using a Costech Elemental Analyzer (EA)
(Valencia, California, USA) connected via a Thermo Scientific ConFlow IV to a Thermo Delta
V (Bremen, Germany) isotope ratio measuring mass spectrometer (IRMS) located at the Stable
Isotope Geochemistry Laboratory at University of Delaware in and near Newark, Delaware.
Stable isotope ratios are reported as δ-values expressed as parts per thousand (‰) derived from
the equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$ 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 δ^{13}C and δ^{15}N values of samples were calibrated against two USGS standards (USGS 40
and USGS 41). Values for δ^{13}C and δ^{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 δ^{13}C and δ^{15}N relative to the Peedee Belemnite
(PDB) and atmospheric N_2 for nitrogen, both of which are assumed equal to 0.0‰. The
analytical precision of the δ^{13}C and δ^{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 δ^{15}N and 0.10
for δ^{13}C, and 0.17 for δ^{15}N and 0.13 for δ^{13}C, respectively. Carbon half-life ($C_{t1/2}$) for C

incorporation to wood thrush plasma was estimated to be roughly 1–2 d 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*, carbon half-life of 2.9 days, Hobson and Clark 1993) and yellow-rumped warblers (*Setophaga coronate*, 0.4-0.7 day, Pearson et al. 2003).

Mixing models were run in the 'siar' package in R (Parnell et al. 2008) using Markov Chain Monte Carlo (MCMC) 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), 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 seven 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 carbon and nitrogen 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 four groups: adult females, adult males, and nestlings in nests without and with cowbird parasitism to assess differences in diets among groups. Sensitivity analyses were conducted by varying trophic enrichment factor values of C from 0 – 2 ‰, and values of N from 0 – 3 ‰. All mean relative contributions to diet differed by a maximum of 4.7 % for all food sources.

To compare diet patterns among groups, I first randomly sampled 100 iterations from posterior distributions from each wood thrush group. I then aggregated food sources a posteriori (i.e., after model runs with all seven 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 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 version 3.1.2 (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. All instances where assumptions of normality were violated, non-parametric tests were used (Zar 2010).

Results

Food resource availability

I 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 B). I 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 1.2). For leaf litter, insect density (5.39 ± 0.60 individuals / L) 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 1.2). In understory vegetation, densities of both caterpillars (0.36 ± 0.06 individuals per g) and insects (0.23 ± 0.03 individuals per g) were greater than spiders (0.08 ± 0.02 individuals per g), and only insect density (individuals per g leaves) differed among sites ($\chi^2 = 28.98$, df = 9, $P < 0.001$) (Table 1.2).

Stable isotopic composition of carbon and nitrogen

Analysis of food sources

I sampled 215 invertebrates comprising 25 families, and 7 classes from leaf litter, understory vegetation, and soil samples for stable isotope analysis (Table 1.3). Overall, mean food source $\delta^{13}C$ and $\delta^{15}N$ values were -25.5 ± 0.21 ‰ and 0.38 ± 0.18 ‰, respectively. I 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 ‰) (Fig. 1.2). I 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 ‰), and earthworms (0.63 ± 0.49 ‰), insects (-0.04 ± 0.39 ‰), myriapods (-1.51 ± 0.54 ‰), and caterpillars (-2.37 ± 0.18 ‰) (Fig. 1.2).

Analysis of blood plasma

I used data from 117 captured and sampled wood thrushes (37 adult females, 36 adult males, 44 nestlings; 33 nestlings without cowbirds, and 11 nestlings with cowbirds). Wood thrush nestlings were sampled from 20 nests, of which 30 % were parasitized. Wood thrush nestling clutch sizes ranged between 1–4, with a mean ± SD of 3.0 ± 0.86. To control for potential bias due to variation in parasite:host nestling ratios, I included only nests with one cowbird nestling in analyses resulting in cowbird nestling to wood thrush nestling ratios that ranged from 0 to ½. 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. I used analysis of variance (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, $P = 0.15$) (Fig. 1.3A). Tukey's post hoc tests revealed that mean plasma $\delta^{15}N$ was greater in 2012 (5.00 ± 0.23 ‰) than 2013 (4.16 ± 0.22 ‰, $P < 0.01$) and 2011 (3.97 ± 0.23 ‰, $P < 0.01$) (Fig. 1.3A). I 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, $P = 0.08$). I 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, $P = 0.89$) (Fig. 1.3B). Mean plasma $\delta^{13}C$ was greater

earlier (-24.5 ± 0.08‰) than later (-25.2 ± 0.15‰) in the breeding season (Fig. 1.3B). Wood thrush blood plasma differed among the four 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 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 cowbirds ($P < 0.01$) and without cowbirds ($P < 0.001$) (Fig. 1.4). Wood thrush nestlings without cowbirds (-25.3 ± 0.17 ‰) had greater plasma $\delta^{13}C$ than nestlings with cowbirds (-26.0 ± 0.28 ‰) ($P < 0.05$) (Fig. 1.4). 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 cowbirds (4.14 ± 0.27 ‰, $P < 0.05$) and without cowbirds (3.34 ± 0.27 ‰, $P < 0.001$) (Fig. 1.4). However, Tukey's post hoc test showed that plasma $\delta^{15}N$ for wood thrush nestlings with and without cowbirds was similar ($P = 0.21$) (Fig. 1.4).

Comparison of wood thrush diets among groups

Wood thrushes ate differing relative proportions among food sources; here I 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 consisted of snails (0.22— 0.36 95 % HDI), spiders (0.25—0.35 95 % HDI), isopods (0.11—0.25 95 % HDI), earthworms (0.04—0.15 95 % HDI), myriapods (0.03—0.13 95 % HDI), insects (0.01—0.07 95 % HDI), and caterpillars (0.0003—0.03 95 % HDI) (Fig. 1.5).

I used a nested ANOVA approach on centerd 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 $= 12$, $P < 0.001$).

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I subsequently used Tukey's post-hoc tests ($P < 0.05$) to determine group differences, and found that wood thrush nestlings in nests without cowbirds ate more Ca-rich foods (0.36—0.55 95 % HDI) and spiders (0.16—0.35 95 % HDI) compared to nestlings in nests with cowbirds (0.28—0.50, 0.15—0.31 95 % HDI, respectively) (Table 1.4). Nestlings in nests without cowbirds ate fewer insects (0.07—0.21 95 % HDI) than nestlings in nests with cowbirds (0.15—0.32 95 % HDI) (Table 1.4). Adult male and female wood thrushes ate similar amounts of all food sources (Table 1.4).

Food availability and resource use

I compared relative diet contributions of seven 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). I 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). I found that food resource use of all wood thrushes combined was independent of available food resources (Fisher's exact 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) (Fig. 1.6). 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) (Fig. 1.6). Wood thrush nestlings without 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) (Fig.

1.6). I found that wood thrush nestlings with cowbirds consumed food sources independent of

food availability ($P < 0.05$), but no pairwise differences were found. All wood thrushes

combined ate 7× the snails, 4× the spiders, and 17× 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 (Fig. 1.6). Nestlings without 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 (Fig. 1.6). Nestlings with cowbirds ate snails,

spiders, isopods, and caterpillars at expected frequencies and ate 1/3 the available insects at less

than expected frequency (Fig 6). Both adult female and male wood thrushes ate 12× the

available snails and 4× the available spiders more frequently than expected, and ate 1/20 the

available caterpillars and insects at less than expected frequency (Fig. 1.6). All wood thrush

groups ate earthworms and myriapods at expected frequencies (Fig. 1.6).

Discussion

Here I show that wood thrush nestlings in nests with cowbirds were fed a lower proportion of snails, isopods, and spiders compared to wood thrush nestlings in the absence of cowbirds. These results support my predictions that 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 to fulfill specific nutritional requirements for optimal growth and development (Weathers 1996, Klasing 1998, Gebhardt-Heinrich and Richner 1998). Based on daily food requirements for a 25 g nestling (Nagy et al. 1999), I used my determined diets (i.e., means and 95 % CIs), and mean Ca content (mg) for food sources (this study), and estimated that the daily Ca intake (mg per day) for wood thrush nestlings parasitized by cowbirds would be reduced by 9–18 % per day compared to wood thrush nestlings in nests without cowbirds. For nestlings in parasitized nests, this corresponds to a reduction in % dietary Ca from 8 % down to 2 %. Reductions of both Ca- and protein-rich food sources in diets of nestlings with cowbirds suggest that 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 comprised of 60 % insects, 16 % caterpillars, 8 % myriapods, 7 % spiders, 6 % earthworms, and 2 % isopods and no

snails. In contrast to all other wood thrush diet analyses published to date, I estimated greater percentages of spiders, snails, and isopods in the diet. Differences among studies of wood thrush diet is 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 I estimated high levels of snails in the diet (ca. 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, 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, 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. I 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, Greenberg and Hollenhorst 2014). These 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 in

small urban forest fragments preferred snails, spiders, and isopods, in contrast to what was

available. This provides further support for the importance of Ca- and protein-rich food sources

for breeding wood thrushes to accommodate nutritional requirements for egg production and nestling provisioning. Mixing models account for invertebrate food sources but I am 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), I think 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 above, would be beneficial.

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Tables

Table 1.1. List of 21 study sites, locations, and areas (ha) within and near Newark, Delaware, USA.

Site Name	ID	Latitude	Longitude	site area (ha)	patch area (ha)
Christina Creek 1	CC1	N 39°39'39.01	W 75°46'14.82	4.2	50.8
Christina Creek 2	CC2	N 39°40'30.67	W 75°46'48.91	8.2	12.7
Coverdale	CD	N 39°41'47.37	W 75°45'5.64	6.2	155.5
Chrysler Woods	CW	N 39°39'33.67	W 75°45'21.27	4.5	5.5
Dorothy Miller	DM	N 39°41'18.01	W 75°44'7.76	4.2	68.8
Ecology Woods	EW	N 39°39'44.15	W 75°44'39.60	16.2	16.6
Folk	FO	N 39°38'43.19	W 75°45'26.75	5.0	150.1
Glasgow 1	GG1	N 39°36'39.99	W 75°43'29.84	5.2	75.6
Glasgow 2	GG2	N 39°36'47.12	W 75°43'54.97	4.7	75.6
Iron Hill 1	IH1	N 39°38'19.57	W 75°44'46.89	5.2	150.1
Iron Hill 2	IH2	N 39°38'19.47	W 75°45'33.24	5.1	150.1
Laird	LA	N 39°41'31.69	W 75°45'32.85	4.5	10.1
Motor Pool	MP	N 39°40'33.05	W 75°44'21.38	5.1	5.9
Phillips	PH	N 39°40'10.80	W 75°45'34.74	3.6	4.6
Reservoir	RE	N 39°41'55.62	W 75°44'36.30	5.0	53.3
Rittenhouse	RH	N 39°39'14.80	W 75°45'29.70	11.0	50.8
Sunset Lake 1	SL1	N 39°37'35.87	W 75°43'46.05	4.5	157.9
Sunset Lake 2	SL2	N 39°37'4.62	W 75°43'48.67	4.6	157.9
White Clay Creek 1	WC1	N 39°42'32.14	W 75°45'58.16	5.2	163.6
White Clay Creek 2	WC2	N 39°42'45.29	W 75°45'53.72	5.4	163.6
Webb Farm	WF	N 39°40'17.90	W 75°44'2.48	8.7	11.1

Table 1.2. Invertebrate density mean (SE) for spiders, insects, caterpillars, snails, myriapods, isopods, and earthworms among 10 forest fragment sites sampled from April to September 2010–2013 in and near Newark, Delaware, USA. Invertebrates were sampled and density was calculated for soil (individuals per m^2), leaf litter (individuals per leaf litter volume L), and understory vegetation (individuals per leaf mass g) sampling substrates. The number of plots is indicated by (*n*). Differences among sites for invertebrate groups are shown by superscript lowercase letters.

Food source	Sampling substrate	*n*	Sites									
			EW	FO	GG2	IH1	IH2	MP	RE	RH	WC1	WC2
			mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)
Spiders	Understory vegetation	111	0.05 (0.02)	0.05 (0.02)	0.12 (0.10)	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)
	Leaf litter	148	0.17 (0.06)	0.13 (0.05)	0.12 (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)
Insects	Understory vegetation	115	0.31^{ab} (0.11)	0.12^{ab} (0.05)	0.13^{b} (0.10)	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)
	Leaf litter	163	3.41^{ab} (0.89)	3.28^{ab} (0.58)	9.12^{a} (2.21)	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)
Caterpillars	Understory vegetation	112	0.37 (0.16)	0.13 (0.05)	0.03 (0.01)	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)
Snails	Leaf litter	143	0.19^{c} (0.08)	0.43^{bc} (0.09)	0.12^{c} (0.08)	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)
Myriapods	Leaf litter	148	0.20^{b} (0.08)	0.32^{b} (0.14)	0.17^{b} (0.07)	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)
Isopods	Leaf litter	148	0.29 (0.16)	0.30 (0.13)	0.10 (0.05)	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)
Earthworms	Soil	30	37.88 (12.40)	65.15 (17.47)	1.52 (1.52)	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)

Table 1.3. Invertebrates (total individuals) sampled during 1 May – 15 August 2011–2013 from sites in and near Newark, Delaware, 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

Table 1.4. Descriptive statistics of wood thrush relative contributions of food sources to diet for adult females and males, and nestlings from nests with and without cowbird parasitism based on estimated posterior distributions from Bayesian mixing models. For each wood thrush group within each of four food sources I 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.

Food source		Adult		Nestling	
		Female	Male	Without cowbirds	With 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.

Figures

Figure 1.1. 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, Delaware, 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).
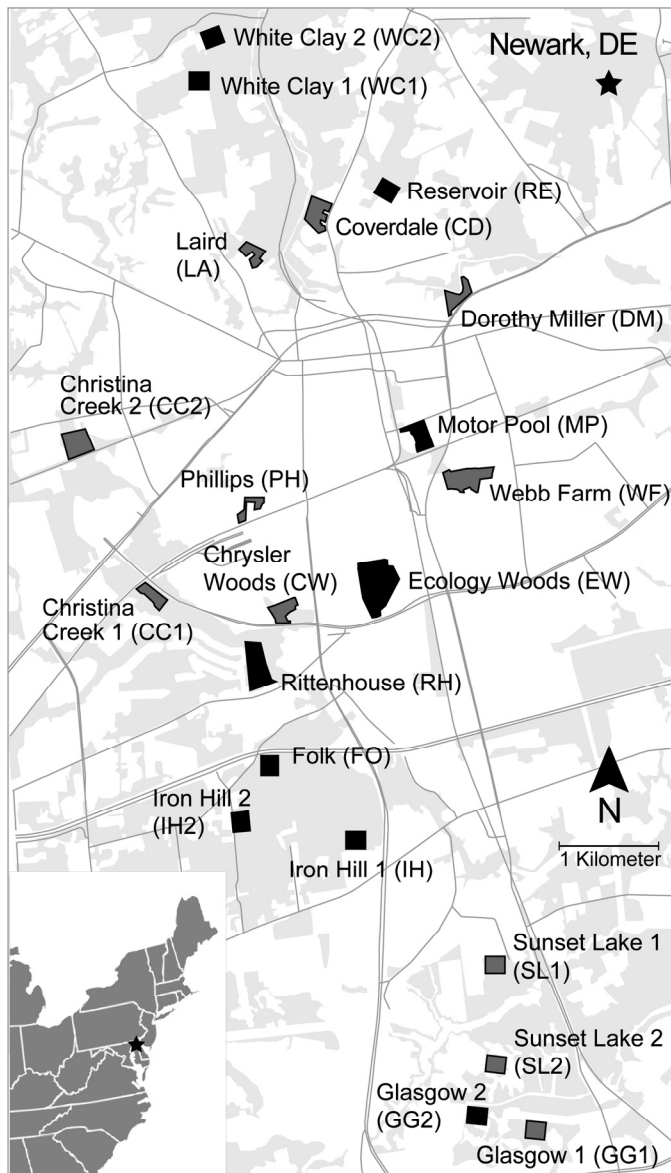
Figure 1.2. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values (mean ± SE) for 7 wood thrush food sources (labeled) sampled during 1 May to 31 August 2011–2013 in and near Newark, Delaware, USA.
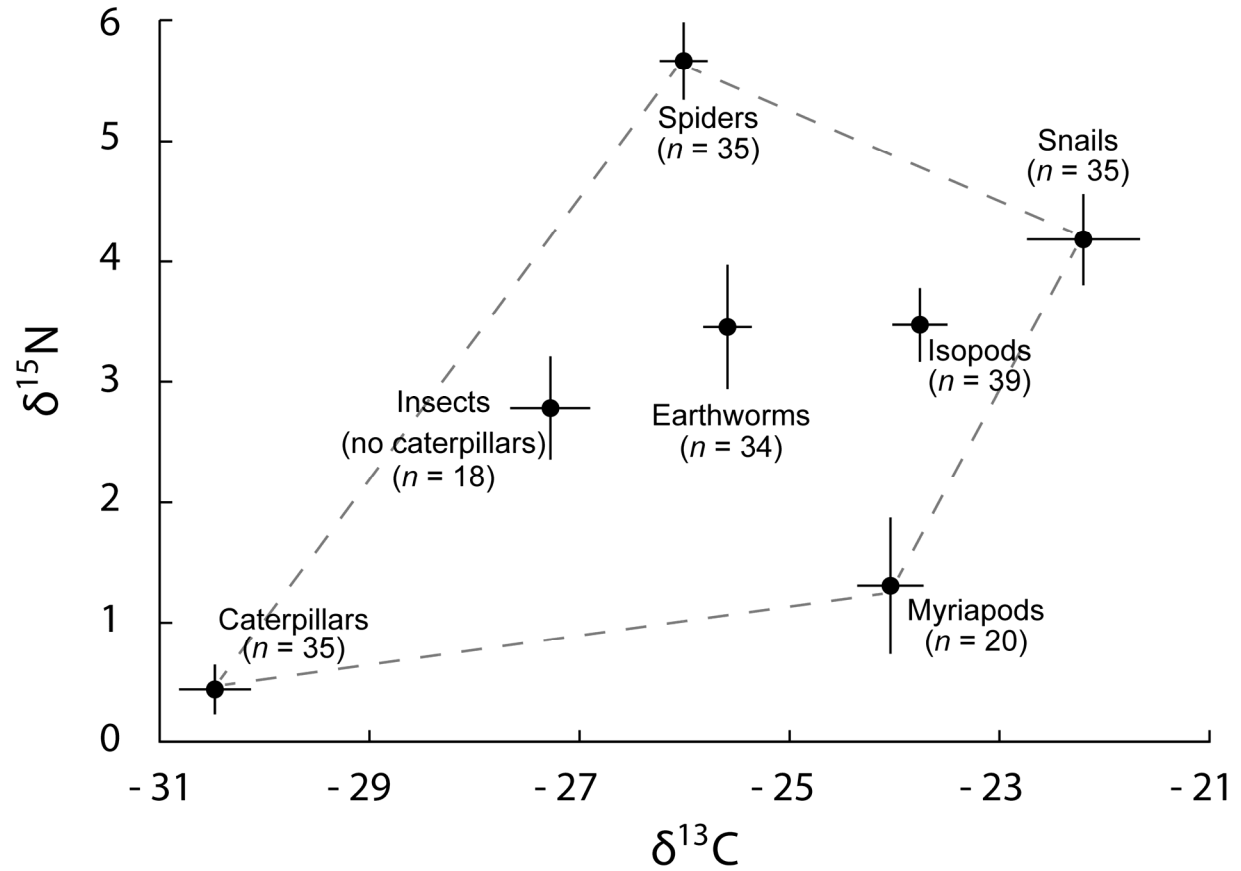
Figure 1.3. Boxplots showing comparisons of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values for blood plasma in A) among years, and B) between early and late season for all wood thrushes sampled during 1 May to 31 August 2011–2013 in and near Newark, Delaware, USA. Asterisks indicate significant differences ($P < 0.05$). Gray boxes, whiskers, and dots indicate inter-quartile ranges, 95 % CIs, and outliers, respectively.
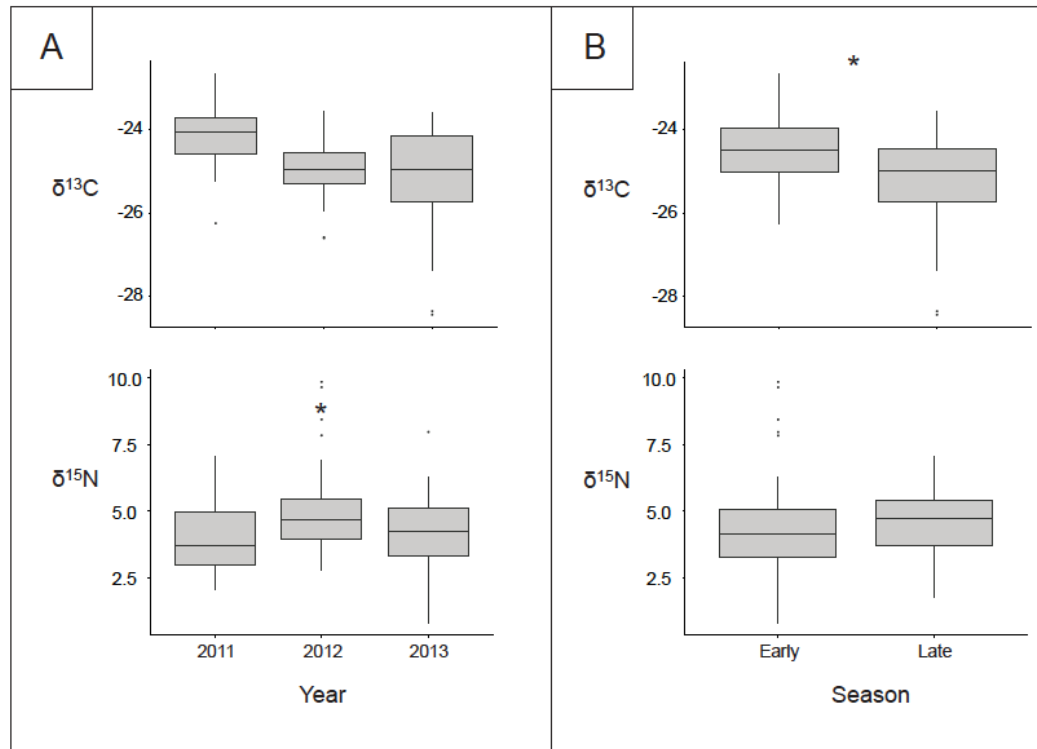
Figure 1.4. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values (mean ± SE) for blood plasma from adult males (black) and females (white), nestlings without cowbirds (light gray) and with cowbirds (dark gray) overlaid on seven food sources (light gray) from wood thrushes sampled during 1 May to 31 August 2011–2013 in and near Newark, Delaware, USA.
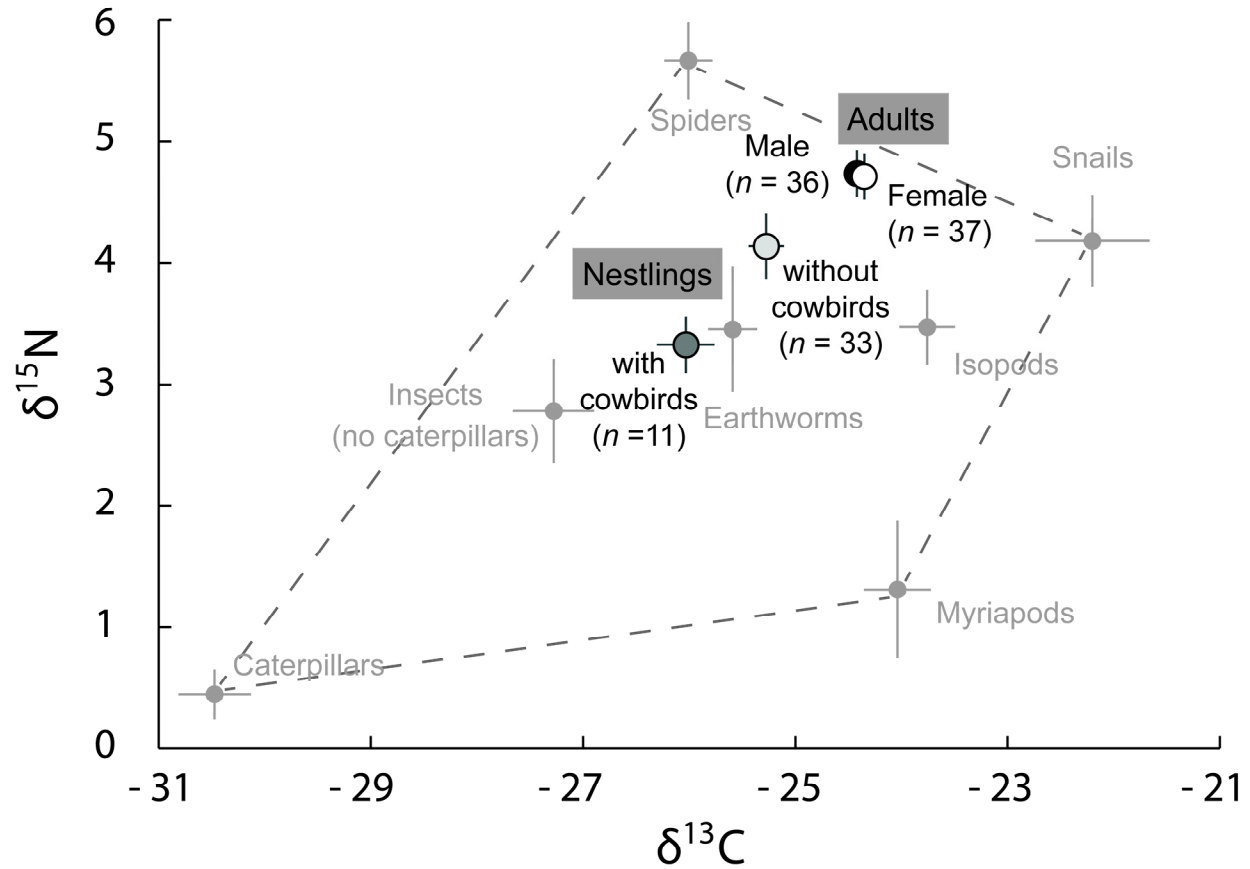
Figure 1.5. Violin plots of posterior distributions showing overall relative contributions of 7 invertebrate food sources to wood thrush diet of all birds combined from birds sampled from 1 May to 31 August 2011–2013 in and near Newark, Delaware, USA. Dark black circles and lines indicate medians and 95 % highest density intervals (HDI) of posterior distributions, respectively.
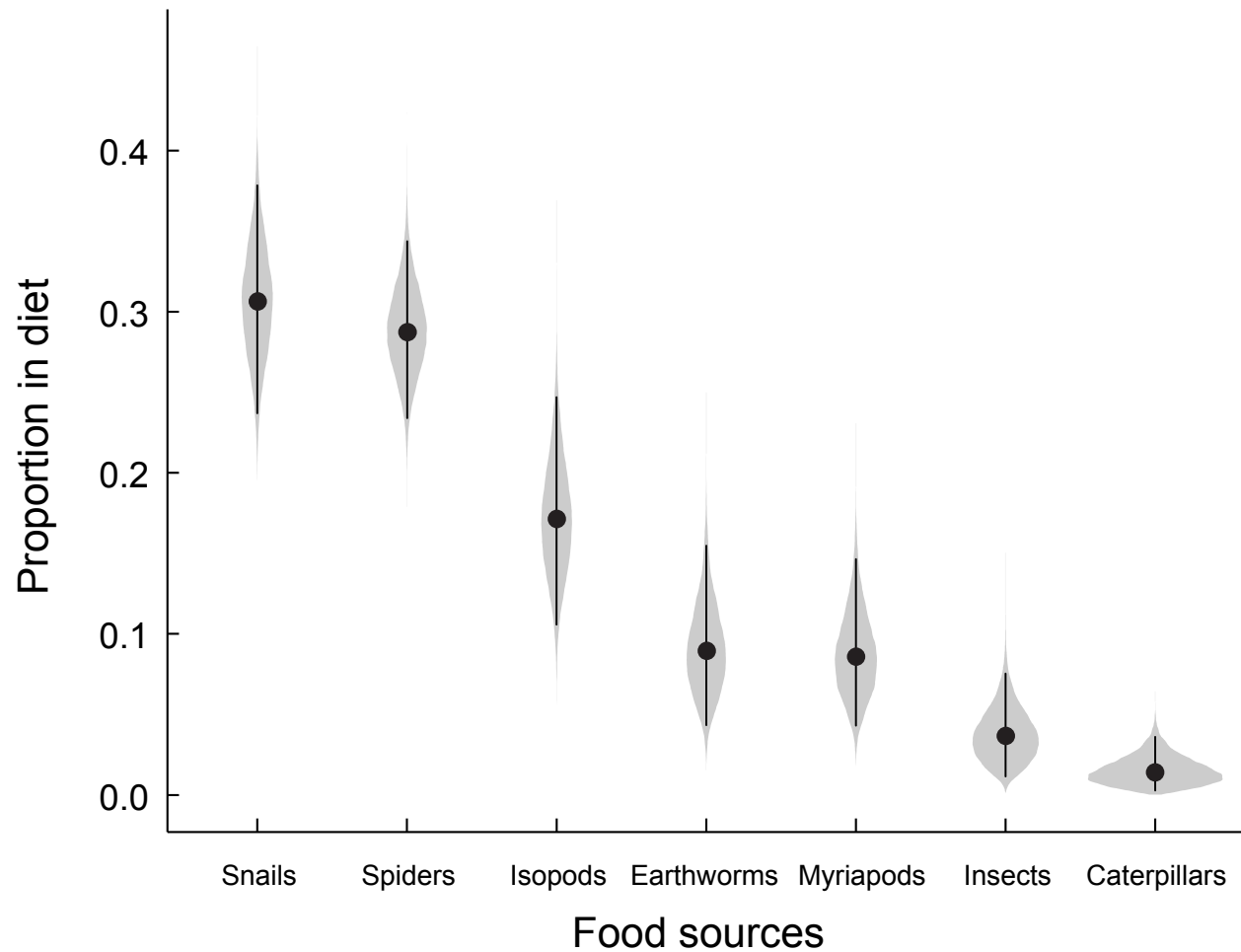
Figure 1.6. Proportion of food resources used by adult females (white), males (black), nestlings without cowbirds (light gray), and nestlings with cowbirds (dark gray) minus proportion of available food resources. Signs above or below bars represent Bonferroni z statistic test results indicating that wood thrushes ate food sources significantly 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.
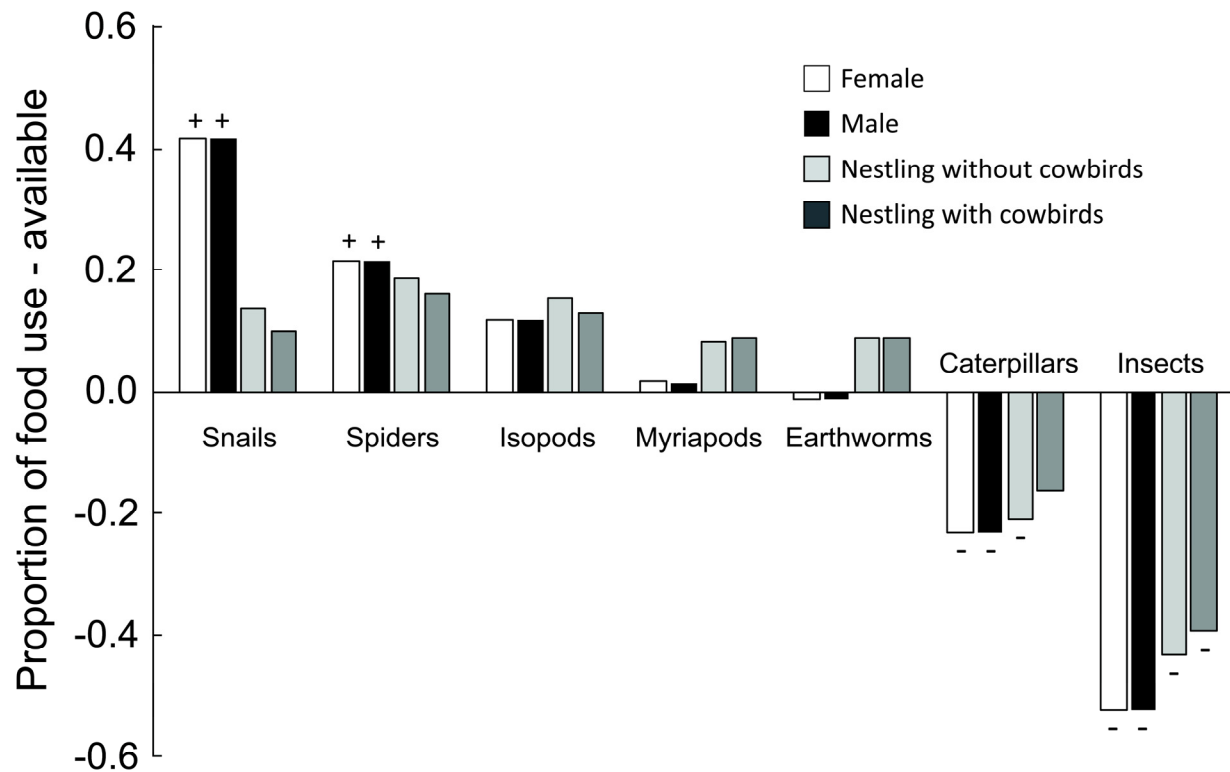
Chapter 2

PANMIXIA AND EXTRA-PAIR PATERNITY OF WOOD THRUSHES IN SMALL URBAN FOREST FRAGMENTS

Abstract

The loss of genetic diversity within populations has been identified as a potential threat to declining species. Reduction of genetic diversity in urban environments is of particular interest given the widespread population declines of species due to anthropogenic environmental and landscape change. Urbanization and habitat fragmentation have been shown to negatively affect population growth rates, and reduce genetic diversity. I studied the genetic structure of a breeding population of wood thrushes within a highly urbanized and fragmented landscape. The range-wide population of the wood thrush (*Hylocichla mustelina*), a Neotropical migratory songbird, has declined by over 50 % in the past 40 years, most likely due to sensitivity to effects of urbanization. I found some genetic structure within the population consisting of three unique clusters that were differentially distributed among discrete forest sites. Mean actual differentiation estimates (D_{est}) among sites ranged between 0–0.29, and I found no relationship between D_{est} and inter-site Euclidean distance (m), suggesting that mating among individuals is not uniform nor constrained by the spatial distribution of breeding locations. Given relatively high annual immigration rates (44 %), the genetic structure I observed is likely the result of a combination of immigration, high site philopatry, and extra-pair mating events. I found that 40 % of nests and 29 % of offspring resulted from extra-pair mating events, some of which involved inter-site forays during the breeding season. Wood thrushes with nests closer to non-forested edges, male wood thrushes with longer wing chord (mm), and males with lower body mass (g) had a higher probability of having offspring through extra-pair matings. These findings suggest that mate selection in wood thrushes breeding in small urban forest fragments might not be

constrained by spatial distributions of breeding sites, and that extra-pair mating events may indeed help alleviate threats from loss of genetic diversity.

Introduction

Habitat loss and fragmentation have been implicated as leading threats to animal populations (Iwamura et al. 2013, Hand et al. 2014, Botello et al. 2015) and have both been shown to reduce genetic flow among sub-populations (Keller and Largiadér 2003), and in turn, may reduce genetic diversity (Eeva et al. 2006, Nöel et al. 2007). Due to the rate and extent of anthropogenic landscape modification (Peterson 2002, Ramachandra et al. 2015) resulting in the loss and fragmentation of habitat, it has become increasingly important to understand how these changes affect wildlife populations. Hence, research on the genetic structure and diversity of populations within urbanized landscapes is critical to improving our understanding and our ability to predict population-level responses to anthropogenic change (Amos et al. 2012, Hansen et al. 2012).

Losses of genetic diversity may be directly related to isolating mechanisms of breeding sub-populations, such as the construction of biological barriers like roads, dams, and buildings which reduce connectivity of suitable habitat on the landscape (Yamamoto et al. 2004, Jha 2015). Without functional corridors connecting discrete patches of breeding habitat, even sub-populations of highly vagile species (e.g., birds) may become isolated (Lussier et al. 2006, Ferrarini 2014, Major et al. 2015). Given these broad concerns, conservation priorities have identified habitat loss and fragmentation as major threats to populations (Faleiro et al. 2013). However, due to the complex nature of synergistically interacting factors related to anthropogenic landscape and environmental change, it remains unclear how populations differentially respond to potential losses of genetic diversity from habitat loss and fragmentation (Runge et al. 2014).

Observed population declines in over 50 species of Neotropical migratory songbirds within the past 50 years (Sauer et al. 2012), are likely related to net reductions of breeding, wintering, and migratory stopover habitat (Sillett and Holmes 2002, Norris and Marra 2007). Among the declining populations of Neotropical migrants, obligate forest-breeding species are particularly vulnerable because of their sensitivity to inherent habitat loss and fragmentation due to increasing rates of urbanization (Faaborg 2014). Studying and understanding how these species' populations are responding to urbanization and the concomitant effects of habitat loss and fragmentation will be imperative for the success of applied conservation efforts.

I investigated the genetic structure and mating system of the wood thrush (*Hylocichla mustelina*), a Neotropical migrant that is sensitive to urbanization (Chace and Walsh 2006, Evans et al. 2011), in an a portion of its breeding rage where regional population declines are severe (Sauer et al. 2012). I was interested in investigating fine-scale genetic structure and the degree of extra-pair paternity of wood thrushes breeding in small urban forest fragments. Despite the wood thrush being a widely-studied species, only a few previous studies have explored aspects of their mating systems as to how extra-pair mating may be influenced by the degree of forest fragmentation on the landscape (Evans et al. 2008, Evans et al. 2009). In general, high prevalence of extra-pair paternity (EPP) has been widely documented within breeding birds despite systems of social monogamy (Griffith et al. 2002), and may confer indirect or direct fitness benefits to individuals (Johnsen et al. 2011, Brouwer et al. 2011, Jacobs et al. 2015), as well as increase levels of genetic diversity within populations (Gohli et al. 2013). Evans et al. (2009) estimated that 40 % of offspring from wood thrushes breeding in forest fragments in Ontario, Canada resulted from EPP compared to 6 % of young within a large contiguous forest in northern Pennsylvania (Evans et al. 2008). Based on these differences, I predicted that EPP rates

for wood thrush in and near Newark, Delaware would be relatively high considering the degree of fragmentation within the study area. Additionally, I was curious to see how estimates of EPP may differ in an area of the breeding range where wood thrushes are regionally declining.

The assessment of population genetic structure and EPP rates of wood thrushes could be used to evaluate if loss of genetic diversity is a consequence of, and potential contributor to observed regional population declines. This research is also unique in that it is greatly informed by a 40-year, ongoing demographic study of wood thrushes within Ecology Woods, a 16-ha forest fragment within the study area (Underwood and Roth 2002). Population trend estimates that have been observed in Ecology Woods (see Fig. 3.1) correspond to both regional and range-wide declines (Sauer et al. 2012). Based on the previous work of Roth and Johnson (1993), and contemporary population trend estimates, I think the breeding population of wood thrushes in and near Newark, Delaware is functionally a sink population, largely supported by stable annual immigration rates (ca. 44 %). However, long-term demographic data from this study area also suggests a relatively high return rate of successfully breeding adults, and in some instances marked individuals have returned in 8 consecutive years, producing over 30 fledglings within a lifetime.

I predicted that the breeding population of wood thrushes in and near Newark, Delaware would exhibit little, if any genetic structuring, and moderate to high levels of extra-pair mating given the combination of steady immigration, high site philopatry (Roth and Johnson 1993), and previous research on wood thrushes in fragmented habitats (Evans et al. 2009). Additionally, I discuss the broader implications of how populations can respond and cope with increasing anthropogenic change and habitat loss and fragmentation.

Methods

Study area and species

This study took place in the mid-Atlantic United States within 21 sites located in18 discrete forest fragments in and around Newark, Delaware, USA (39°41'1N 75°44'58W) (Fig 1, Chapter 1). Wood thrushes breed in deciduous forest from southeastern Canada throughout the eastern United States and winter in Central America (Evans et al. 2011). Throughout their breeding range, wood thrushes are typically found nesting in under- and mid-story vegetation within forest patches ranging in size from 1 ha to >1000 ha (Keller and Yahner 2007), and often raise two broods per season (Evans et al. 2011). Study area description and site selection details can be found in Chapter 1.

Wood thrush demographic data

Nest monitoring and capture techniques

See methods for nest monitoring and capture techniques in Chapter 1

Blood collection for genetic analysis

Blood samples of adult and nestling wood thrushes were collected from birds via brachial artery puncture using 27 gauge, 1.27 cm syringes in heparinized capillary tubes (75 μL) according to University of Delaware IACUC regulations, under permit #: 1129-2012-2 (Appendix A). Capillary tubes containing blood were sealed with crito-seal clay and stored immediately on ice in the field. Blood samples were transferred to 1.5 mL cryo-vials and stored frozen at -80°C within 2-3 hours of collection.

DNA extraction and PCR methods

I extracted deoxyribonucleic acid (DNA) from blood samples using Qiagen DNeasy kit (Qiagen, Venlo, Netherlands), and used polymerase chain reaction (PCR) in Bio Rad T100 thermal cyclers (Bio Rad, Hercules, CA, USA) to amplify five neutral polymorphic microsatellite loci, that have been previously used in genetic studies of wood thrushes (Evans 2008). I amplified the microsatellite loci: Cuμ 02, Cuμ 05, Cuμ 28, Cuμ 32 (Gibbs et al. 1999), and Dpμ 05 (Dawson et al. 1997) (see Table 2.1) using 25 μl PCR reactions that consisted of 1 μl DNA (ca. 50 ng), 0.2 μl Taq polymerase, 1–3 μl of 25 mM MgCl$_2$, 1.25 μl of fluorescent dye-labeled (i.e., 6-FAM, VIC, NED, PET) forward and reverse primer (Invitrogen, Carlsbad, CA, USA), 0.375 μl of 10 mM dNTPS, 2.5 μl of 10× PCR buffer, and 15.425 μl of distilled and deionized H$_2$O. I varied annealing temperatures (Table 2.1) and MgCl$_2$ amounts independently for each locus to optimize successful PCR reactions. Florescent dye-labeled PCR products were analyzed at the Delaware Biotechnology Institute using fragment analysis on a ABI Prism 3130XL Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). I genotyped individuals by scoring alleles using GeneMapper (ver. 3.5) software (Applied Biosystems).

Wood thrush population structure and differentiation

I used the program Structure (ver. 2.3.4) (Pritchard et al. 2003) to determine the degree of genetic structure in the population of wood thrushes breeding in and near Newark, Delaware. I used the admixture ancestry model with sampling location information, an alpha value of 1 (i.e., Dirichlet parameter for the degree of admixture), and assumed that allele frequencies were correlated among subpopulations (Pritchard et al. 2003). Markov-chain Monte Carlo (MCMC) simulations were initially run in Structure for 1,000,000 iterations, with a burn-in period of

100,000 iterations, and thinned posterior distributions by retaining every 10th iteration. I set k (i.e., the number of potential population clusters) to range between 1 and 13, which is the maximum number of sites that individual wood thrushes were sampled from within the study area, and ran 3 simulations for each value of k (1 to 13) to account for Markov chain stochasticity. I subsequently used the program Structure Harvester (Web v0.6.94) to estimate the number of k-population clusters using the Evanno method (Earl and vonHoldt 2012). Following determination of the most-likely number of clusters (k), I ran Structure again for 30 simulations using the same parameter settings, with k set to 3 clusters to estimate precision. I used the program CLUMPP (ver. 1.1.2) to estimate and visualize mean cluster membership per site (Jakobsson and Rosenberg 2007). I then visualized most-likely iterations for individuals and mean cluster membership using the program DISTRUCT (ver. 1.1) (Rosenberg 2004).

I initially used the program Genetix (ver. 4.05.2) (Belkhir et al. 1996) to estimate F_{ST} (Weir and Cockerham 1984) and G_{ST} (Nei 1973, Nei 1978) diversity indices, along with corresponding sub-population distance matrices independently for the following groups: all wood thrushes combined, all adults, adult females, adult males, and offspring. However, recent concerns have arisen over the mathematical behavior of traditional F_{ST} and G_{ST} indices that lead to potentially spurious interpretation of diversity estimates when using genetic markers with high mutation rates (e.g., microsatellite loci), and in populations with high allelic diversity (Pearse and Crandall 2004, Jost 2008). Therefore, I subsequently computed Jost's (2008) D_{est} (estimator of actual differentiation) using the program Software for the Measurement of Genetic Diversity (SMOGD, ver. 2.6) (Crawford 2010). I then used the R package 'ecodist' (Goslee and Urban 2010) to test for differences between matrices (Mantel 1967) of between-site D_{est} values, and

Euclidean distances (m) between all site pairs to asses if genetic similarity between sites was related to isolation by distance.

Wood thrush paternity analysis

I assigned paternity to offspring using the program Cervus (ver. 3.0.7) and estimated extra-pair paternity rates (Kalinowski et al. 2007). The combined non-exclusion probability for offspring given a known mother was < 0.0001, and allele frequencies did not deviate from Hardy-Weinberg equilibrium, except at the Cuμ 05 locus (Table 2.2). However, I excluded all offspring where known mothers and offspring had mismatching alleles, potentially due to the presence of null alleles, from the paternity analysis to reduce the potential for false paternity assignment. Additionally, I restricted assignment of offspring resulting from extra-pair matings to genetic fathers in cases where candidate fathers were estimated with 95 % confidence or 80 % confidence in cases where males were either not captured in the same nesting year or when inter-site distances were less than 3 km. I chose a threshold of 3 km since previous research has suggested that male and female wood thrushes can make off-territory forays of several kilometers (Evans et al. 2008).

Results

I sampled 301 individual wood thrushes and followed the fates of 184 active wood thrush nests during the breeding seasons from 2011–2013. Wood thrush clutch size (mean ± SE) was 2.19 ± 0.1, and ranged from 0 to 4. The number of fledglings per nest (mean ± SE) was 0.92 ± 0.11, and like clutch size, ranged from 0 to 4. Cowbirds parasitized 35 % of wood thrush nests that resulted, on average (mean ± SE), in 0.75 ± 0.09 cowbird eggs laid per nest, and 0.20 ± 0.04 cowbird fledglings per nest. Nest density (number of nests per ha; mean ± SE) from 2011–2013 among sites where breeding occurred was 0.62 ± 0.08, varied across sites, and ranged between 0.11 and 1.93.

Population genetic structure

Using data from 301 genotyped individuals (i.e., 76 females, 101 males, and 124 nestlings), I found the breeding population of wood thrushes in the study area to consist of 3 unique clusters. Numbers of individuals sampled per site were as follows: CC2 (*n* = 2), EW (*n* = 80), FO (*n* = 32), GG2 (*n* = 5), IH1 (*n* =44), IH2 (*n* =25), MP (*n* = 7), RE (*n* = 13), RH (*n* = 20), SL2 (*n* = 7), WC1 (*n* = 28), WC2 (*n* = 37), and WF (*n* =1). Although there was considerable mixing of the three identified clusters among sites, both group (mean) and individual proportions of membership to each cluster differed among 13 sites (Figs. 2.1 and 2.2, respectively). Wood thrushes from IH1, WC1, and RE showed similar relative proportions of cluster membership, as did IH2, SL2, FO, RH, WC2, and GG2. Sites CC2, EW, WF, and MP formed a third natural grouping based on visual inspection, however contained more variation than the two previously mentioned groups (Fig. 2.1). The degree of intra-site structural variation among individuals also differed among sites, where EW showed the greatest amount individual variation, and GG2 the

least (Fig. 2.2). However, differences among sites are potentially due to the number of birds sampled at each site, and the nature of the relationships among sampled birds. For example, GG2 shows data for 5 individuals consisting of an adult male and female pair, and their three offspring.

Wood thrush population differentiation

I found that diversity indices (i.e., F_{ST}, G_{ST}, and D_{est}) provided different estimates for population differentiation among wood thrush groups sampled from 13 sub-populations (i.e., site locations) that were analyzed (Table 2.3). My intention here was not to compare these estimators and their interpretation, but to provide them for reference, and show further support for using D_{est} as an index of population differentiation. Harmonic mean values of D_{est} differed among wood thrush groups, and were highest for offspring (0.18), whereas adult males and females showed no differentiation ($D_{est} = 0$) (Table 2.3). D_{est} for all individuals when analyzed collectively was 0.073, suggesting a relatively high degree of similarity among sub-populations. Bootstrapping estimates based on 1000 permutations had a SE of 0.002, indicating a high level of precision of D_{est} estimates. Ranges of mean inter-site D_{est} estimates differed among all wood thrush (0–0.29), adults (0–0.16), females (0–0.06), males (0–0.13), and offspring (0–0.45) (see Table 2.6 for all pair-wise estimates).

I found no correlations (Mantel 1967) between distance matrices of population differentiation (D_{est}) and inter-site distances (m) among groups for all wood thrush ($r = 0.19$, $P = 0.89$), adults ($r = -0.08$, $P = 0.56$), females ($r = -0.19$, $P = 0.26$), males ($r = -0.05$, $P = 0.72$), or offspring ($r = 0.15$, $P = 0.47$).

Estimates of wood thrush extra-pair paternity rates

I attempted to assign paternity to 105 genotyped wood thrush offspring from 35 known mothers, and a pool of 101 candidate adult males. For these individuals, allele frequencies did not deviate from Hardy-Weinberg equilibrium, except at locus Cuμ 05 (Table 2.2). The combined non-exclusion probability when considering the mother–father pair, was < 0.0001. I successfully assigned paternity to 41 offspring from 25 nests. Offspring from extra-pair matings were overwhelmingly the result of intra-site pairings of adults (71 %) within each breeding season. However, I also found 14 % of offspring resulting from extra-pair mating between adults captured in different years within the same sites, 10 % from adults captured in different years at different sites, and 5 % (n =2) that resulted from inter-site extra-pair mating events. While I was unable to determine the sex of solicitous adult individuals (i.e., the directionality) of extra-pair copulations with these data, the results provide evidence of several alternative pathways of genetic flow via extra-pair copulation for wood thrushes breeding in urbanized and fragmented landscapes.

Morphological relationships to extra-pair paternity

Using multivariate logistic regression, I found no year (χ^2 = 0.2, df = 13, P = 0.66), month (χ^2 = 0.007, df = 13, P = 1.0), or site (χ^2 = 0.56, df = 13, P = 1.0) effects on the probability of extra-pair paternity. I examined the potential influence of morphometric, patch, nest, and age factors on extra-pair paternity rates using mixed-effects logistic regression models (Table 2.5). I found that males with longer wing chord (mm) had a higher probability of siring offspring through extra-pair mating events (χ^2 = 4.6, df = 8, P < 0.05) (Fig. 2.3A, Table 2.5). Males with lower body mass (g) also had a higher probability of siring offspring through extra-pair mating (χ^2 =

4.9, df = 8, *P* < 0.05) (Fig. 2.3B, Table 2.5). Within the patch effects model, I found that nests

located greater distances from non-forest edge (m) had a lower probability of containing young

resulting from extra-pair mating events (χ^2 = 4.10, df = 3, *P* < 0.05) (Fig. 2.3C, Table 2.5). I also

found the increased likelihood of older males (ASY) siring offspring *via* extra-pair matings to be

marginally significant (χ^2 = 3.3, df = 1, *P* = 0.07) (Fig. 2.3D, Table 2.5).

Discussion

I found weak genetic structure within the population of wood thrushes in contrast to my predictions of complete panmixis given relatively high annual immigration rates. However, the countervailing effects from high site philopatry of successfully breeding adults seem plausible for the level of structure ($k = 3$ clusters), and spatial distribution of mean and individual cluster membership I observed. The similarity among clusters was not related to pair-wise distances between sites. For example, mean population structure was more similar between IH1 and WC1 (7.9 km), than between WC1 and WC2 (0.48 km). Interestingly, EW, which is centrally located within the study area, showed the greatest amount of within-site variation and consisted of individuals with similar clustering patterns to both of the other natural groups (i.e., IH1, WC1, RE, and IH2, SL2, FO, RH, WC2, GG2).

Results of population genetic structure were supported by actual genetic differentiation (D_{est}) estimates, indicating overall, a high degree of relatedness among all individuals (particularly among adults). The lack of correlation between Euclidean inter-site distances (m) and D_{est} estimates lend further support of the non-uniformity I observe in weak spatial structuring of k-cluster membership among sites. Inter-site estimates of D_{est}, provide valuable information on the most-likely pathways of genetic flow within the study area, and could be used in future analyses to validate habitat-based models of genetic flow within fragmented landscapes using matrix-resistance methods in programs such as Circuitscape (McRae and Shah 2009, Cushman et al. 2012). Two potential pathways for genetic flow that I have identified in this study are the inter-site movement of breeding adults in differing years, and the inter-site forays that may occur during the breeding season within a given year. For example, in both scenarios, inter-site D_{est} estimates support the results from paternity analyses. For the former situation, inter-site D_{est} estimates ranged between 0.02–0.17 where extra-pair mating occurred between

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adults from IH1–FO, WC1–RE, and GG2–RH pairings in differing years, and for the latter within-breeding season extra-pair matings, D$_{est}$ estimates were 0.02 between IH1–FO, and 0.05 between EW–IH1.

Extra-pair paternity may confer fitness advantages to individuals avoiding inbreeding (Blomqvist et al. 2002, Foerster et al. 2003), however these patterns are not unequivocal among species (Hansson et al. 2004, Kokko and Ots 2006, Reid et al. 2015) or populations (Evans et al. 2009). For example, within the study area, a pedigree analysis using 39 years of demographic from EW, indicated that in two instances parents socially paired with their own offspring in subsequent breeding seasons. These "inbreeding" events occurred during two periods of peak rates of immigration into EW, which could potentially explain mating behavior resulting from avoidance of outbreeding. However, these mating events might also only be social pairings of two genetically non-related individuals, as I demonstrated in this study, that 29 % of offspring were the result of extra-pair matings.

Extra-pair paternity was predicted by lower male body mass (g), longer male wing chord (mm), and by age-class of the social father. Collectively, these patterns suggest that older, more experienced males have a higher probability of engaging in either solicitation of extra-pair matings or being solicited by females making off-territory forays. Past research has demonstrated that older and more experienced males may be preferentially selected by fertile females (Sundberg and Dixon 1996), and that female promiscuity is inversely related to the amount of potential available mates (Moller 1992). This may give rise to patterns where longer-lived males have a higher probability of being selected by females compared to shorter lived males. I did not detect any relationship of male wing chord (mm), body mass (g), or age class (SY or ASY) to fecundity given the small sample size of individuals that I assigned putatively

paternity to. However, using linear regression on data from marked and recaptured males ($n =$ 282) sampled during 1973–2013 in EW, I found that male age was positively related to the number of mean fledglings per year ($F = 13.6$, df = 1, $P < 0.001$; Fig. 2.4).

I found that offspring from extra-pair matings were more likely to occur in nests closer to non-forested edges, implying that males with territories closer to non-forested edges may encounter solicitous females more often, or perhaps engage in more frequent off-territory forays themselves. Other research suggests that territory density and breeding synchrony can also influence the number of potential mates for females at a given point in time, which can in turn, affect rates of extra-pair mating (Westneat et al. 1990, Stutchbury and Morton 1995). However, I did not detect any effect of territory density on the probability of EPP, despite varying territory densities ranging between 0.11–1.93 among sites and years, and a territory density (mean ± SE) of 0.62 ± 0.08, which is very similar to breeding wood thrush densities that Evans et al. (2009) report.

In order to achieve established conservation goals for the wood thrush, and other sensitive forest-breeding species we must gain a better understanding of how populations are responding to anthropogenic stressors such as habitat loss and fragmentation. By studying sink populations within highly urbanized landscapes, like the mid-Atlantic United States, where populations are declining at alarming rates, we can better inform conservation-based decision making and actions for the wood thrush. These results suggest that breeding wood thrushes in and near Newark, Delaware have considerable genetic flow among breeding sites, and that discrete forest patches are functionally more connected than was previously thought given personal observations from the field, and patterns in mark-recapture data. However, there remains a need to understand the drivers of the genetic structure I did observe, as this will allow

us to predict how populations may respond in light of the continued increasing rate of urbanization within the mid-Atlantic region of the United States.

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Tables

Table 2.1. Summary of genetic characteristics of primer sequences for 5 wood thrush microsatellite loci.

Locus	Repeat motif	No. of alleles	Fragment size range (bp)	t_m (ºC)	Primer sequence	Dye label	Source (GenBank accension no.)
Dpμ 01	$(CA)_{22}$	10	140-168	53, 57	F-TGGATTCACACCCCAAAATT R-AGAAGTATATAGTGCCGCTTGC	6-FAM	Dawson et al. 1997 (unknown)
Cuμ 02	$(TG)_{15}$	8	130-152	53, 57	F-CCTTGGATTGCTTCCAAATG R-CCAATTTCCTGCAGACTCTTTC	VIC	Gibbs et al. 1999 (AF122890)
Cuμ 05	$(GT)GC(GT)_2GC(GT)_8$	24	142-206	50, 57	F-ACCTCTAAATACCTGTGAGTGC R-ACTGTGGTATTCTTTACCTAGCA	NED	Gibbs et al. 1999 (AF122892)
Cuμ 28	$(CA)_{12}$	14	158-190	53, 55	F-GAGGCACAGAAATGTGAATT R-TAAGTAGAAGGACTTGATGGCT	VIC	Gibbs et al. 1999 (AF122894)
Cuμ 32	$(GT)TT(GT)_9$	13	136-176	53, 55	F-AGGAGAGTGAAAGAAAAGGG R-GAATTCTCAGCATGACAAATC	PET	Gibbs et al. 1999 (AF122895)

Table 2.2. Number of alleles (k), number of genotyped individuals (N), observed (HO) and expected (HE) heterozygosity, polymorphic information content (PIC), and frequency of null alleles (F(Null)) at 5 microsatellite loci for 241 wood thrushes sampled from 2011–2013 in and near Newark, Delaware, USA.

Locus	k	N	H_O	H_E	PIC	F(Null)
Cuu02	9	229	0.598	0.664	0.616	0.0526
Cuu05	32	204	0.706*	0.932*	0.926	0.1372
Cuu28	15	235	0.809	0.816	0.795	0.0038
Cuu32	18	235	0.736	0.791	0.762	0.0388
Dpu01	19	229	0.69	0.78	0.767	0.0636

*Significant deviation from Hardy-Weinberg equilibrium ($P < 0.01$)

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Table 2.3. Population differentiation indices (i.e., FST, GST, and Dest) and respective harmonic mean estimates among analyzed wood thrush groups: all individuals, adults, adult females, adult males, and offspring sampled during 2011–2013 breeding seasons in and near Newark, Delaware, USA.

Group	N	F_{ST}	G_{ST}	Dest
All	301	0.017	0.115	0.073
Adults	177	0.005	0.116	0.007
Female	76	0	0.133	0
Male	101	0.004	0.166	0
Offspring	124	0.038	0.133	0.178

Table 2.4. Proportion of wood thrush nests and mean proportion of offspring per site resulting from extra-pair mating events within 10 sites sampled from 2011–2013 in and near Newark, Delaware, USA.

Site	n nests	Proportion of nests	n offspring	Proportion of offspring
EW	10	0.4	17	0.29 (0.11)
FO	1	0	2	0
GG2	1	1	2	0.5
IH1	2	1	2	1
IH2	1	0	1	0
MP	2	0	4	0
RE	1	1	2	1
RH	2	0	3	0
WC1	2	1	2	1
WC2	3	0	6	0
All sites	25	0.4	41	0.29 (0.07)

Table 2.5. Multivariate logistic regression models and associated variables, Beta (β) coefficients, Wald Chi-square statistics (χ2), and P values. Significant predictors (α = 0.05) of the probability of extra-pair paternity are indicated by asterisks.

Model	Variable	β	Wald χ^2	P value
Morphometric	Male mass (g)	-0.74	4.90	0.03*
	Male wing chord (mm)	0.82	4.60	0.03*
	Male tarsus length (mm)	-0.27	1.80	0.17
	Male tail length (mm)	-0.20	1.20	0.27
	Female mass (g)	0.05	0.09	0.77
	Female wing chord (mm)	0.28	1.00	0.31
	Female tarsus length (mm)	-0.08	0.11	0.74
	Female tail length (mm)	-0.16	0.41	0.52
Patch	Distance to edge (m)	-0.01	4.10	0.04*
	Patch size (ha)	0.00	0.39	0.53
	Nest density (nests per ha)	1.07	0.53	0.47
Nest	Nest success	-0.05	0.03	0.87
	Cowbird parasitism	-17.94	< 0.01	1.00
	Wood thrush clutch size	-1.11	1.50	0.22
	Wood thrush nestlings	0.55	0.13	0.71
	Wood thrush fledge	0.36	0.11	0.97
	Cowbird eggs	30.83	< 0.01	1.00
	Cowbird nestlings	6.84	< 0.01	1.00
	Cowbird fledge	-37.61	< 0.01	0.74
Parent age (SY or ASY)	Age of social father	-1.30	3.30	0.07
	Age of social mother	-1.23	2.60	0.11
	Age of candidate father	-0.27	0.14	0.71

Table 2.6. Half-matrices of esitmators of actual differentiation (Dest) showing the degree of genetic similarity among sites. Dest estimates are highlighted in light gray (Dest $\geq$ 0.1), gray (Dest $\geq$ 0.2), and dark gray (Dest $\geq$ 0.3) boxes.

Group

All individuals	–	CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2
	CC2	–	–	–	–	–	–	–	–	–	–	–	–
	EW	0	–	–	–	–	–	–	–	–	–	–	–
	FO	0	0.04	–	–	–	–	–	–	–	–	–	–
	GG2	0.02	0.26	0.20	–	–	–	–	–	–	–	–	–
	IH1	0	0.05	0.02	0.14	–	–	–	–	–	–	–	–
	IH2	0	0.03	0	0.18	0.01	–	–	–	–	–	–	–
	MP	0.02	0.13	0.10	0.21	0.15	0.16	–	–	–	–	–	–
	RE	0	0.13	0.10	0.29	0.10	0.04	0.07	–	–	–	–	–
	RH	0	0.04	0.01	0.17	0.06	0.04	0.09	0.09	–	–	–	–
	SL2	0	0.02	0	0.11	0.01	0	0.14	0.02	0.01	–	–	–
	WC1	0	0.02	0.05	0.18	0.03	0.01	0.20	0.12	0.06	0	–	–
	WC2	0	0.02	0.02	0.17	0.02	0	0.12	0.06	0.01	0	0.015	–
	WF	–	0	0.04	0.02	0.05	0	0.08	0	0.02	0	0.022	0

Adults	–	CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2
	CC2	–	–	–	–	–	–	–	–	–	–	–	–
	EW	0	–	–	–	–	–	–	–	–	–	–	–
	FO	0	0.01	–	–	–	–	–	–	–	–	–	–
	GG2	–	0	0	–	–	–	–	–	–	–	–	–
	IH1	0	0.04	0	0	–	–	–	–	–	–	–	–
	IH2	0	0.04	0	0	0	–	–	–	–	–	–	–
	MP	0	0.01	0	0	0.02	0.07	–	–	–	–	–	–
	RE	0	0.16	0.04	0	0.04	0.04	0	–	–	–	–	–
	RH	0	0	0	0	0	0	0	0.06	–	–	–	–
	SL2	0	0.05	0	0	0.01	0	0	0	0	–	–	–
	WC1	0	0	0	0	0	0.01	0.02	0.12	0	0	–	–
	WC2	0	0.02	0	0	0	0	0.01	0.03	0	0	0.01	–
	WF	–	0	0.01	–	0.05	0	0.02	0	0.03	0	0.01	0

Table continued

Female	–	CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2
	CC2	–	–	–	–	–	–	–	–	–	–	–	–
	EW,	–	–	–	–	–	–	–	–	–	–	–	–
	FO,	–	0	–	–	–	–	–	–	–	–	–	–
	GG2,	–	0	0	–	–	–	–	–	–	–	–	–
	IH1,	–	0.01	0	0	–	–	–	–	–	–	–	–
	IH2,	–	0.01	0	0	0	–	–	–	–	–	–	–
	MP,	–	0	0	0	0	0.06	–	–	–	–	–	–
	RE,	–	0.06	0	0	0	0.05	0	–	–	–	–	–
	RH,	–	0	0	0	0.02	0.01	0	0.03	–	–	–	–
	SL2	–	–	–	–	–	–	–	–	–	–	–	–
	WC1,	–	0	0	0	0	0	0	0.05	0	–	–	–
	WC2,	–	0.01	0	0	0	0	0	0.02	0	–	0	–
	WF	–	–	–	–	–	–	–	–	–	–	–	–
Male		CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2
	CC2	–	–	–	–	–	–	–	–	–	–	–	–
	EW	0	–	–	–	–	–	–	–	–	–	–	–
	FO	0	0.02	–	–	–	–	–	–	–	–	–	–
	GG2	–	0	0	–	–	–	–	–	–	–	–	–
	IH1	0	0.07	0	0	–	–	–	–	–	–	–	–
	IH2	0	0.05	0	0	0	–	–	–	–	–	–	–
	MP	–	0	0	–	0	0	–	–	–	–	–	–
	RE	0	0.13	0.02	0	0.05	0.02	0	–	–	–	–	–
	RH	0	0	0	0	0	0	0	0.01	–	–	–	–
	SL2	0	0.08	0	0	0	0	0	0	0	–	–	–
	WC1	0	0	0.01	0	0.06	0.03	0	0.07	0	0	–	–
	WC2	0	0.02	0	0	0	0	0	0	0	0	0.04	–

Table continued

Offspring	–	CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2
	CC2	–	–	–	–	–	–	–	–	–	–	–	–
	EW	–	–	–	–	–	–	–	–	–	–	–	–
	FO	–	0.05	–	–	–	–	–	–	–	–	–	–
	GG2	–	0.24	0.08	–	–	–	–	–	–	–	–	–
	IH1	–	0.07	0.05	0.12	–	–	–	–	–	–	–	–
	IH2	–	0.00	0.02	0.28	0.03	–	–	–	–	–	–	–
	MP	–	0.04	0.04	0.24	0.14	0.07	–	–	–	–	–	–
	RE	–	0.28	0.37	0.45	0.23	0.08	0.23	–	–	–	–	–
	RH	–	0.21	0.06	0.20	0.19	0.10	0.02	0.34	–	–	–	–
	SL2	–	–	–	–	–	–	–	–	–	–	–	–
	WC1	–	0.03	0.13	0.15	0.04	0.00	0.10	0.12	0.23	–	–	–
	WC2	–	0.01	0.02	0.09	0.05	0.00	0.05	0.17	0.09	–	0.02	–
	WF	–	–	–	–	–	–	–	–	–	–	–	–

Figure 2.1. Stacked bar chart (Q-matrix) showing the mean population genetic structure among 13 sites from wood thrushes sampled during the breeding seasons from 2011–2013 in and near Newark, Delaware, USA.
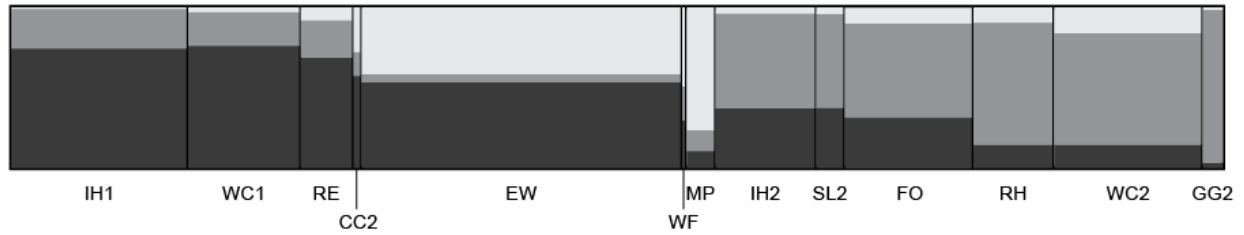
Figure 2.2. Stacked bar chart showing individual membership coefficients (Q-matrix for k = 3 clusters) for 301 wood thrushes sampled from 13 sites during the breeding seasons from 2011–2013 in and near Newark, Delaware, USA.
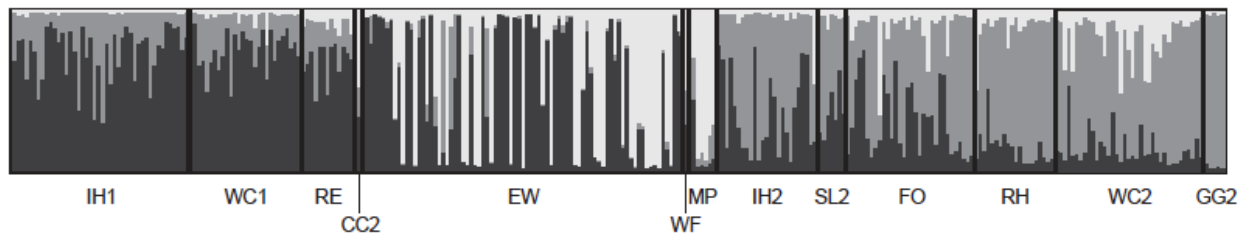
Figure 2.3. Logistic regression models showing the relationship of A) male wing chord (mm), B) male body mass (g), C) distance from nest location to non-forested edge, and D) age class of social father (SY, ASY) to the probability of offspring resulting from extra-pair paternity (EPP) or social mating events.
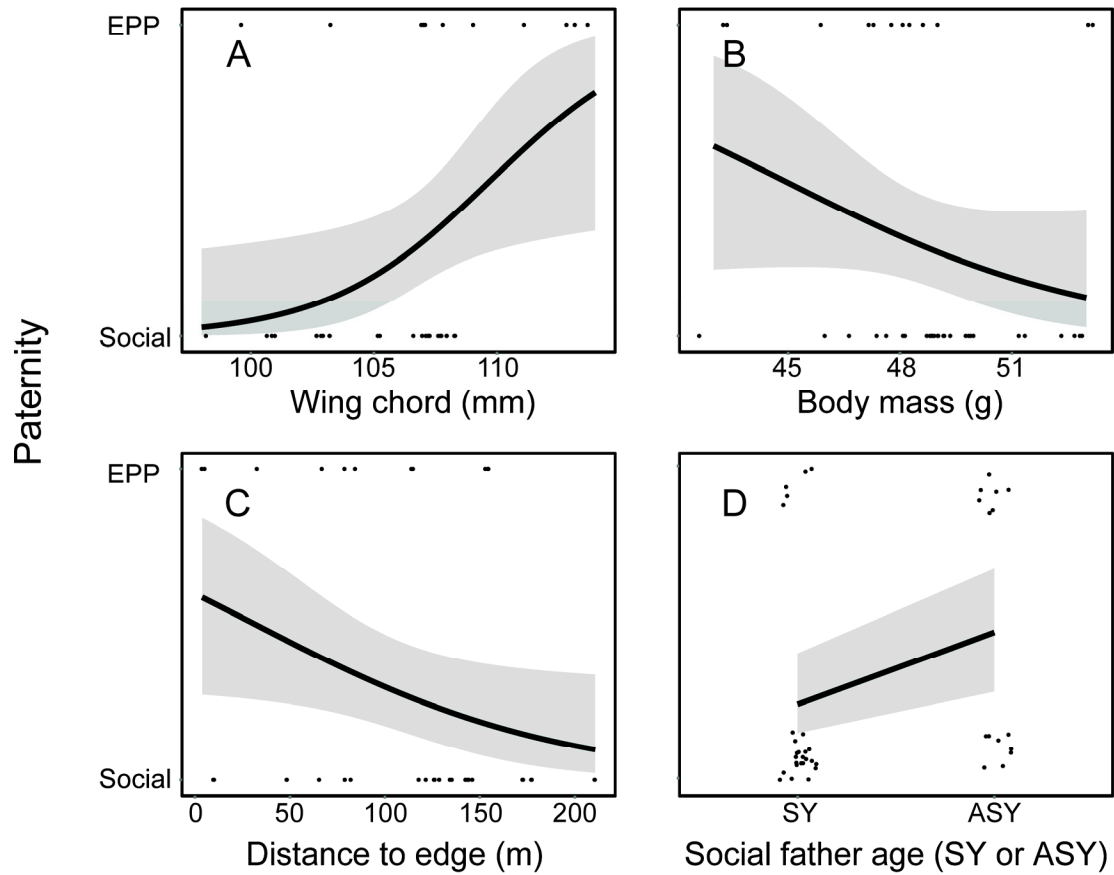
Figure 2.4. Positive linear relationship between male age (years) and mean number of fledglings per year from marked males ($n = 282$) breeding in Ecology Woods (EW) from 1973–2013 in and near Newark, Delaware, USA.
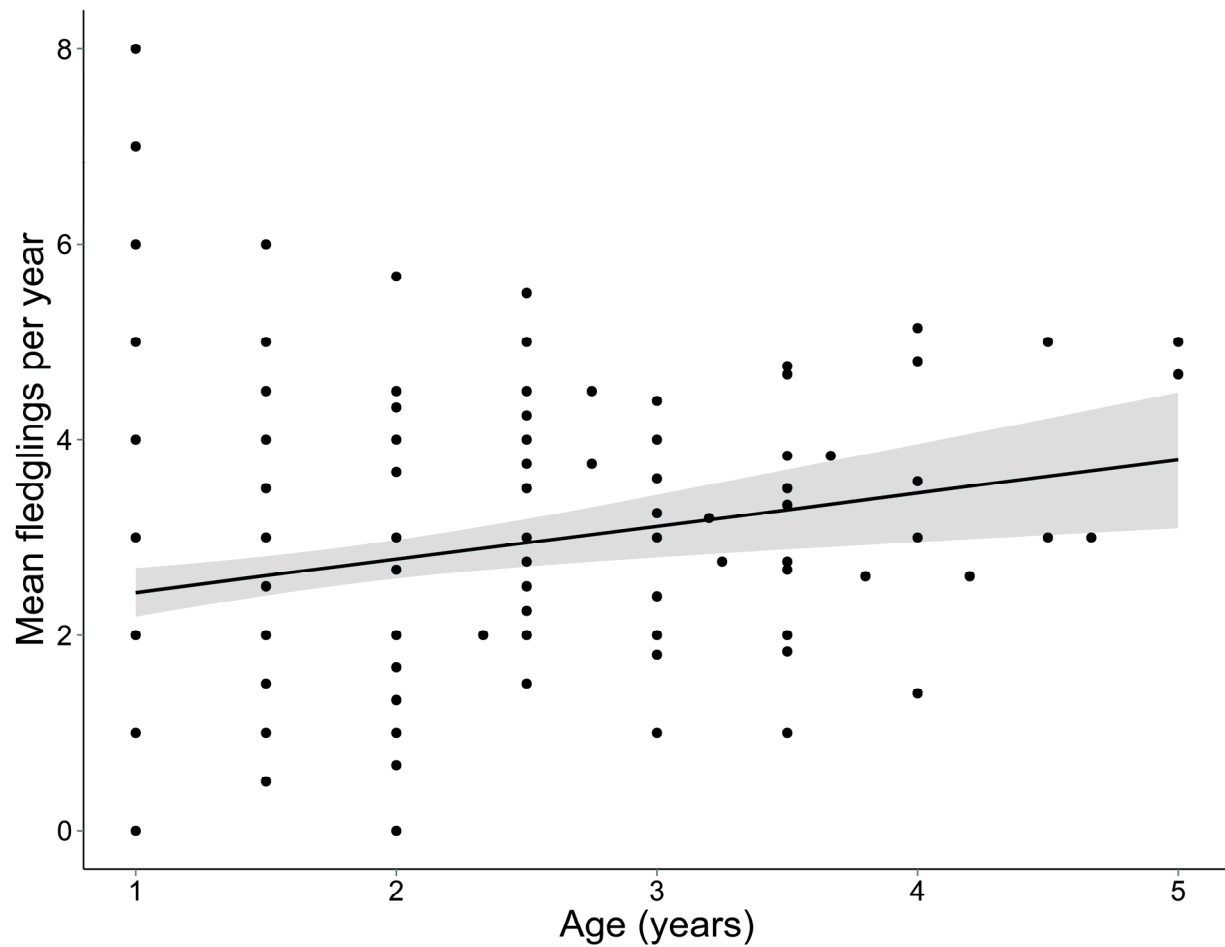
Chapter 3

PLUGGING THE URBAN SINK: SIMULATING METAPOPULATION RESPONSES OF BREEDING WOOD THRUSHES TO CONSERVATION EFFORTS IN URBAN LANDSCAPES

Abstract

Loss of forest habitat to urbanization is a primary cause of forest-breeding songbird population declines; a process that will continue as human dominated landscapes expand. Understanding the relative effects of different mitigation strategies is necessary to stop population declines for sensitive species. I studied the wood thrush (*Hylocichla mustelina*), a declining forest-breeding Neotropical migratory species that is sensitive to urbanization. I used an integrative approach linking 40 years of demographic data with contemporary metapopulation model simulations of breeding wood thrushes to predict population responses to differing conservation scenarios. I compared four conservation scenarios over a 30-year time period (2014 – 2044) representing A) current observed state (null model), B) reduced impervious surface, C) reduced Brown-headed Cowbird (*Molothrus ater*) parasitism pressure, and D) simultaneous reduction in both impervious surface and cowbird pressure. Compared to the null model, the reduced impervious surface scenario increased mean annual population trends by 54 %, the reduced cowbird pressure scenario increased mean annual population trends by 38 %, and the scenario with reductions in both impervious surface and cowbird pressure increased mean annual population trends by 98 %. Mean annual growth rates (λ) per site were greater in models with reductions of impervious surface ($\lambda = 0.94$) and cowbird pressure ($\lambda = 0.92$) compared to the null model ($\lambda = 0.88$). However, only by combining the positive effects of reduced impervious surface and reduced cowbird pressure did wood thrush populations stop declining ($\lambda = 1.00$). These results suggest that independently reducing the proportion of impervious surface around forest patches and cowbird parasitism pressure may slow current negative population trends. However, conservation efforts that combine reductions in impervious surface and cowbird parasitism, at both regional and local scales, respectively, can potentially stabilize populations of breeding

wood thrushes within urbanized fragmented landscapes that typify the mid-Atlantic United

States.

Introduction

Species and the conservation efforts necessary to maintain them, face multiple anthropogenic factors that can negatively affect populations across multiple scales (Jarzyna et al. 2015). Understanding and predicting how populations will respond to regional and local factors is essential for defining priorities and achieving conservation goals (Walsh et al. 2014). Using empirically-based integrated population models (Abadi et al. 2010), predictive site occupancy models (Meineri et al. 2015), and individual-based metapopulation models (Hanski and Ovaskainen 2003) to model the effects of different factors on population dynamics can improve our understanding and predictions of population responses to conservation efforts.

Since 1966, 49 % of Neotropical migratory songbird species have undergone significant population declines (Sauer et al. 2012). Evidence suggests that these populations are negatively affected by a synergy of habitat loss and fragmentation (Hoover et al. 1995, Burke and Nol 2000), which is exacerbated by urbanization (Suarez-Rubio et al. 2011). Preventing continued population declines will require empirically-based models designed to predict how species will respond to conservation efforts across multiple scales (review in Walther et al. 2002, Faaborg 2014). Spatially-explicit metapopulation models and their extensions (e.g., source-sink models) have been successfully used for this problem, particularly in fragmented landscapes (Pulliam 1988, Hanski 1999). Central to these models is the examination of how populations comprised of subpopulations respond to landscape patterns (Hanski and Gaggiotti 2004). The incorporation of habitat sources and sinks into population models expands on the Levins model (1969), emphasizing propagule movement among discrete patches (Pulliam 1988, Hanski 1999). Source-sink models simultaneously considering births, immigration, deaths, and emigration (BIDE; Cohen 1969) represent a shift in emphasis from colonization and extinction of patches by individuals to inter-patch movement through immigration or emigration. Metapopulation

ecology has provided a powerful set of tools for applied conservation (Soulé et al. 1988), and is ideally suited for modeling population responses to anthropogenic stressors such as urbanization, habitat loss, and fragmentation (Kawecki 2004).

At regional scales, wood thrush (*Hylocichla mustelina*) occupancy and abundance are positively related to the extent of forest habitat on the landscape (Smith et al. 2011). Locally, wood thrush breeding density and fecundity are negatively related to human development (e.g., impervious surface; Phillips et al. 2005, Richmond et al. 2012) and nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) (hereafter cowbird) (Hoover et al. 1995). Previous studies of long-term localized wood thrush population demographics (Roth and Johnson 1993, Holmes 2011) and regional source-sink dynamics (Lloyd et al. 2005, Tittler et al. 2006) suggest that multiple-scale approaches should be used to determine critical linkages between population dynamics and the conservation and management of forest ecosystems (Bonnot et al. 2011). I used a long-term demographic study of the wood thrush, a declining forest-breeding migratory songbird, to improve our understanding of how mitigating habitat loss and cowbird parasitism affects population growth thereby reducing population declines.

I constructed a spatially-explicit individual-based model for breeding wood thrushes that assumed heterogeneity among site quality and differential inter-site transition probabilities, to evaluate how landscape and site-level characteristics would influence metapopulation dynamics (Ovaskainen and Hanski 2004). Through the integration of 40 years of demographic information and contemporary site occupancy models, I evaluated population responses to four conservation scenarios and their respective effects on population growth rates of breeding wood thrushes. I predicted that conservation scenarios would have a positive effect on population growth rates. However, I was unsure of the magnitudes of population responses corresponding

to respective conservation scenarios. Here I present a predictive metapopulation model that
evaluates alternative conservation strategies that can be used as a tool in guiding conservation
and management decisions at both regional and local scales.

Methods

Study species and area

The study took place in the mid-Atlantic United States within 21 sites located in18 discrete forest fragments in and around Newark, Delaware, USA (39°41'1N 75°44'58W) (Fig. 1.1 in Chapter 1). Wood thrushes breed in deciduous forest from southeastern Canada throughout the eastern United States and winter in Central America (Evans et al. 2011). Throughout their breeding range, wood thrushes are typically found nesting in under- and mid-story vegetation within forest patches ranging in size from 1 ha to >1000 ha (Keller and Yahner 2007), and often raise two broods per season (Evans et al. 2011). Study area description and site selection details can be found in Chapter 1.

Integrated population model (IPM)

I estimated wood thrush demographic parameters (i.e., adult survival, recruitment, fecundity, and immigration) using an integrated population model (IPM) (Kéry and Schaub 2012, Schaub et al. 2013). I used 40 years (1973 – 2013) of mark-recapture, population census, and fecundity data containing information from 2,592 marked individuals and 1,692 nests collected annually within Ecology Woods (EW; Fig. 1.1 in Chapter 1), a 16-ha forest patch within the study area (Roth and Johnson 1993), to run a female-based, age-structured population model using the R package 'R2WinBUGS' (Sturtz et al. 2005) and WinBUGS (ver. 1.4.3) (Lunn et al. 2000). I used data on cowbird parasitism of wood thrush nests in EW from 1974–2013 to build regression models correlating cowbird parasitism pressure (i.e., mean proportion of parasitized nests and mean number of cowbird eggs per nest) with IPM estimated wood thrush survival, fecundity, and recruitment.

Estimating transition probabilities among sites

To determine transition probabilities among sites, I genotyped individuals using five microsatellite loci and estimated the average relatedness between site pairs. To genotype individuals, I collected blood samples via brachial artery puncture using 27 gauge, 1.27 cm syringes in heparinized capillary tubes (75 µL) according to University of Delaware IACUC regulations, under permit #: 1129-2012-2 (Appendix A). I sealed capillary tubes containing blood with crito-seal clay and stored immediately on ice in the field. I then transferred blood samples to 1.5 mL cryo-vials and stored frozen at -80°C within 2–3 hr of collection. I extracted deoxyribonucleic acid (DNA) from blood samples using Qiagen DNeasy kit (Qiagen, Venlo, Netherlands), and used polymerase chain reaction (PCR) in Bio Rad T100 thermal cyclers (Bio Rad, Hercules, CA, USA) to amplify five neutral polymorphic microsatellite loci, that have been previously used in genetic studies of wood thrushes (Dawson et al. 1997, Gibbs et al. 1999, Evans et al. 2008). I analyzed florescent dye-labeled PCR products at the Delaware Biotechnology Institute using fragment analysis on an ABI Prism 3130XL Genetic Analyzer (Applied Biosystems, Foster City, CA, USA). I then used the program BayesAss (Ranala 2007) to estimate genetic distances and compute transition probabilities of wood thrushes among sites (Wilson et al. 2003). Pair-wise site transition probabilities were then averaged between all site pairings and used to construct a transition matrix (Table 3.1, Appendix C).

Wood thrush occupancy and abundance estimates

To estimate site occupancy and abundance, I conducted fixed-radius point count surveys (Buckland 1987, Ralph et al. 1995) between 30 minutes before and five hours after dawn from 1 May – 15 August 2011—2012 at one central point in each of the 21 sites. I visited all points 5

times every two weeks during each year. To account for observer bias, observers did not visit the same point consecutively. I divided each 10-minute survey into four 2.5 minute intervals, during each of which observers recorded every bird detected within a 100 m radius, and recorded the sex of individuals where discernible, how individual birds were detected (i.e., visual observation, singing bird, or calling bird), and if the bird was detected within 0—50 m or 50—100 m distance bands.

To analyze point count data, I used the 'unmarked' (Fiske and Chandler 2011) package in R (R Core Development Team 2014). I converted raw count data to binomial detections (i.e., 0 or 1) to estimate wood thrush occupancy, fit models using the 'occu' function (MacKenzie et al. 2002), which assumes population closure during the duration of surveys, and included 'year' as a random covariate. These models contained the detection covariate (Julian day) and the following site-level covariates: year, forest patch size (ha), proportion impervious surface within 500 m buffer, proportion of agricultural land cover within 500 m buffer, mean forest site age, mean woody stems, and mean exchangeable soil calcium (Ca) (meq/100 g). I computed the site-level covariates (i.e., forest patch size (ha), proportion impervious surface within 500 m buffer, and proportion of agricultural land cover within 500 m buffer) in ArcMap (ver. 10.1) using the National Land Cover Data (NLCD) 2006 raster data. I compared 11 models to capture the potential influence of both landscape and patch-level covariates on wood thrush patch occupancy (Table 3.2).

I used corrected Akaike's information criterion (AICc) (Akaike 1974, Hurvich and Tsai 1989) with ΔAICc values ≤ 2 as a criterion to compare models predicting wood thrush site occupancy and abundance. I included the detection covariate (Julian day) and the following site-level covariates: year, forest patch size (ha), proportion impervious surface within 500 m buffer,

proportion of agricultural land cover within 500 m buffer, mean forest site age, mean number of woody stems, and mean exchangeable soil calcium (Ca) (meq/100 g) in the models. I compared 11 models to capture the potential influence of both landscape- and patch-level covariates on wood thrush site occupancy.

I estimated wood thrush abundance using point count data (see above) using the package 'unmarked' (Fiske and Chandler 2011) with the function 'pcount' which fits hierarchical N-mixture models to estimate abundance at each point surveyed (Royle 2004). I used the null model to estimate mean wood thrush abundance per hectare. I extrapolated a conservative population estimate to establish the initial conditions for model simulations by multiplying the estimated wood thrush density (i.e., individuals per ha) by the total area (ha) of forest habitat within the study area, and halved this number to effectively relax the assumption of homogeneity of wood thrush distribution on the landscape.

Metapopulation model structure

I modeled wood thrush metapopulation dynamics among 21 discrete sites within the study area and used a 22nd site to represent emigration (i.e., removal from the study area) as a discrete-time Markov process in Mathematica 10.1 (Wolfram Research 2014). This mimicked a stochastic process where the probability of future states of the population were dependent on the current state at a given time step t (Caswell and Cohen 1991, Verboom et al. 1991, Hanski and Ovaskainen 2003). I initialized the model by distributing 400 birds (based on abundance estimates) by observed relative proportions among the 21 sites. At each time step (i.e., years), the number of birds per site (φ_i^t) for all 22 sites, was computed by multiplying the number of birds per site i at time step t by the probabilities of individuals moving between site i and any of

the other sites (Table 3.1, Appendix D), and then subsequently multiplying φ_i^t independently by

adult survival, recruitment, and immigration rates to compute the number of returning adults,

recruited individuals, and immigrants, respectively with the equations:

$$Returns_i^{t+1} = \varphi_i^t \times P(\text{adult survival}_i^t) \tag{1}$$

$$Recruits_i^{t+1} = \varphi_i^t \times P(\text{recruitment}_i^t) \tag{2}$$

$$Immigrants_i^{t+1} = \varphi_i^t \times \text{proportion of immigrants}_i^t \tag{3}$$

where φ_i^t is the number of birds in site i and $P(\text{adult survival}_i^t)$, $P(\text{recruitment}_i^t)$, and

proportion of immigrants$_i^t$ were estimated for each site i at each time step t, by randomly

drawing values from uniform distributions with means and 95 % CIs taken from IPM-estimated

means for adult survival, recruitment, and immigration rates from 2002–2012. I defined

recruited individuals in the model as birds that were born in and returned to the study area as

sexually mature (i.e., ≥ 1 year old). For each of 22 sites, the total number of birds at time ($t + 1$)

was computed with the equation:

$$N^{t+1} = \sum_{i=1}^{\text{\# sites}} \begin{pmatrix} Returns_i^{t+1} + Recruits_i^{t+1} + \\ Immigrants_i^{t+1} \end{pmatrix} \tag{4}$$

I computed the annual growth rate lambda (λ_i) within each site i with the equation:

$$\lambda_i = \frac{N_i^{t+1}}{N_i^t} \tag{5}$$

where N_i^{t+1} and N_i^t are the total number of birds per site i (from Equation 4) at time step $(t +$ 1) and t, respectively. To estimate metapopulation annual growth rate (λ) for each model scenario, I summed the number of birds across 21 sites at each time step (Equation 4), and divided the total number of birds in the study area at time step (N^{t+1}) by the total number of birds from the previous time step (N^t). I calculated mean annual growth rates (λ_i) per year at each site i before averaging across 21 sites (excluding emigrants in site 22) for each ensemble of 10,000 model iterations. I calculated the probability of lambda ($\lambda_i \geq 1$) for each model scenario by tallying the number of sites where the local annual growth rate was equal to or greater than 1 at each time step and dividing by the total number of sites. I estimated population trends (mean % annual change) for each model scenario using the equation:

$$r = log\left(\frac{Ne}{No}\right) \times \frac{100}{T}$$
(6)

where N_e is the number of birds at the end time step, N_o is the number of birds at the initial time step (t_o), and T is the total number of years the model is run for. I also estimated mean annual site occupancy by dividing the number of occupied sites per year (defined as having at least two individuals) by the number of years.

I simulated four conservation scenarios by varying model parameters using regression functions that represented Scenario A) the null model, akin to no conservation efforts under current observed conditions, Scenario B) reductions in the proportion of impervious surface, Scenario C) reduced cowbird parasitism pressure, and Scenario D) coincident reductions in both impervious surface and cowbird parasitism.

Metapopulation model scenario descriptions

Scenario A: Null model

Null model parameters were independently estimated for each site by randomly sampling from uniform distributions constrained by upper and lower 95 % CI around the means of IPM annual estimates from 2002—2012 in EW for adult survival, recruitment, and fecundity (i.e., number of fledglings per female). Similarly, I estimated the proportion of immigrants at each time step (held equal across all sites) by randomly drawing from a uniform distribution with a mean and SD taken from IPM estimates. To model current observed conditions within the study area, I limited breeding (i.e., fecundity = 0), and allowed fewer immigrants (i.e., 1 % of total birds per site) to enter initially unoccupied patches at (t_o), while allowing birds full immigration into currently occupied sites with currently observed fecundity.

Scenario B: Reduced impervious surface

I modeled the effect of reducing the proportion of impervious surface on wood thrush metapopulation dynamics by nearly doubling the annual mean proportion of immigrants and allowing 90 % of immigrants to enter into and effectively breed (i.e., no reduction of fecundity) in previously unoccupied sites in response to concomitant reductions in impervious surface from ca. 0.8 (null model) to around 0.05 using a predictive site occupancy model from the R package 'unmarked' (Fiske and Chandler 2011). Adult survival, recruitment, and fecundity were all estimated using the methods described above for the null model.

Scenario C: Reduced cowbird parasitism pressure

I modeled a reduction in cowbird parasitism pressure using beta regression models to increase the probability of adult survival corresponding to a reduction in the proportion of cowbird nests parasitized from 0.65 (current observed parasitism rate) to range between (0.25—0.0). I estimated and increased mean fecundity (i.e., number of fledglings per female) from 0.97 (current observed fecundity) to 1.19 using a linear model representing a reduction of the mean cowbird eggs laid per nest. I additionally increased mean recruitment based on the linear model relationship between the proportion of cowbird parasitized nests and annual number of recruited individuals. In this model, immigration probabilities and fecundity in initially unoccupied sites were the same as in the null model.

Scenario D: Combined reduced impervious surface and cowbird pressure

I modeled the simultaneous effects of reducing impervious surface and cowbird parasitism pressure by using regression-based models to estimate according increases in immigration probabilities to all sites, and allowed breeding in all sites (as described in the reduced impervious surface model above). Under this model scenario, I used parameters estimated for adult survival, fecundity, and recruitment following the methods described above for the reduced cowbird parasitism model, and immigration probabilities were estimated as a function of reduced impervious surface (as stated above).

All model simulations were run for 30 years into the future with a $P(\text{emigration}_i^t) =$ 0.03 held constant for all sites. I simulated each scenario 10,000 times to account for the

stochastic nature of the model. All model simulations started from an initial distribution of birds across sites following the observed distribution of birds (i.e., from this study 2011—2013) among 13 known occupied sites within the study area, and 9 empty sites (including the idealized 22nd site representing emigration). After testing all data for departures from normality with a Shapiro-Wilk test, I used one-way analysis of variance (ANOVA) with Tukey's post-hoc tests to test for differences in population trend, mean annual growth rate (λ), and mean site occupancy among the four model scenarios.

Relating impervious surface and cowbird parasitism pressure to annual growth rate (λ)

I used Equations 1–3 to convert the simulated site occupancy, adult survival, and fecundity to the proportion of impervious surface, proportion of parasitized nests, and mean cowbird eggs laid per nest, respectively. I multiplied the proportion of parasitized nests by mean cowbird eggs laid to derive a parasitism pressure index (hereafter, cowbird index). I calculated mean estimates for impervious surface, cowbird index, and lambda by site (λ_i) for each model scenario.

Results

IPM model results

I used IPM-derived population estimates (Fig. 3.1), annual adult survival and recruitment (Fig. 3.2), fecundity (Fig. 3.3), and immigration rates (Fig. 3.4) for wood thrushes in EW from 1974—2013 to build regression models relating demographic estimates and quantified cowbird parasitism rates and mean eggs per nest (Fig. 3.5). I computed contemporary demographic parameters (mean ± SD) to simulate metapopulation dynamics over a 30-year time period (2014–2044), by averaging ten years of IPM annual estimates from 2002—2012 for adult survival, fecundity, recruitment, and immigration (Table 3.3). The proportion of parasitized wood thrush nests (mean ± SD) increased by over 400 % between the periods of 1974—1984 and 2002—2012 (Fig. 3.2). Beta regression and a subsequent likelihood ratio test in the R packages 'betareg' (Zeileis et al. 2013) and 'lmtest' (Hothorn et al. 2014), respectively, showed that parasitism was positively related to years ($\chi^2 = 22.3$, df $= 3$, $P < 0.001$) (Fig. 3.5).

Transition matrix

I estimated transition probabilities among sites inferred from probabilities of relatedness using microsatellite data from 177 genotyped adult wood thrushes sampled from 13 discrete sites (see Appendix C). The final normalized transition matrix contained estimated transition probabilities from the 13 sampled sites, transition probabilities of 0.008 and 0.85 for leaving and remaining in a site, respectively for the 8 initially unoccupied sites, and a 22nd site with a transition probability of 0.03 representing emigration out of the study area (Appendix D).

Occupancy model selection results

The impervious surface model explained 62 % of the variation in these data as indicated by AICc model comparison (Table 3.4). Site occupancy was negatively related to the proportion of impervious surface within a 500 m buffer around forest sites (Fig 6A), and differed from the null model according to the likelihood ratio test (Kent 1982) ($\chi^2 = 11.6$, df = 1, $P < 0.01$). From the significant correlation between impervious surface within a 500 m buffer around sites and wood thrush site occupancy, I derived the equation:

$$logit \; (y) = -1.31x + 1.01$$

(7)

representing the predicted probability of patch occupancy (y) given the proportion of impervious surface (x) within a 500 m buffer around a forest patch (Fig. 3.6A). I estimated mean immigration probability to sites (0.41 ± 0.01) for a corresponding reduction of the proportion of impervious surface to 0.05 in model scenarios simulating reductions in impervious surface around forest sites (Table 3.3).

Regression model results

The proportion of cowbird parasitized wood thrush nests (mean ± SD) increased over 400 % from 1974—1984 (0.13 ± 0.14) to 2002—2012 (0.65 ± 0.16) in EW (Fig. 3.5). Beta regression and a subsequent likelihood ratio test in the R packages 'betareg' (Zeileis et al. 2013) and 'lrtest' (Fox 2014), respectively, showed that parasitism was positively related to years ($X^2 = 22.3$, df = 3, $P < 0.001$) (Fig. 3.5). Beta regression and a likelihood ratio test revealed that the annual probability of adult wood thrush survival from 1974—2012 was negatively related the proportion

of cowbird parasitized nests ($X^2 = 80.1$, df $= 3$, $P < 0.01$) (Fig. 3.6B). I inferred the following

equation from the beta regression model:

$$logit\,(y) = -0.24x + 0.067$$

(8)

where y is annual adult survival and x is the proportion of cowbird parasitized wood thrush

nests, to estimate a mean adult survival (0.51 ± 0.01) corresponding to a reduction in the

proportion of parasitized nests by 62 % for simulating reduced cowbird parasitism (Table 3.3). I

used linear regression in the 'stats' R package and found that wood thrush annual fecundity (i.e.,

number of offspring produced per female) was negatively related to mean cowbird eggs laid per

nest ($F = 9.72$, df $= 37$, $P < 0.01$) (Fig. 3.6C). With the governing linear regression equation:

$$y = -0.25x + 1.25$$

(9)

where y is predicted wood thrush fecundity and x is the mean cowbird eggs laid per nest, I

estimated a mean fecundity (1.19 ± 0.04) given a reduction in the mean number of cowbird eggs

per nest from 1.18 (2002—2012 mean) to 0.5 in model scenarios with reduced cowbird

parasitism pressure (Table 3.3). Linear regression also indicated that simulations involving the

mean number of recruited wood thrushes annually in EW was negatively related to the

proportion of cowbird parasitized wood thrush nests ($F = 5.61$, df $= 37$, $P < 0.05$) (Fig. 3.6D).

The following linear model equation:

$$y = -1.37x + 1.57$$

(10)

where y is the number of recruited birds and x is proportion of cowbird parasitized nests was

subsequently used to estimate the mean number of recruited individuals related to reductions in

the proportion of parasitized nests in model simulations. I simulated increases in annual wood

thrush recruitment rates by randomly drawing values from a uniform distribution with mean and SD of 0.085 ± 0.01 (Table 3.3).

Metapopulation simulation results

I used ANOVA and subsequent post-hoc tests and found that metapopulation annual growth rates (λ) (mean ± SD) differed among all model scenarios (F = 567.1, df = 3, P < 0.001) (Table 3.5), and were lowest for Scenario A (0.88 ± 0.01) after 30 years (Table 3.5, Fig. 3.7). The annual growth rate for Scenario C (0.92 ± 0.02) was lower than in Scenario B (0.94 ± 0.01), and both were lower than Scenario D (1.0 ± 0.01) (Table 3.5).

I found differences in annual growth rates per site (λ_i) (mean ± SD) among model scenarios (F = 46.3, df = 3, P < 0.001) (Table 3.5). Tukey's post-hoc tests showed that mean growth rates per site for Scenario A (0.92 ± 0.03) were lower than all other scenarios, and mean growth rate per site for Scenario C (0.99 ± 0.04) was lower than both Scenarios B (1.02 ± 0.06), and D (1.05 ± 0.08) (Table 3.5). Besides, I found that the probability that site-level mean annual growth rates (λ_i) were greater than 1 over the 30-year simulation period was lower for Scenario A (0.06 ± 0.05) compared to Scenarios C, B, and D (0.33 ± 0.26, 0.52 ± 0.08, and 0.89 ± 0.2, respectively) (Table 3.5, Fig. 3.7).

I used ANOVA in R (R Core Development Team 2014) and found that annual population trend estimates (mean ± SE) differed among the four model scenarios (F = 61.1, df = 3, P < 0.001) (Table 3.6). Trend estimates were lower for Scenario A (-11.7 ± 0.40) compared to all other scenarios, and both Scenario C (-5.68 ± 0.65) and B (-3.79 ± 0.87), were lower than Scenario D (1.92 ± 0.85) (Table 3.6).

I compared mean proportions of occupied sites (χ^2, df = 3, 7.815) with multiple pair-wise comparisons between model scenarios (Marascuilo 1966) and found site occupancy for Scenario A (0.42 ± 0.36) to be independent of Scenarios B and D (0.98 ± 0.17, for both models), but not of Scenario C (0.67 ± 0.36). Comparisons indicated that both proportions of site occupancy for Scenarios B and C were independent of each other, and Scenarios C and D were independent of one another. However, I found no such independence between Scenarios B and D (Table 3.5).

Correlations of model parameters to annual growth rate (λ)

I found that for Scenario A the number of immigrants ($R^2 = 0.39$), number of recruited individuals ($R^2 = 0.39$), and number of returning adults ($R^2 = 0.34$) were all correlated with annual growth rate (λ) ($r = 0.63, 0.63$, and 0.58, respectively with $P < 0.001$ in all cases; Table 3.7). In Scenario B, number of immigrants ($R^2 = 0.16$) was correlated with annual growth rate (λ) ($r = 0.39$, $P < 0.05$; Table 3.7). In Scenario C, the number of immigrants ($R^2 = 0.53$), number of recruited individuals ($R^2 = 0.53$), and the number of returning adults ($R^2 = 0.46$) were all significantly correlated with annual growth rate (λ) ($r = 0.73, 0.73$, and 0.68, respectively with $P < 0.001$ in all cases). In Scenario D, the number of immigrants ($R^2 = 0.20$) and number of emigrants ($R^2 = 0.94$), were both correlated with annual growth rate (λ) ($r = 0.45$, and - 0.97, respectively with $P < 0.05$ in both cases; Table 3.7).

Relating impervious surface and cowbird parasitism pressure to annual growth rate (λ)

The relationship of combinations of proportions of impervious surface (ranging from 0–0.35) and cowbird index (ranging between 0–0.5) to mean annual growth rate per site (λ_i) is shown in Fig. 3.8. Mean annual growth rate (λ_i) was lowest (< 0.94) when both impervious surface and

cowbird index increased to 0.35 and 0.5, respectively (Fig. 3.8). Annual growth rate was stable

(i.e., $\lambda_i = 1$) between 0.05–0.15 impervious surface over the range of cowbird index values, and

mean annual growth rate was positive ($\lambda_i > 1$) between 0.02–0.10 impervious surface over the

range of cowbird index values (Fig. 3.8).

Discussion

Conservation scenarios had a positive effect on Wood Thrush population growth rates. These results suggest that coincident reductions of the proportion of impervious surface on the landscape and cowbird parasitism pressure locally (Scenario D), would benefit increasing wood thrush population growth rates. Although both conservation measures (Scenarios B and C) had positive effects on wood thrush population growth, they were insufficient to stabilize population growth when implemented individually. I think wood thrush conservation efforts of in the New England/mid-Atlantic region should combine local and regional strategies to reduce current rates of regional population declines and stabilize the population.

The implementation plan for the New England/mid-Atlantic Coast Bird Conservation Region 30 (BCR 30; characterized by a highly developed landscape), has identified habitat loss, degradation, and fragmentation as the greatest threat to bird species, and has designated the wood thrush as a species of "Highest Priority" with a regional population estimate 1/3 lower than objective goals (Atlantic Coast Joint Venture 2012). I estimated that 23 % of all forest habitat within BCR 30 (590,794 ha), is contained in forest fragments ≤ 20 ha that can provide valuable breeding and stopover habitat for the wood thrush and other forest-breeding Neotropical migrants. Given observed wood thrush occupancy across a range of patch sizes (Keller & Yahner 2007, MacIntosh et al. 2011), I think that solely focusing conservation efforts on larger forest patches and discounting forest patches ≤ 20 ha, would be a mistake in attempting to achieve the stated population goals for the wood thrush in BCR 30.

We compared population trends among model scenarios and 40 years of empirical data from EW (-2.79 % per year), which were similar to Breeding Bird Survey (BBS) route regression trend estimates from data from 1966–2012 for the New England/mid-Atlantic Coast (-2.77 % per year) and the state of Delaware (-2.1 % per year) (Sauer et al. 2012). However, more

recent trends from 2002–2012 have decreased to -8.42 % per year in EW, and to -3.73 % per year, and -10.52 % per year for BBS trends from New England/mid-Atlantic Coast and Delaware, respectively (Sauer et al. 2012). *In silico* population trends for simulations 30 years into the future were also similar for Scenario A in EW (-11.5 % per year), and for the overall study area (-12.8 % per year). Continuity among regional BBS, locally observed, and *in silico* population trends implies that our model was accurately calibrated, providing confidence in simulated population-trend estimates under modeled conservation scenarios. Given the disparity among growth rates throughout the breeding range (Sauer et al. 2012), conservation efforts for the Wood Thrush should address both regional and local factors that drive source-sink dynamics, and implement strategies aimed at creating, promoting, and sustaining source habitats (Keagy et al. 2005).

The proportion of impervious surface on the landscape can have profound effects on watersheds, ecosystems, habitat quality, and species occurrence and dispersal (Kaplan & Ayers 2001). Clear links between proportion of impervious surface and human development has been documented as a leading stressor on landbird community structure (Donnelly & Marzluff 2006, Schlesinger et al. 2008), abundance (Lussier et al. 2006), and dispersal (Whittaker & Marzluff 2012). The potential negative effects of urbanization and increasing proportion of impervious surface on wood thrushes within our study area seems to be an important driver of site occupancy (Longcore & Jones 1969, Roth & Johnson 1993, this study). My *in silico* experiments suggest that by reducing the proportion of impervious surface from 0.60 (in Scenario A) to 0.05 (Scenarios B and D), we could expect an 88.5 % increase in the probability of ($\lambda \geq 1$) resulting in positive annual growth, and a 57 % increase in site occupancy. I found

that mean annual growth rate per site ($\lambda_i \geq 1$) was below an upper threshold for the proportion of impervious surface within a 500 m buffer around sites of 0.17 (Fig. 3.4).

Cowbird parasitism can have negative effects on host songbird species by reducing fecundity and thereby contributing to population-level declines (Mayfield 1977, Kilpatrick 2002). Our simulation of reduced parasitism pressure showed that reducing the mean proportion of parasitized nests within the study area from 0.65 (Scenario A) to between 0.25—0.0 (Scenario C), resulted in a 4.3 % increase in overall annual growth rate (λ) for the metapopulation, a 7.1 % increase in mean annual growth rates per site (λ_i), and an 82 % increase in the probability that λ ≥ 1. Additionally, I observed a 37 % increase in site occupancy under Scenario C. Given the increasing population trend for cowbirds between 2002–2012 in the New England/mid-Atlantic (1.2 % per year; Sauer et al. 2012) and the demonstrated efficacy of removing cowbirds and benefits to host populations (e.g., Kirtland's warblers (*Dendroica kirtlandii*); Siegle & Ahlers 2004, McLeod & Koronkiewicz 2014), I propose that cowbird removal be tested at a local scale to evaluate model predictions. For example, we found the index of cowbird parasitism was inversely related to mean annual growth rate.

My simulations of wood thrush population responses to reductions in impervious surface and cowbird parasitism pressure could be used as a predictive tool (e.g., Fig. 3.4) to estimate growth rates for known combinations of impervious surface and parasitism rates. I held transition probabilities constant over time, so our metapopulation model does not specifically account for other potentially contributing factors to wood thrush breeding population dynamics, and they simplify variation in habitat quality among our sites within the metapopulation framework. Future models could improve these shortcomings by modifying transition probabilities and emigration rates through time according to predicted changes in habitat quality.

Predicting bird population responses to future land-use change (Martinuzzi et al. 2015), and mitigation of negative effects of urbanization using sustainable landscape planning tools (Mason et al. 2007, Lerman et al. 2014, Gagné et al. 2015) will be paramount for the successful conservation of Wood Thrushes and other declining Neotropical migrants. Based on these findings through the integration of long-term demographic, predictive occupancy, and metapopulation models, I recommend that conservation strategies for breeding wood thrushes in the New England/mid-Atlantic coastal region focus on reducing both negative effects of cowbirds and impervious surface across spatial scales.

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Tables

Table 3.1. Example transition matrix containing probabilities of dispersal movement (Θ) among 21 discrete forest patches and functional emigration (ε) from the study area.

Patch	1	2	3	$\cdots$	21	ε
1	$\Theta_{1,1}$	$\Theta_{2,1}$	$\Theta_{3,1}$	$\cdots$	$\Theta_{21,1}$	ε_1
2	$\Theta_{1,2}$	$\Theta_{2,2}$	$\Theta_{3,2}$	$\cdots$	$\Theta_{21,2}$	ε_2
3	$\Theta_{1,3}$	$\Theta_{2,3}$	$\Theta_{3,3}$	$\cdots$	$\Theta_{21,3}$	ε_3
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\ddots$	$\vdots$	$\vdots$
21	$\Theta_{1,21}$	$\Theta_{2,21}$	$\Theta_{3,21}$	$\cdots$	$\Theta_{21,21}$	ε_{21}
ε	0	0	0	...	0	1

Table 3.2. List of occupancy models and covariates used to determine covariates affecting the probability of wood thrush patch occupancy within the study area in and near Newark, Delaware, USA.

Model	Covariates (~ detection ~ site-level)
Null	occu (~ 1 ~ 1)
Day	occu (~ day ~ 1)
Year	occu (~ 1 ~ year)
Landscape	occu (~ 1 ~ patch area + impervious surface + agriculture)
Patch area	occu (~ 1 ~ patch area)
Impervious surface	occu (~ 1 ~ impervious surface)
Agriculture	occu (~ 1 ~ agriculture)
Mean stand age	occu (~ 1 ~ tree core mean)
Vegetation	occu (~ 1 ~ mean woody stems)
Soil calcium	occu (~ 1 ~ exchangeable Ca)
Global	occu (~ day ~ year + exchangeable Ca + mean woody stems + tree core mean + patch area + impervious surface + agriculture)

Table 3.3. Parameter estimate means (SD) used in four metapopulation model scenarios for wood thrushes breeding in small urban forest fragments.

	Models			
Model parameter	Null	Reduce impervious surface	Reduce cowbirds	Reduce impervious surface & cowbirds
Adult survival	0.49 (0.03)	0.49 (0.03)	0.51 (0.01)	0.51 (0.01)
Recruitment	0.06 (0.003)	0.06 (0.003)	0.085 (0.01)	0.085 (0.01)
Fecundity	0.97 (0.29)	0.97 (0.29)	1.19 (0.04)	1.19 (0.04)
Immigration	0.23 (0.01)	0.41 (0.01)	0.23 (0.01)	0.41 (0.01)

Table 3.4. Occupancy model comparison based on AICc ranking using the R package 'unmarked' for 11 models.

Model	n Parameters	AICc	delta	AIC weight	Cumulative weight
Impervious surface	3	227.8	0	0.6237	0.62
Mean stand age	3	230.1	2.34	0.1936	0.82
Landscape	5	231.8	3.99	0.0848	0.90
Patch area	3	232.4	4.64	0.0613	0.96
Global	10	235.6	7.79	0.0127	0.98
Agriculture	3	237.1	9.30	0.006	0.98
Null	2	237.4	9.59	0.0052	0.99
Soil calcium	3	237.6	9.88	0.0045	0.99
Vegetation	3	237.7	9.93	0.0044	1
Year	3	239.2	11.47	0.002	1
Day	3	239.3	11.57	0.0019	1

Table 3.5. Model estimated means (SD) for metapopulation lambda (λ), lambda per site (λ_i), probability $\lambda \geq 1$, annual population trend (%), and the proportion of occupied patches for four model scenarios.

	Models			
Model derived estimates	Null	Reduce impervious surface	Reduce cowbirds	Reduce impervious surface & cowbirds
Metapopulation lambda (λ)	0.88 (0.01)	0.94 (0.01)	0.92 (0.02)	1.00 (0.01)
Lambda per site (λ_i)	0.92 (0.03)	1.02 (0.06)	0.99 (0.04)	1.05 (0.08)
Prob ($\lambda \geq 1$)	0.06 (0.05)	0.52 (0.08)	0.33 (0.26)	0.89 (0.2)
Metapopulation trend	-12.8 (1.15)	-5.93 (0.30)	-7.92 (0.68)	-0.32 (0.21)
Population trend per site	-11.7 (1.84)	-3.79 (3.98)	-5.68 (2.96)	1.92 (3.90)
Proportion of occupied sites	0.42 (0.36)	0.98 (0.17)	0.67 (0.36)	0.98 (0.17)

Table 3.6. Annual population trend estimates by site that show comparisons among four model scenarios representing responses of breeding wood thrushes to differing conservation scenarios.

Site name	Site abbreviation	Model			
		Null	Reduce impervious surface	Reduce cowbirds	Reduce impervious surface & cowbirds
Christina Creek 1	CC1	-11.3	0.3	-2.8	6.0
Christina Creek 2	CC2	-11.8	-3.0	-5.0	2.6
Chrysler Woods	CW	-11.4	0.3	-2.9	5.9
Coverdale	CD	-10.8	0.3	-2.9	5.9
Dorothy Miller	DM	-11.6	0.2	-2.8	5.8
Ecology Woods	EW	-11.5	-6.4	-7.2	-0.6
Folk	FO	-14.1	-9.0	-9.7	-3.2
Glasgow 1	GG1	-10.8	0.2	-3.0	5.9
Glasgow 2	GG2	-11.1	-5.9	-6.8	-0.1
Iron Hill 1	IH1	-14.4	-9.4	-10.2	-3.7
Iron Hill 2	IH2	-14.3	-9.2	-9.9	-3.4
Laird	LA	-11.8	0.5	-2.9	6.0
Motor Pool	MP	-8.1	-2.7	-3.6	3.2
Phillips	PH	-10.9	0.5	-3.1	5.9
Reservoir	RE	-10.4	-5.3	-6.3	0.5
Rittenhouse	RH	-11.5	-6.5	-7.4	-0.6
Sunset Lake 1	SL1	-11.2	0.3	-3.0	5.9
Sunset Lake 2	SL2	-8.3	-3.4	-4.2	2.5
Webb Farm	WF	-10.8	-2.1	-4.6	3.5
White Clay Creek 1	WC1	-14.5	-9.5	-10.2	-3.6
White Clay Creek 2	WC2	-14.9	-9.8	-10.6	-4.1

Table 3.7. Linear model-based correlations (R-squared values) of metapopulation model estimates to lambda (λ). Greatest correlations for each model scenario are indicated in bold.

Parameter correlation with lambda (λ)	Models			
	Null	Reduce impervious surface	Reduce cowbirds	Reduce impervious surface & cowbirds
Number of immigrants	0.39*	**0.16***	**0.53***	0.20*
Number of emigrants	0.07	0.01	0.13	**0.94***
Number of recruited	**0.40***	0.13	**0.53***	0.0001
Number of returns	0.34*	0.13	0.46*	0.0001
Adult survival	0.003	0.0004	0.0004	0.023
Fecundity	0.04	0.09	0.01	0.01
Mean recruitment	0.07	0.10	0.004	0.01

*Pearson correlation P value ≤ 0.05

Figures

Figure 3.1. Annual population estimates (mean ± SD) of breeding female wood thrushes showing annual counts (gray dashed line) and integrated population model (IPM) estimates (solid black line) from 1974–2013 in Ecology Woods (EW) in and near Newark, Delaware, USA.
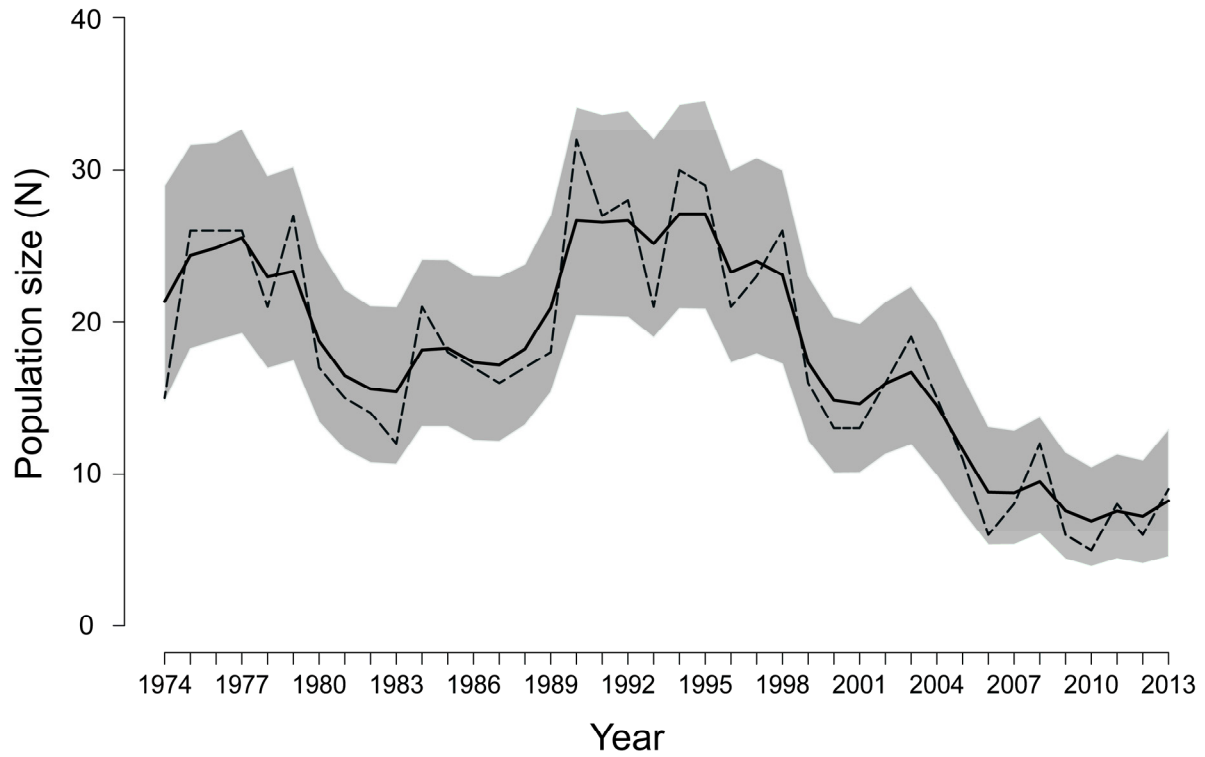
Figure 3.2. Estimated annual survival probabilities (mean ± SD) for adult female (open circles) and recruited (filled circles) wood thrushes from 1974–2013 in Ecology Woods (EW) in and near Newark, Delaware, USA. Overall mean and 95 % CI are shown by dark gray dashed lines.
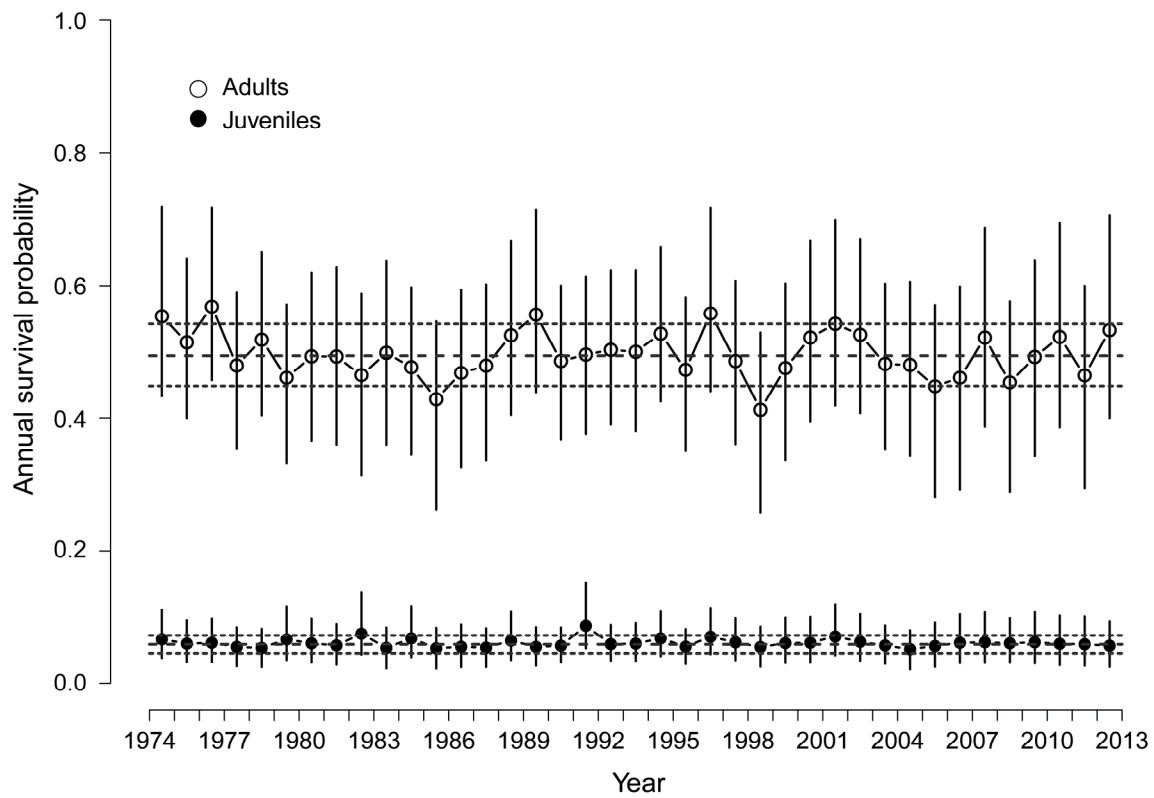
Figure 3.3. Estimated annual fecundity (i.e., number of fledglings per female) (mean ± SD) for
from 1974–2013 in Ecology Woods (EW) in and near Newark, Delaware, USA. Overall mean
and 95 % CI are shown by dark gray dashed lines.
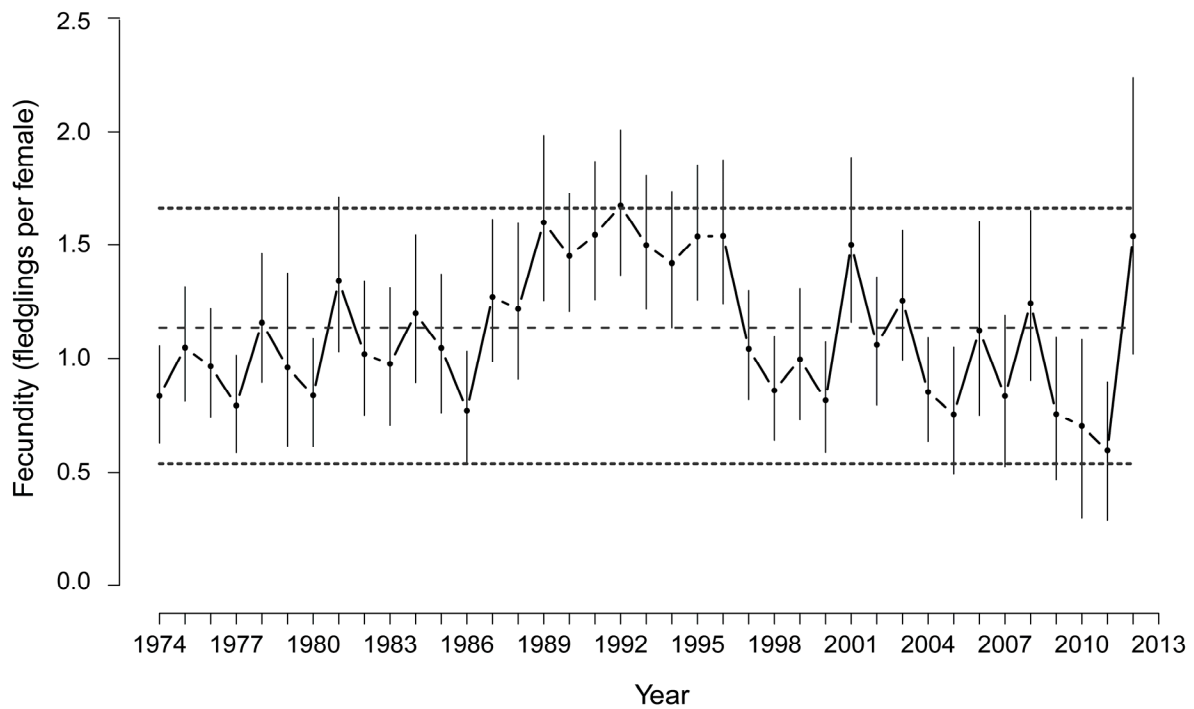
Figure 3.4. Estimated annual proportion of immigrants (mean ± SD) for adult female wood thrushes from 1974–2013 in Ecology Woods (EW) in and near Newark, Delaware, USA. Overall mean and 95 % CI are shown by dark gray dashed lines.
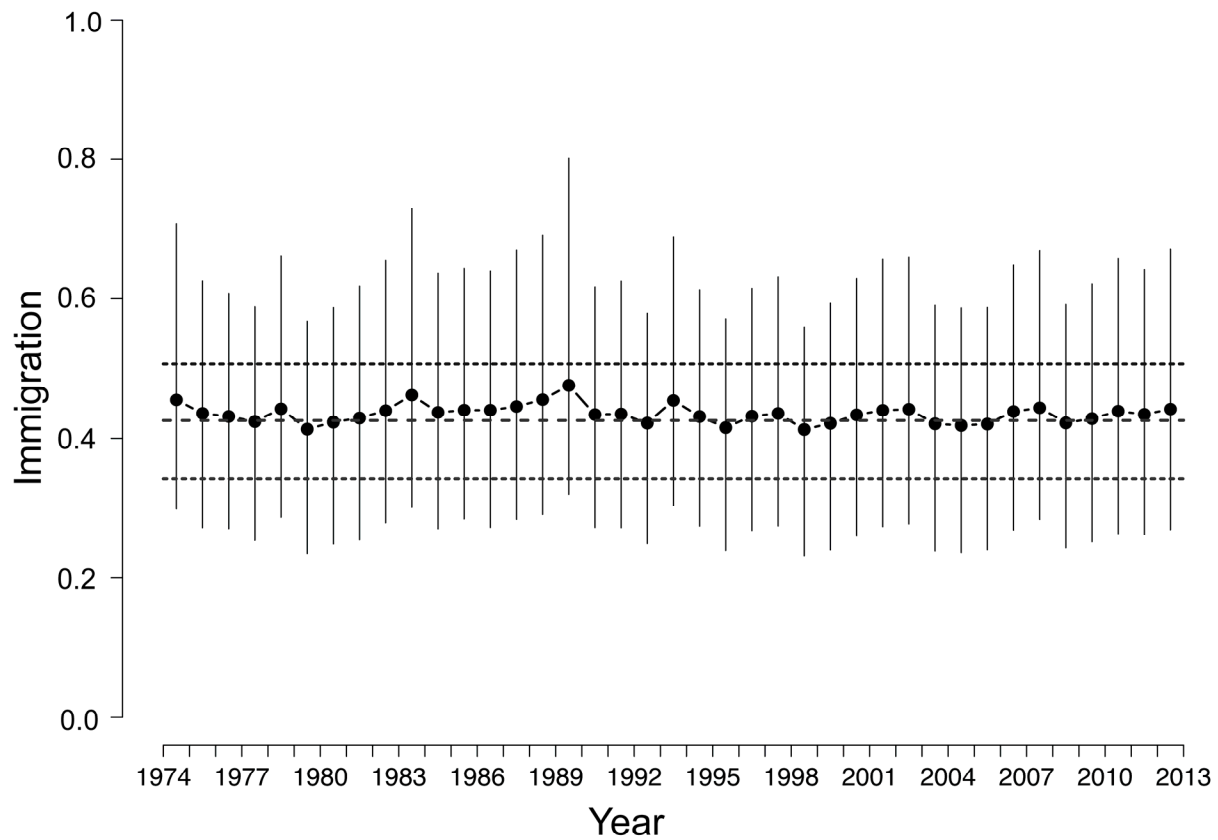
Figure 3.5. Beta regression model showing the rate of increase in the proportion of cowbird parasitized wood thrush nests from 1974–2012 in Ecology Woods (EW) in and near Newark, Delaware, USA.
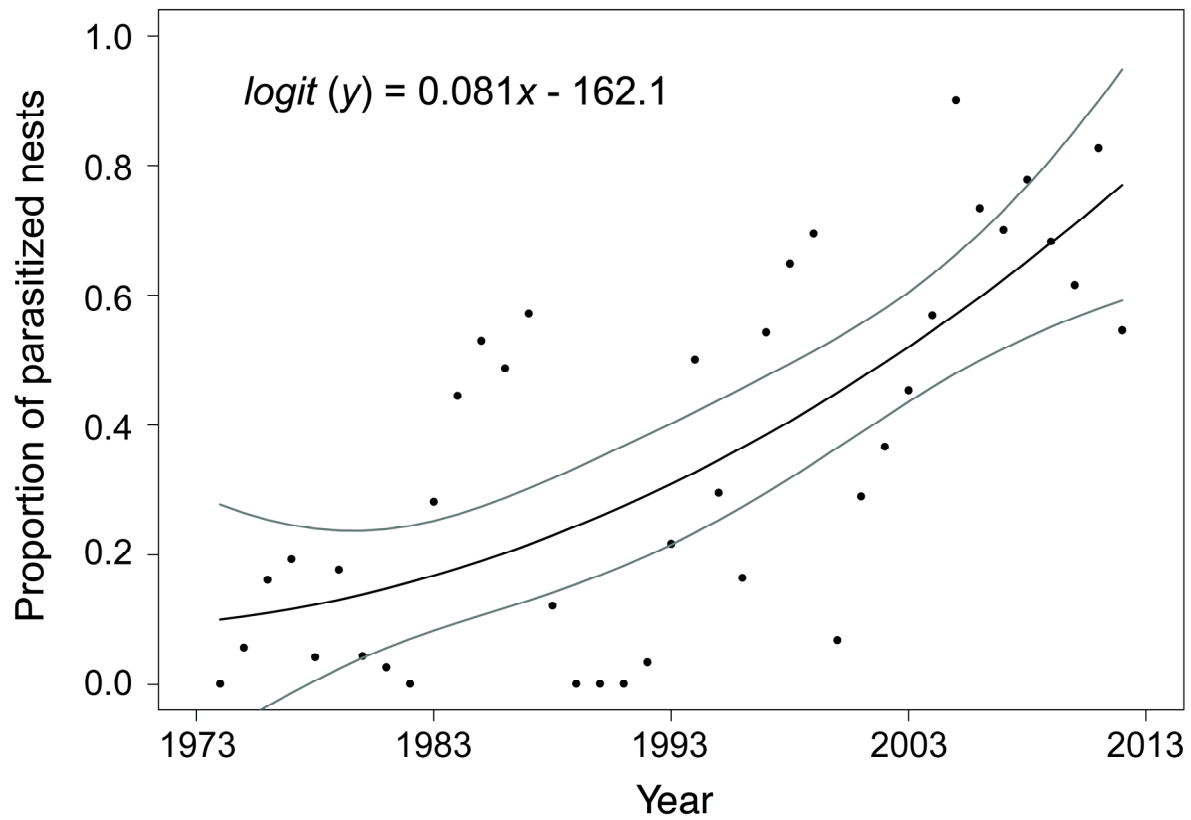
Figure 3.6. Regression models showing relationships between A) proportion of impervious surface (within 500 m patch buffer) and patch occupancy, B) proportion of cowbird parasitized nests and adult wood thrush survival, C) mean cowbird eggs laid per nest and wood thrush fecundity (mean fledglings per female), and D) proportion of cowbird parasitized nests and mean number of recruited individuals per year.
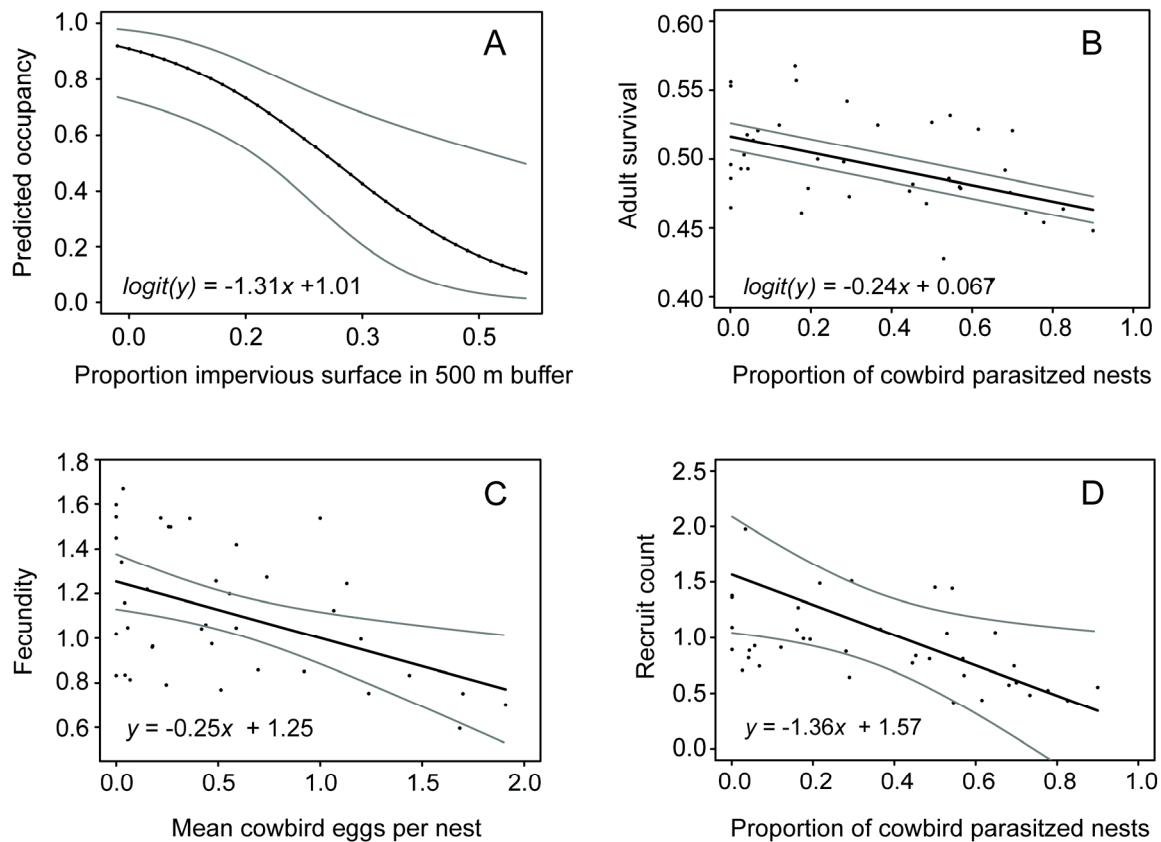
Figure 3.7. Wood thrush population size (N) estimates (mean and 95 % CI) over a 30 year period under four model scenarios: A) null (light gray), B) reduce impervious surface (dark gray), C) reduce cowbirds (gray), and D) reduce impervious surface and cowbirds (black).
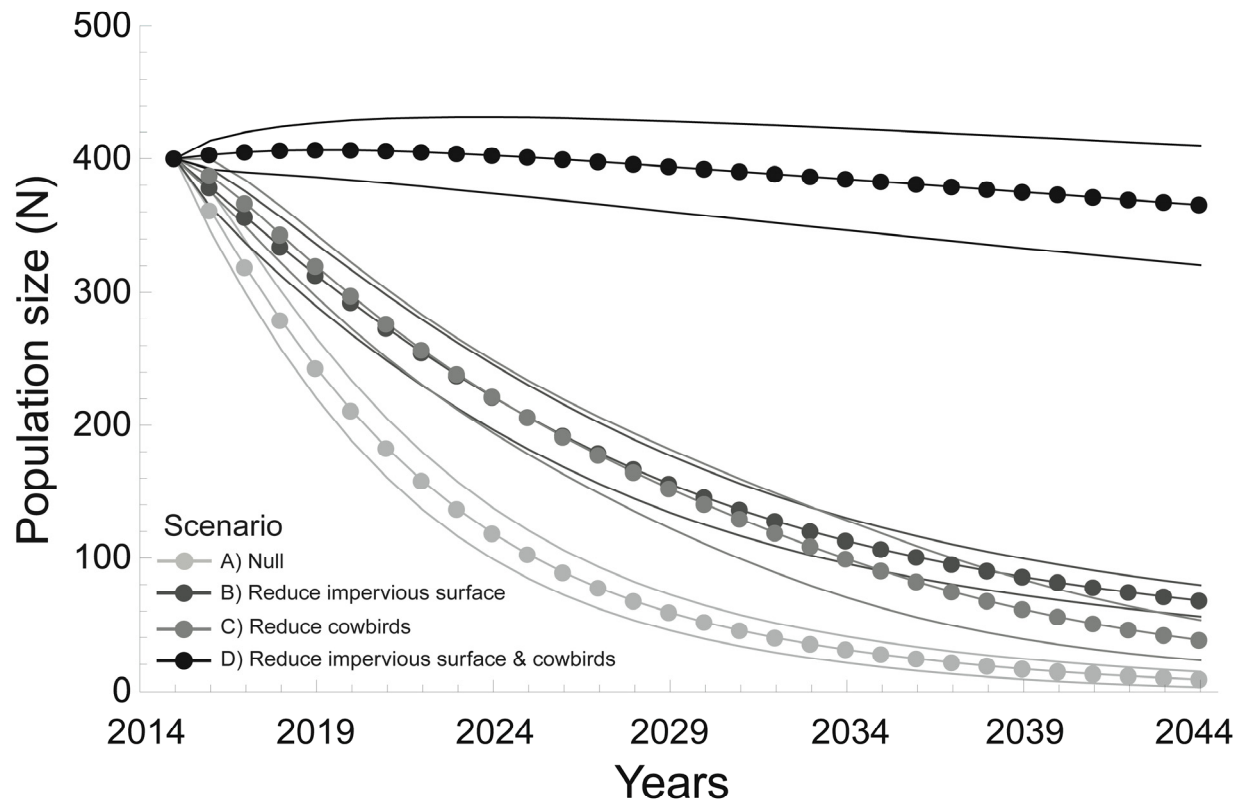
Figure 3.8. Contour plot showing the relationship of combinations of proportions of impervious surface and index of cowbird parasitism (i.e., proportion of cowbird parasitized nests × number of cowbird eggs per nest) to mean annual growth rate per site (λi).
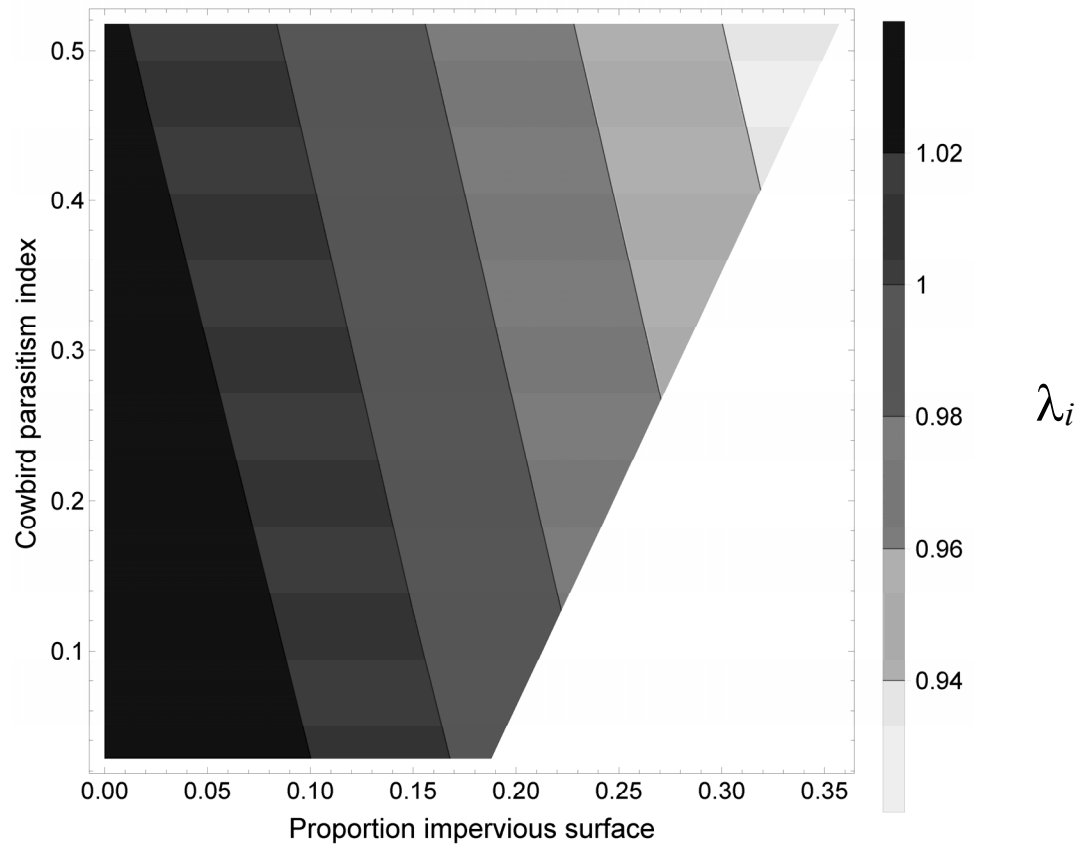
Appendix A

UNIVERSITY OF DELAWARE INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC) ANNUAL REVIEW PERMIT.

University of Delaware
Institutional Animal Care and Use Committee
Annual Review

(Please complete below using Arial, size 12 Font.)

Title of Protocol: Long-term Dynamics of a Wood Thrush Population in a Forest Fragment

AUP Number: 1129-2012-2 | ← **(4 digits only)**

Principal Investigator: W. Gregory Shriver

Common Name: Wood Thrush

Genus Species: *Hylocicila mustelina*

Pain Category: *(please mark one)*

USDA PAIN CATEGORY:	*(Note change of categories from previous form)*
Category	**Description**
☐ **B**	Breeding or holding where NO research is conducted
X C	Procedure involving momentary or no pain or distress
☐ **D**	Procedure where pain or distress is alleviated by appropriate means (analgesics, tranquilizers, euthanasia etc.)
☐ **E**	Procedure where pain or distress cannot be alleviated, as this would adversely affect the procedures, results or interpretation

---

Official Use Only

IACUC Approval Signature: _____

Date of Approval: 2/1/12 _____

Principal Investigator Assurance

1. I agree to abide by all applicable federal, state, and local laws and regulations, and UD policies and procedures.

2. I understand that deviations from an approved protocol or violations of applicable policies, guidelines, or laws could result in immediate suspension of the protocol and may be reportable to the Office of Laboratory Animal Welfare (OLAW).

3. I understand that the Attending Veterinarian or his/her designee must be consulted in the planning of any research or procedural changes that may cause more than momentary or slight pain or distress to the animals.

4. I declare that all experiments involving live animals will be performed under my supervision or that of another qualified scientist listed on this AUP. All listed personnel will be trained and certified in the proper humane methods of animal care and use prior to conducting experimentation.

5. I understand that emergency veterinary care will be administered to animals showing evidence of discomfort, ailment, or illness.

6. I declare that the information provided in this application is accurate to the best of my knowledge. If this project is funded by an extramural source, I certify that this application accurately reflects all currently planned procedures involving animals described in the proposal to the funding agency.

7. I assure that any modifications to the protocol will be submitted to the UD-IACUC and I understand that they must be approved by the IACUC prior to initiation of such changes.

8. I understand that the approval of this project is for a maximum of one year from the date of UD-IACUC approval and that I must re-apply to continue the project beyond that period.

9. I understand that any unanticipated adverse events, morbidity, or mortality must be reported to the UD-IACUC immediately.

10. I assure that the experimental design has been developed with **consideration of the three Rs: reduction, refinement, and replacement, to reduce animal pain and/or distress and the number of animals used in the laboratory.**

11. I assure that the proposed research does not unnecessarily duplicate previous experiments. *(Teaching Protocols Exempt)*

12. I understand that by signing, I agree to these assurances.

_____   1/20/2012
Signature of Principal Investigator   Date

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SIGNATURE(S) OF ALL PERSONS LISTED ON THIS PROTOCOL

I certify that I have read this protocol, accept my responsibility and will perform only the procedures that have been approved by the IACUC.

	Name	Signature
1.	Zachary Ladin	*(signature)*
2.		
3.		
4.		
5.		
6.		
7.		
8.		
9.		
10.		
11.		
12.		
13.		
14.		
15.		

IACUC approval of animal protocols must be renewed on an annual basis.

1. Previous Approval Date: 24 February 2011

   Is Funding Source the same as on original, approved AUP?

   X Yes   ☐ No

   If no, please state Funding Source and Award Number:

2. **Record of Animal Use:**

Common Name	Genus Species	Total Number Previously Approved	Number Used To Date
1. Wood Thrush	*Hylocichla mustelina*	150	25
2.			
3.			
4.			
5.			

3. **Protocol Status:** *(Please indicate by check mark the status of project.)*

   Request for Protocol Continuance:

   X   A. Active: Project ongoing

   ☐ B. Currently inactive: Project was initiated but is presently inactive

   ☐ C. Inactive: Project never initiated but anticipated starting date is:

   Request for Protocol Termination:

   ☐ D. Inactive: Project never initiated

   ☐ E. Completed: No further activities with animals will be done.

4. **Project Personnel:** Have there been any personnel changes since the last IACUC approval? ☐ Yes   X No

   If Yes, fill out the Amendment to Add/Delete Personnel form to "Add" Personnel.

Project Personnel Deletions:

Name	Effective Date
1.	
2.	

5. **Progress Report:** If the status of this project is 3.A or 3.B, please provide a brief update on the progress made in achieving the aims of the protocol.

We are approaching the 40th year of this project by continuing Roland Roth's Wood Thrush research in the UD ecology woods which is the longest continuously operating demographic study of this species. In the 2011 field season (May – August) only 13 new Wood Thrush were banded.

6. **Problems or Adverse Effects:** If the status of this project is 3.A or 3.B, please describe any unanticipated adverse events, morbidity, or mortality, the cause if known, and how these problems were resolved. If there were none, this should be indicated.

I am happy to report that we did not see any adverse effects or problems while conducting our research.

Appendix B

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, DELAWARE, 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	-	1277	-
		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	-
		Campodeidae	-	9	-
		Cantharidae	-	11	9
		Carabidae	-	27	2
		Ceraphronidae	-	3	-
		Chironomidae	-	2	-
		Chrysomelidae	-	7	4
		Cicadellidae	-	1	41
		Cleridae	-	1	-
		Coreidae	-	1	1
		Cryptophagidae	-	1	-
Table continued					

Invertebrate group	Class	Family	Soil	Leaf Litter	Understory
Insects (8688)	Insecta	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	-	1064	29
		Gryllidae	-	8	65
		Heleomyzidae	-	4	-
		Histeridae	-	1	-
		Hypogastruridae	-	111	-
		Ichneumonidae	-	5	-
		Isotomidae	-	2035	-
		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	-	1065	-
		Pentatomidae	-	7	5
		Phlaeothripidae	-	118	-
		Phoridae	-	15	1
		Platygastridae	-	10	-
		Pselaphidae	-	12	-
		Psychodidae	-	3	-
		Pteromalidae	-	2	-
		Ptiliidae	-	1	-
		Ptilodactylidae	-	4	-

Table continued

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Invertebrate group	Class	Family	Soil	Leaf Litter	Understory
Insects (8688)	Insecta	Reduviidae	-	0	12
		Rhinotermitidae	-	15	-
		Rhyparochromidae	-	1	-
		Scarabaeidae	-	15	-
		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	-	1520	-
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	11395	540

Appendix C

ESTIMATED TRANSITION PROBABILITIES (MEAN ± SD) FOR WOOD THRUSHES AMONG 13 SAMPLED SITES IN AND NEAR NEWARK, DELAWARE, USA

Site i to j	Transition probability	Site j to i	Transition probability
CC2—CC2	0.6898 (0.02)		-
EW—CC2	0.0238 (0.02)	CC2—EW	0.0218 (0.02)
FO—CC2	0.007 (0.01)	CC2—FO	0.0361 (0.03)
GG2—CC2	0.0225 (0.02)	CC2—GG2	0.0218 (0.02)
IH1—CC2	0.0106 (0.01)	CC2—IH1	0.0244 (0.02)
IH2—CC2	0.0101 (0.01)	CC2—IH2	0.0278 (0.02)
MP—CC2	0.0083 (0.01)	CC2—MP	0.0321 (0.03)
RE—CC2	0.0204 (0.02)	CC2—RE	0.0223 (0.02)
RH—CC2	0.0142 (0.01)	CC2—RH	0.0224 (0.02)
SL2—CC2	0.0133 (0.01)	CC2—SL2	0.0217 (0.02)
WC1—CC2	0.0172 (0.02)	CC2—WC1	0.0217 (0.02)
WC2—CC2	0.0115 (0.01)	CC2—WC2	0.0292 (0.02)
WF—CC2	0.0107 (0.01)	CC2—WF	0.0289 (0.03)
CC2—EW	0.0218 (0.02)	EW—CC2	0.0238 (0.02)
EW—EW	0.6913 (0.02)		-
FO—EW	0.0072 (0.01)	EW—FO	0.0426 (0.03)
GG2—EW	0.0232 (0.02)	EW—GG2	0.0236 (0.02)
IH1—EW	0.0105 (0.01)	EW—IH1	0.0245 (0.02)
IH2—EW	0.0097 (0.01)	EW—IH2	0.0249 (0.02)
MP—EW	0.0085 (0.01)	EW—MP	0.0238 (0.02)
RE—EW	0.0205 (0.02)	EW—RE	0.0233 (0.02)
RH—EW	0.0143 (0.01)	EW—RH	0.0234 (0.02)
SL2—EW	0.0125 (0.01)	EW—SL2	0.0234 (0.02)
WC1—EW	0.0174 (0.02)	EW—WC1	0.0233 (0.02)
WC2—EW	0.011 (0.01)	EW—WC2	0.0261 (0.02)
WF—EW	0.0108 (0.01)	EW—WF	0.0259 (0.02)
CC2—FO	0.0361 (0.03)	FO—CC2	0.007 (0.01)
EW—FO	0.0426 (0.03)	FO—EW	0.0072 (0.01)
FO—FO	0.7222 (0.04)		-
GG2—FO	0.0233 (0.02)	FO—GG2	0.007 (0.01)
IH1—FO	0.0326 (0.02)	FO—IH1	0.021 (0.02)
IH2—FO	0.0164 (0.01)	FO—IH2	0.0132 (0.01)
MP—FO	0.0184 (0.02)	FO—MP	0.1115 (0.03)
RE—FO	0.0351 (0.03)	FO—RE	0.0072 (0.01)
RH—FO	0.0225 (0.02)	FO—RH	0.0073 (0.01)
SL2—FO	0.0324 (0.02)	FO—SL2	0.0093 (0.01)
Table continued			

Site i to j	Transition probability	Site j to i	Transition probability
WC1—FO	0.0194 (0.02)	FO—WC1	0.0075 (0.01)
WC2—FO	0.0238 (0.02)	FO—WC2	0.0164 (0.02)
WF—FO	0.0235 (0.02)	FO—WF	0.0632 (0.04)
CC2—GG2	0.0218 (0.02)	GG2—CC2	0.0225 (0.02)
EW—GG2	0.0236 (0.02)	GG2—EW	0.0232 (0.02)
FO—GG2	0.007 (0.01)	GG2—FO	0.0233 (0.02)
GG2—GG2	0.6897 (0.02)	-	
IH1—GG2	0.0106 (0.01)	GG2—IH1	0.0238 (0.02)
IH2—GG2	0.0097 (0.01)	GG2—IH2	0.0224 (0.02)
MP—GG2	0.0076 (0.01)	GG2—MP	0.0417 (0.03)
RE—GG2	0.021 (0.02)	GG2—RE	0.0219 (0.02)
RH—GG2	0.0144 (0.01)	GG2—RH	0.0219 (0.02)
SL2—GG2	0.0128 (0.01)	GG2—SL2	0.0228 (0.02)
WC1—GG2	0.0169 (0.02)	GG2—WC1	0.0225 (0.02)
WC2—GG2	0.0112 (0.01)	GG2—WC2	0.0372 (0.03)
WF—GG2	0.0109 (0.01)	GG2—WF	0.0273 (0.02)
CC2—IH1	0.0244 (0.02)	IH1—CC2	0.0106 (0.01)
EW—IH1	0.0245 (0.02)	IH1—EW	0.0105 (0.01)
FO—IH1	0.021 (0.02)	IH1—FO	0.0326 (0.02)
GG2—IH1	0.0238 (0.02)	IH1—GG2	0.0106 (0.01)
IH1—IH1	0.6846 (0.02)	-	
IH2—IH1	0.0292 (0.02)	IH1—IH2	0.0655 (0.04)
MP—IH1	0.0342 (0.02)	IH1—MP	0.0359 (0.03)
RE—IH1	0.0395 (0.03)	IH1—RE	0.0109 (0.01)
RH—IH1	0.0823 (0.03)	IH1—RH	0.0105 (0.01)
SL2—IH1	0.0269 (0.02)	IH1—SL2	0.0113 (0.01)
WC1—IH1	0.0374 (0.03)	IH1—WC1	0.0102 (0.01)
WC2—IH1	0.0254 (0.02)	IH1—WC2	0.0483 (0.03)
WF—IH1	0.031 (0.02)	IH1—WF	0.0585 (0.04)
CC2—IH2	0.0278 (0.02)	IH2—CC2	0.0101 (0.01)
EW—IH2	0.0249 (0.02)	IH2—EW	0.0097 (0.01)
FO—IH2	0.0132 (0.01)	IH2—FO	0.0164 (0.01)
GG2—IH2	0.0224 (0.02)	IH2—GG2	0.0097 (0.01)
IH1—IH2	0.0655 (0.04)	IH2—IH1	0.0292 (0.02)
IH2—IH2	0.7231 (0.03)	-	
MP—IH2	0.0416 (0.03)	IH2—MP	0.08 (0.03)
RE—IH2	0.0234 (0.02)	IH2—RE	0.0101 (0.01)
RH—IH2	0.0166 (0.02)	IH2—RH	0.0112 (0.01)
SL2—IH2	0.0241 (0.02)	IH2—SL2	0.0106 (0.01)
WC1—IH2	0.0203 (0.02)	IH2—WC1	0.01 (0.01)
WC2—IH2	0.0234 (0.02)	IH2—WC2	0.0436 (0.03)
WF—IH2	0.0205 (0.02)	IH2—WF	0.0365 (0.03)
CC2—MP	0.0321 (0.03)	MP—CC2	0.0083 (0.01)
EW—MP	0.0238 (0.02)	MP—EW	0.0085 (0.01)
Table continued			

Site i to j	Transition probability	Site j to i	Transition probability
FO—MP	0.1115 (0.03)	MP—FO	0.0184 (0.02)
GG2—MP	0.0417 (0.03)	MP—GG2	0.0076 (0.01)
IH1—MP	0.0359 (0.03)	MP—IH1	0.0342 (0.02)
IH2—MP	0.08 (0.03)	MP—IH2	0.0416 (0.03)
MP—MP	0.758 (0.03)	-	
RE—MP	0.0406 (0.03)	MP—RE	0.0073 (0.01)
RH—MP	0.017 (0.02)	MP—RH	0.0085 (0.01)
SL2—MP	0.095 (0.04)	MP—SL2	0.0094 (0.01)
WC1—MP	0.0489 (0.03)	MP—WC1	0.0082 (0.01)
WC2—MP	0.0731 (0.04)	MP—WC2	0.0369 (0.02)
WF—MP	0.1353 (0.04)	MP—WF	0.053 (0.04)
CC2—RE	0.0223 (0.02)	RE—CC2	0.0204 (0.02)
EW—RE	0.0233 (0.02)	RE—EW	0.0205 (0.02)
FO—RE	0.0072 (0.01)	RE—FO	0.0351 (0.03)
GG2—RE	0.0219 (0.02)	RE—GG2	0.021 (0.02)
IH1—RE	0.0109 (0.01)	RE—IH1	0.0395 (0.03)
IH2—RE	0.0101 (0.01)	RE—IH2	0.0234 (0.02)
MP—RE	0.0073 (0.01)	RE—MP	0.0406 (0.03)
RE—RE	0.6882 (0.02)	-	
RH—RE	0.0152 (0.01)	RE—RH	0.0208 (0.02)
SL2—RE	0.0134 (0.01)	RE—SL2	0.0217 (0.02)
WC1—RE	0.0175 (0.02)	RE—WC1	0.0198 (0.02)
WC2—RE	0.0118 (0.01)	RE—WC2	0.0263 (0.02)
WF—RE	0.0106 (0.01)	RE—WF	0.0227 (0.02)
CC2—RH	0.0224 (0.02)	RH—CC2	0.0142 (0.01)
EW—RH	0.0234 (0.02)	RH—EW	0.0143 (0.01)
FO—RH	0.0073 (0.01)	RH—FO	0.0225 (0.02)
GG2—RH	0.0219 (0.02)	RH—GG2	0.0144 (0.01)
IH1—RH	0.0105 (0.01)	RH—IH1	0.0823 (0.03)
IH2—RH	0.0112 (0.01)	RH—IH2	0.0166 (0.02)
MP—RH	0.0085 (0.01)	RH—MP	0.017 (0.02)
RE—RH	0.0208 (0.02)	RH—RE	0.0152 (0.01)
RH—RH	0.6813 (0.01)	-	
SL2—RH	0.0118 (0.01)	RH—SL2	0.0156 (0.02)
WC1—RH	0.0176 (0.02)	RH—WC1	0.0141 (0.01)
WC2—RH	0.0109 (0.01)	RH—WC2	0.0713 (0.03)
WF—RH	0.0106 (0.01)	RH—WF	0.0211 (0.02)
CC2—SL2	0.0217 (0.02)	SL2—CC2	0.0133 (0.01)
EW—SL2	0.0234 (0.02)	SL2—EW	0.0125 (0.01)
FO—SL2	0.0093 (0.01)	SL2—FO	0.0324 (0.02)
GG2—SL2	0.0228 (0.02)	SL2—GG2	0.0128 (0.01)
IH1—SL2	0.0113 (0.01)	SL2—IH1	0.0269 (0.02)
IH2—SL2	0.0106 (0.01)	SL2—IH2	0.0241 (0.02)
MP—SL2	0.0094 (0.01)	SL2—MP	0.095 (0.04)

Table continued

Site i to j	Transition probability	Site j to i	Transition probability
RE—SL2	0.0217 (0.02)	SL2—RE	0.0134 (0.01)
RH—SL2	0.0156 (0.02)	SL2—RH	0.0118 (0.01)
SL2—SL2	0.6806 (0.01)	-	
WC1—SL2	0.0188 (0.02)	SL2—WC1	0.0123 (0.01)
WC2—SL2	0.0141 (0.02)	SL2—WC2	0.0415 (0.03)
WF—SL2	0.0132 (0.01)	SL2—WF	0.0234 (0.02)
CC2—WC1	0.0217 (0.02)	WC1—CC2	0.0172 (0.02)
EW—WC1	0.0233 (0.02)	WC1—EW	0.0174 (0.02)
FO—WC1	0.0075 (0.01)	WC1—FO	0.0194 (0.02)
GG2—WC1	0.0225 (0.02)	WC1—GG2	0.0169 (0.02)
IH1—WC1	0.0102 (0.01)	WC1—IH1	0.0374 (0.03)
IH2—WC1	0.01 (0.01)	WC1—IH2	0.0203 (0.02)
MP—WC1	0.0082 (0.01)	WC1—MP	0.0489 (0.03)
RE—WC1	0.0198 (0.02)	WC1—RE	0.0175 (0.02)
RH—WC1	0.0141 (0.01)	WC1—RH	0.0176 (0.02)
SL2—WC1	0.0123 (0.01)	WC1—SL2	0.0188 (0.02)
WC1—WC1	0.6841 (0.02)	-	
WC2—WC1	0.0115 (0.01)	WC1—WC2	0.0565 (0.03)
WF—WC1	0.0111 (0.01)	WC1—WF	0.0281 (0.02)
CC2—WC2	0.0292 (0.02)	WC2—CC2	0.0115 (0.01)
EW—WC2	0.0261 (0.02)	WC2—EW	0.011 (0.01)
FO—WC2	0.0164 (0.02)	WC2—FO	0.0238 (0.02)
GG2—WC2	0.0372 (0.03)	WC2—GG2	0.0112 (0.01)
IH1—WC2	0.0483 (0.03)	WC2—IH1	0.0254 (0.02)
IH2—WC2	0.0436 (0.03)	WC2—IH2	0.0234 (0.02)
MP—WC2	0.0369 (0.02)	WC2—MP	0.0731 (0.04)
RE—WC2	0.0263 (0.02)	WC2—RE	0.0118 (0.01)
RH—WC2	0.0713 (0.03)	WC2—RH	0.0109 (0.01)
SL2—WC2	0.0415 (0.03)	WC2—SL2	0.0141 (0.02)
WC1—WC2	0.0565 (0.03)	WC2—WC1	0.0115 (0.01)
WC2—WC2	0.7223 (0.04)	-	
WF—WC2	0.0249 (0.02)	WC2—WF	0.0501 (0.04)
CC2—WF	0.0289 (0.03)	WF—CC2	0.0107 (0.01)
EW—WF	0.0259 (0.02)	WF—EW	0.0108 (0.01)
FO—WF	0.0632 (0.04)	WF—FO	0.0235 (0.02)
GG2—WF	0.0273 (0.02)	WF—GG2	0.0109 (0.01)
IH1—WF	0.0585 (0.04)	WF—IH1	0.031 (0.02)
IH2—WF	0.0365 (0.03)	WF—IH2	0.0205 (0.02)
MP—WF	0.053 (0.04)	WF—MP	0.1353 (0.04)
RE—WF	0.0227 (0.02)	WF—RE	0.0106 (0.01)
RH—WF	0.0211 (0.02)	WF—RH	0.0106 (0.01)
SL2—WF	0.0234 (0.02)	WF—SL2	0.0132 (0.01)
WC1—WF	0.0281 (0.02)	WF—WC1	0.0111 (0.01)
WC2—WF	0.0501 (0.04)	WF—WC2	0.0249 (0.02)
WF—WF	0.6869 (0.02)	-	

Appendix D

NORMALIZED TRANSITION MATRIX USED IN METAPOPULATION MODEL SIMULATIONS WITH TRANSITION PROBABILITIES FOR WOOD THRUSHES AMONG 13 OCCUPIED AND 8 UNOCCUPIED PATCHES, IN ADDITION TO ONE IDEALIZED PATCH REPRESENTING EMIGRATION FROM THE STUDY AREA. PATCHES ARE IDENTIFIED ALONG ROW AND COLUMN NAMES BY SITE ABBREVIATIONS (SEE STUDY AREA DESCRIPTION, CHAPTER 1).

Site	CC2	EW	FO	GG2	IH1	IH2	MP	RE	RH	SL2	WC1	WC2	WF	CC1	CD	CW	DM	GG1	LA	PH	SL1	Emigration
CC2	0.69	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
EW	0.02	0.66	0.01	0.01	0.06	0.02	0.02	0.01	0.02	0.01	0.04	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
FO	0.02	0.01	0.66	0.01	0.06	0.04	0.02	0.01	0.02	0.01	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
GG2	0.02	0.02	0.02	0.69	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
IH1	0.02	0.05	0.05	0.02	0.58	0.03	0.02	0.01	0.04	0.02	0.07	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
IH2	0.02	0.02	0.04	0.02	0.03	0.62	0.02	0.04	0.02	0.02	0.04	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
MP	0.02	0.02	0.02	0.02	0.02	0.03	0.69	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
RE	0.02	0.01	0.01	0.02	0.01	0.05	0.02	0.68	0.01	0.02	0.02	0.04	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
RH	0.02	0.02	0.02	0.02	0.05	0.02	0.02	0.01	0.68	0.02	0.02	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
SL2	0.02	0.01	0.02	0.02	0.03	0.02	0.02	0.02	0.02	0.69	0.02	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
WC1	0.02	0.04	0.03	0.02	0.08	0.04	0.01	0.01	0.02	0.02	0.61	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
WC2	0.02	0.02	0.03	0.02	0.05	0.03	0.02	0.04	0.02	0.03	0.03	0.62	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
WF	0.02	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.69	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
CC1	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03
CD	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.01	0.01	0.01	0.01	0.03
CW	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.01	0.01	0.01	0.03
DM	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.01	0.01	0.03
GG1	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.01	0.03
LA	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.01	0.03
PH	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.01	0.03
SL1	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.85	0.03
Emigration	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1