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Habitat use of the declining Wood Thrush in coastal Virginia

Vitek Jirinec

Prague, Czech Republic

Wildlife Biology, Humboldt State University, 2010

A Thesis presented to the Graduate Faculty
of the College of William and Mary in Candidacy for the Degree of
Master of Science

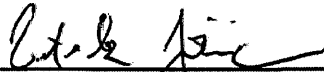
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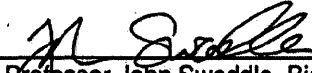
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ABSTRACT

Following the trend in many populations of migratory songbirds, the charismatic Wood Thrush has experienced long-term range-wide declines over the last few decades. A number of studies indicate that the species is area-sensitive: nest success and probability of occurrence decline with decreasing forest patch size. However, our five-year bird census in suburban and rural areas in coastal Virginia provides little evidence for decreased probability of occurrence in smaller forest fragments. Perhaps then, housing development per se is not necessarily detrimental to Wood Thrush, as long as certain habitat requirements are met. Although the species has been extensively researched, there is little information on why birds use a particular area, and knowledge of which environmental features explain concentrated bird use is therefore limited. This is a missed opportunity for identification of critical factors necessary for the conservation of this species. We captured and radio-tracked 37 male birds over two breeding seasons (2013, 2014) in tandem with vegetation and food prey availability sampling. Our models reveal bird activity increases with biomass of invertebrate prey and availability of certain habitat features. Bird presence is thus likely tied with access to these environmental factors, which are in turn affected by their own suite of predictors.

However, whether knowledge of bird habitat requirements derived from daytime-only observations is sufficient necessarily depends on birds using same areas at night. We therefore captured 10 female mates of 2014 males and examined roosting positions in relation to bird daytime home ranges, vegetation density, and nest status. Nocturnal tracking revealed males slept outside their daytime home ranges in areas with significantly higher vegetation density while females sleep on nests. However, without active nests, males guarded females at night, presumably to ensure paternity during periods of female fertility. These results provide novel natural history information for this enigmatic species, and provide additional tools for reversal of its population decline.

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Thesis topic introduction

Populations of many Neartic-Neotropical migratory songbirds are declining (Ballard et al. 2003). Researchers have long recognized that effective conservation of birds requires a thorough understanding of their habitat requirements. For migrants, this calls for knowledge across the annual cycle as declines have been connected with events occurring on the breeding grounds (Rodenhouse and Holmes 1992), wintering regions (Holmes and Sherry 2001, Norris et al. 2004), and migratory stopover areas (Leu and Thompson 2002, Packett and Dunning 2009). Researchers generally infer habitat requirements for target species from daytime observations at one or more of the above areas. This approach would be satisfactory if daytime habitat requirements matched nighttime habitat requirements. However, selective pressures shaping bird behavior are considerably different during the day than at night, when even non-anatid species transform into sitting ducks. A highly-mobile, visually-oriented animal becomes relatively unaware of its surroundings and thus exposed to nocturnal predators. Habitat offering optimal foraging opportunities during the day might be useless at the night when diurnal birds do not eat, and cover from predators becomes crucial.

With exposure to nocturnal predation in mind, it is perhaps unsurprising that observations of migratory songbirds moving away from their daytime use areas to disjunct roosting sites have been documented for at least four species on their wintering grounds (Jirinec et al. 2011, Smith et al. 2008, Townsend et al. 2009, Warkentin and Morton 1995). In three of these studies, researchers suggested predation pressure as the reason for such commutes to roost sites. Often, birds moved to areas with high vegetation density, which presumably conferred cover from visual nocturnal predators. Regardless

of ultimate causes for roosts commutes, focusing solely on diurnal habitat requirements provides often-incomplete natural history information on birds. Importantly, both daytime and nocturnal areas have to be considered for effective conservation of migratory birds that use separate roosting habitat.

Diurnal habitat selection of breeding birds remains one of the central questions in ornithology (Battin and Lawler 2006). Along with much of biodiversity, habitat loss and degradation is the leading threat to birds. This reality often channels limited conservation funds to studies of habitat quality to focal species of concern (Johnson 2007). Knowledge of habitat requirements for non-focal species is therefore often limited. Following the general understanding that birds select habitat hierarchically (Battin and Lawler 2006), researchers have commonly focused on large-scale associations between landscape features and bird habitat quality. Such studies are often easier and cheaper to conduct than small-scale studies requiring tracking of individual birds. I have found only two studies that attempted to identify breeding songbird microhabitat requirements based on within-home range space use patterns via rigorous tracking of individually-marked birds (Anich et al. 2012, Barg et al. 2006), and none that include considerations of food availability. Because this is the scale at which birds interact with their environment during arguably the most crucial time in the year – the breeding season – this is a missed opportunity for identification of critical habitat requirements.

In this thesis, I have explored roosting ecology (Chapter 1) and examined microhabitat associations (Chapter 2) of the declining Wood Thrush (*Hylocichla mustelina*). Despite the oft-studied status of this migratory species, populations of the Wood Thrush have declined by about 50% just in the last 5 decades (Sauer et al. 2014).

Although the Wood Thrush is the subject of much research, roosting ecology of this species is completely unknown, while microhabitat requirements have not been given a thorough investigation. I captured and tracked 37 Wood Thrush males over the 2013 and 2014 breeding seasons to examine where birds sleep and which environmental features typify areas with concentrated use. In addition to the 37 males, I have included 10 females in 2014 that have been primarily captured for an undergraduate honors thesis by Akshay Deverakonda. All birds were fitted with leg color bands and radio transmitters which allowed for individual tracking throughout the breeding season.

I believe the findings described below provide novel natural history information for the charismatic Wood Thrush. Only preservation of areas meeting both diurnal and nocturnal demands of this familiar vocalist will ensure its song will continue to be heard.

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CHAPTER 1

Mismatch between daytime activity regions and roosting areas in the Wood Thrush: why are males sleeping around?

Abstract

Despite its necessary importance for understanding the complete avian circadian cycle, behavior of roosting birds has received little attention from ornithologists. We examined the spatial arrangement of roosts in relation to diurnal home ranges for the declining Wood Thrush (*Hylocichla mustelina*) on its breeding grounds in coastal Virginia. To our knowledge, this is the first broad description of roosting ecology for a North American migratory passerine during the breeding season. The primary objective of this study was to determine if day and night use regions overlap. Secondly, we tested the hypothesis that birds roost at sites with higher local vegetation density using LiDAR and explored the effect of nest status on roosting pattern in bird pairs. We captured and radio-tracked 37 males to construct 95% kernel diurnal home ranges. In 10 home ranges we also tagged female mates. Both sexes were tracked at night to roosting locations. Of 74 male roosts, 31% were located outside diurnal home ranges. LiDAR-derived vegetation density was ~7% higher at roost sites than at random points within diurnal home ranges, and young birds roosted farther from peak diurnal use areas than older birds, suggesting a role of roost habitat quality. Nest status had a significant effect on pair roosting pattern, as females with active nests roosted exclusively in nest cups while males roosted an average of 121.8 m (CI = 72.6 – 204.2, $n = 11$) away on equivalent nights. Once nests fledged or failed, males roosted within diurnal home ranges while guarding females. We propose

that the observed mismatch in male diurnal home ranges and nocturnal roost sites may be based on optimal roosting conditions at those sites, but male solicitation of extra-pair copulations from fertile neighboring females during the morning and evening insemination windows should also be considered.

Introduction

All animals sleep, yet it is one of the less studied behavior (Lima et al. 2005). In forest birds, roosting has been examined primarily in the context of activity at communal roosting sites (Marzluff et al. 1996, McGowan et al. 2006), and behavior of cavity-utilizing species (Steinmeyer et al. 2010, Wang and Weathers 2009). However, many aspects of roosting ecology are of great interest to biologists. For example, zoonotic disease transmission potential has been linked with roost characteristics of American Robins, where West Nile virus vectors preferentially fed on individuals higher in forest canopy but risk of infection decreased for birds roosting in groups (Janousek et al. 2014). In Jamaican coffee farms, nearby forest appears to provision the delivery of economically-substantial ecosystem service by Black-throated Blue Warblers as birds forage on coffee pests during the day (Kellermann et al. 2008), after commuting from nocturnal roosts in the woods and large shade trees (Jirinec et al. 2011).

Comprehensive knowledge of habitat requirements might be the chief reason to study bird roosting. Declines of Neotropical migratory songbirds indicate the need to consider habitat requirements of individual species and highlight the need for understanding habitat use over the entire annual cycle. Migratory songbird declines are connected with events occurring on the breeding grounds (Rodenhouse and Holmes

1992), wintering regions (Holmes and Sherry 2001, Norris et al. 2004, Robbins et al. 1989), and migratory stopover areas (Leu and Thompson 2002, Packett and Dunning 2009), and are ultimately associated with local habitat quality. Information about bird ecology, such as habitat requirements, is commonly inferred from habitat associations derived from daytime observations at one or more of the above areas. This approach would be satisfactory only if daytime and nocturnal use regions overlapped. Wintering Ovenbirds (*Seiurus aurocapilla*) appear to roost in their core diurnal activity area (Brown and Sherry 2008), which suggests roosting is correlated with daytime use patterns in some species. However, evidence is mounting that many forest migrants roost away from their daylight activity ranges. To our knowledge, this phenomenon has been specifically documented on the wintering grounds for the Prothonotary Warbler (*Protonotaria citrea*; Warkentin and Morton 1995), Northern Waterthrush (*Parkesia noveboracensis*; Smith et al. 2008), Black-throated Blue Warbler (*Setophaga caerulescens*; Jirinec et al. 2011), and the Bicknell's Thrush (*Catharus bicknelli*; Townsend et al. 2009). Additionally, recent report provides some evidence for Yellow-rumped Warbler (*Setophaga coronata*) commutes during the migratory stopover period (Slager and Rodewald 2015). Furthermore, anecdotal observations suggest many more Nearctic-Neotropical migrants conduct off-home range commutes to roost sites (see Smith et al. 2008 for review).

One hypothesis for roost commute is movement to quality roosting habitat. Predation risk to sleeping birds is elevated as roosting birds are relatively unresponsive to cues alerting them to predator presence (Amo et al. 2011, Lima et al. 2005). Areas offering optimal foraging opportunities where vigilance is sufficient to reduce predation may be too dangerous for sleeping birds, and natural selection should thus favor a change

in habitat use (Clark and Shutler 1999). Townsend et al. (2009) documented 9% mortality over ~30 days by introduced rats at roosts of Bicknell's Thrushes on the wintering grounds. Although thrushes appeared to never use pine forest during the day, 68% of roosts were in pine where rat relative abundance was significantly lower. Although night predation risk studies are limited for birds (Lima et al. 2005), research on primates suggests safety is principal in sleeping site selection (Qihai et al. 2009, Ramakrishnan and Coss 2001). Regardless of the ultimate selection pressure driving divergent temporal habitat use, understanding nighttime habitat demands is essential for bird conservation as population status is inextricably linked with quality of such habitat across the annual cycle. This raises the need for research that quantifies space use of individually-marked birds during the entire 24-hour period. Increased logistical difficulties and personnel demands likely contribute to the inadequate number of such studies. Nevertheless, understanding whether diurnal and nocturnal use areas overlap is the first step in determining whether roosting habitat should be considered independently.

In this study, we consider the physical space utilized by birds during the daytime hours and define it as the "diurnal home range" (DHR). Although a home range has been defined as all used areas (Burt 1943), nighttime use patterns of diurnal bird species are largely unknown, rendering this definition without knowledge of roosting areas potentially misleading. We outlined DHRs by the 95% kernel boundary, which includes an actively defended territory as well as adjacent areas used opportunistically during the day.

In contrast to DHR, we define a “roost” as the location where a bird spends nighttime hours, regardless of whether it is alone or near conspecifics. Our assumption is within-night roost location does not change unless a bird is disturbed.

We delineated DHRs and roosts for the Wood Thrush (*Hylocichla mustelina*) during the breeding season. Populations of this migratory songbird show significant, long-term and range-wide declines ($-2\% \text{ yr}^{-1}$ from 1966 to 2012; Sauer et al. 2014), partly attributed to decreased nest success in smaller forest fragments (e.g., Lloyd et al. 2005). On the breeding grounds, areas with frequent daytime Wood Thrush detections have been related to upland deciduous and mixed forests with moderate subcanopy, semi-open floor with decaying litter, and a wide variety of tall deciduous tree species (Roth et al. 2011). Despite that this species’ breeding ecology is well studied, knowledge of Wood Thrush nocturnal behavior is limited to anecdotal observations of nesting females (Roth et al. 2011).

The primary objective of this study was to determine if the Wood Thrush roosts within its diurnal home range, followed by two secondary objectives: to test the hypothesis that local vegetation density differs between roost sites and random sites within diurnal home range, and compare roosting locations of males and females during times when nests are active and inactive. In pair analyses, we examined the effect of nest status both on intra-pair roost distance and mate roost positions within diurnal home range.

Methods

Study Area

For broader land cover representation of this wide-ranging species, we captured and tracked individual birds at eight parks and one military base located in the coastal plain of southeastern Virginia (37° 15' N, 76° 40' W). Birds were tracked on property managed by the National Park Service, College of William and Mary, Colonial Williamsburg, City of Newport News, City of Williamsburg, York County, James City County, Kingsmill Resort, York River State Park, and the U.S. Navy.

The region is moderately covered with eastern deciduous and mixed forest, but encroaching urbanization has fragmented many of the wooded study sites (Monette and Ware 1983). We surveyed vegetation at six circular plots (15 m radius) within study bird DHRs ($n = 222$ plots). On average, highest tree density was represented by tulip poplar (*Liriodendron tulipifera*; $51.6 \pm \text{SE} = 4.6$ trees ha^{-1}), American beech (*Fagus grandifolia*; 49.6 ± 3.9 trees ha^{-1}), and American holly (*Ilex opaca*; 45.2 ± 4.5 trees ha^{-1}), with mean diameter at breast-height (cm) at 39.7 ± 0.8 , 25.5 ± 0.6 , 13.8 ± 0.2 , respectively. Ground was generally open with deciduous leaf-litter carpeting most of the forest floor ($62 \pm 2\%$). Pawpaw (*Asimina triloba*), along with saplings of *I. opaca* and *F. grandifolia* comprised the highest counts of understory woody vegetation.

Bird Capture and Marking

We tracked 47 birds using radio telemetry over two breeding seasons (2013 to 2014). Males ($n = 37$) were captured in May 15 – June 3 of both years using mist nets (30 mm mesh) with conspecific song playback (Angelier et al. 2010). Target netting allowed us to

capture individuals with established territories and avoid floaters which could quickly depart the survey area. Female mates ($n = 9$) were added to a subset of study males in 2014, and we included observations of one banded (but not radio-tagged) female from 2013. Females were captured throughout the breeding season using passive netting near newly-discovered nests of tagged males in order to ensure correct pair assignment. We never observed nest abandonment due to such disturbance. Sex was determined by the presence of brood patch and cloacal protuberance (Pyle 1997). We subsequently monitored nests of radio-tagged pairs about every 3 days to determine nest status for analyses involving nest stage. We estimated stage (incubation or nestling) based on observations of parental behavior and known stage intervals summarized in Roth et al. (2011). Increased personnel in 2014 allowed for age determination based on molt limits in greater coverts without excessive bird handling. Birds with evidence of juvenal greater coverts were classified as second-year (SY), while birds without definitive aging characteristics were classified as after-hatch-year birds (AHY, Pyle 1997). For each bird, we affixed a USGS aluminum band along with a unique set of three color bands for identification in case of premature transmitter detachment.

We used a figure-eight leg harness (Rappole and Tipton 1991) to attach a 1.3 g VHF transmitter (BD-2; Holohil Systems Ltd., Carp, Ontario, Canada) to each bird. We used 0.7 mm Stretch Magic (Pepperell Braiding, Pepperell, Massachusetts, USA) jewelry cord for harness (intraloop distance = 57.5 mm), and observed no injurious rubbing on individuals ($n = 6$) recaptured up to 46 days after initial transmitter deployment. Two birds were recaptured in order to reattach a lost transmitter due to fractured harness, suggesting birds eventually lose tags during normal wear.

Diurnal Home Range Estimation

DHRs were derived from diurnal radio telemetry locations (Marzluff et al. 2004). Birds were tracked from May 16 through July 25 of both years (mean 11.9 ± 0.8 unique days) between 0630 and 2030 EDT until transmitter battery depletion (average battery life ~ 60 days). We obtained at least one location per bird each hour between 0800 – 2000 to account for variation in temporal space use (Anich et al. 2012); otherwise locations were distributed throughout daytime hours. To ensure biological independence between locations (defined as interval long enough to reach any point within DHR, Barg et al. 2005), points were recorded ≥ 20 min apart. This interval is equal or larger than in similar studies with three warbler species (Anich et al. 2012), and we believe it is adequate as birds often moved substantially between relocations, easily traversing their DHRs. Final bird location was determined by observers equipped with 3-element Yagi antennas and receivers (TRX-1000S and TRX-3000S; Wildlife Materials, Murphysboro, Illinois, USA). To avoid telemetry bias due to observer disturbance, we homed in to ≤ 50 m of target, then projected bird position in GPS units (GPSMAP 62; Garmin, Olathe, Kansas, USA) using compass bearing and distance with a laser range finder (400LH; Opti-Logic, Tullahoma, Tennessee, USA). In cases where birds moved beyond detection radius (Lang et al. 2002), we performed extensive ground searches with twin truck-mounted antennas along with aerial telemetry using a fixed-wing aircraft.

We base diurnal home ranges on utilization distributions generated from 95% kernel density estimations (Barg et al. 2005, Marzluff et al. 2004, Worton 1989). Utilization distribution is a representation of individual's space use as a function of telemetry location density, thus portraying the relative use levels (hereafter relative

percent diurnal use) within each pixel of its activity area (Horne and Garton 2006, Marzluff et al. 2004). We used inverse isopleths (i.e. quantiles of kernel estimates) of the utilization distribution to represent relative percent diurnal use (0 – 100%; Figure 1). DHR edge thus corresponds to 5% relative use for a conservative area estimate (Pechacek and Nelson 2004), whereas areas outside DHR had 0% relative diurnal use, and the most-used sections within DHR approach peak relative use (100%). For analyses where designation of DHR center was necessary, we considered the uppermost kernel value as DHR center – peak relative diurnal use. Because males defend territories and pair DHR highly overlaps (A. Deverakonda personal observation), we used male DHR for pair roost analyses. Although the least-squares cross-validation (LSCVh) is commonly used as the kernel bandwidth selection method (Gitzen and Millspaugh 2003), we found this approach did not perform well for individual birds with multiple frequently-used areas. An alternative to LSCVh is the likelihood cross-validation (CVh), which has been shown to generally yield estimates with better fit and less variability than LSCVh, and to perform better with smaller sample sizes (Horne and Garton 2006). Barg et al. (2005) recommended 50 animal locations as the lower limit for LSCVh kernels. We used on average 53.9 ± 1.3 locations (range 50 – 80) to construct DHRs. Kernel density estimation and subsequent utilization distribution isopleths were constructed in Geospatial Modeling Environment (Beyer 2011).

Roost Site Location Estimation

We tracked birds to roosts throughout the breeding season. Roosts for individual birds were located on separate nights throughout the diurnal tracking period such that DHRs

and roosting areas were biologically coupled. Nocturnal tracking began at least one hour after sunset and continued no later than one hour before sunrise (Jirinec et al. 2011). We made sure birds were settled in for the night by confirming signal immobility prior to recording roost locations. We located roosts in a similar manner to diurnal tracking by homing as close as possible to a signal source, then carefully attempted to locate roosting bird. For each roost, we attempted to visually locate birds using headlamps. In cases of visual confirmation, we recorded roost height, tree species, and whether conspecifics were nearby. To avoid bird disturbance, we projected roost coordinates from a distance (see Diurnal Home Range Estimation) and obtained above-ground roost height using the height function in the rangefinders. In most cases we were unable to see the target bird (61%), particularly if the roost was high up or obscured by foliage. We therefore triangulated its radio signal (from ≤ 50 m away) and considered signal strength before estimating roost location and height. For males, we obtained two roost locations per bird for a total of 74 male-only roosts. For marked pairs ($n = 10$), we attempted to get two roosts per sex with pair locations recorded on the same night. In cases where females were captured after male roost collection was already underway, we collected additional male roosts to complement same-night female locations.

Roost Habitat

We used discrete return Light Detection and Ranging (LiDAR) data to test the hypothesis that Wood Thrush roosts were located in densely vegetated areas. LiDAR has been used to quantify three-dimensional forest structure at relatively high resolutions (Lefsky et al. 2002), including detailed vertical biomass distribution (Vierling et al. 2008).

The LiDAR data were collected in 22 April – 10 May, 2010, and 21 – 31 March, 2013. Therefore, data corresponding to ~30% of bird sites occurred in late March – before the arrival of most birds. The leaf area index is lower in March than in June when most roosts were identified. However, vegetative parts of trees and shrubs should be correlated with density of woody stems and branches, and our pairwise analysis (see Analysis) controlled for temporal differences in return density.

We computed vegetation density in LAStools software (version 150202; Martin Isenburg). Percent vegetation density was calculated as the number of returns ≥ 1 m aboveground divided by the number of all returns at 2-m resolution. We removed low-lying LiDAR points (< 1 m) to avoid understory vegetation unused for roosting. To accommodate telemetry error (i.e. GPS and location error), we averaged vegetation density within a 10-m circular neighborhood using focal statistics in a Geographic Information System (ArcMap 10.1; ESRI, Redlands, California, USA).

Analysis

Male-only roosts were analyzed separately from pair roosts. Male-only roosts ($n = 74$) were used to determine if DHR and roosting areas overlapped, and to test the hypothesis that local vegetation density explains roost site selection. Pair roost locations ($n = 36$) were used to explore the effect of nesting status on pair roosting pattern. In case of > 2 roosts per male in pairs with late-caught females, we used the first two roosts to determine DHR overlap and to test the vegetation density hypothesis. Only roosts collected for both sexes on the same nights were used for pair roost analysis.

Spatial relationships between roosting positions and DHR were determined in ArcMap 10.1 and examined using multiple statistical tests. We chose tests and parameters based on tests of normality (Shapiro and Wilk 1965) and homogeneity of variance (Levene 1960) assumptions after histogram and boxplot evaluation. In cases of non-normal data, we used natural-log transformation for analyses with parametric tests, or we resorted to non-parametric testing if transformations failed to produce normal datasets. We used a χ^2 test to see whether the positions of observed roosts matched roost positions expected in case birds used local area in proportion to its availability. We therefore divided DHR into five bins based on levels of relative use – five to retain a sufficient number of observations per bin (≥ 5) – and calculated the expected roost number by multiplying the sum of all within-DHR roosts by the proportion of bin area (Isdell et al. 2015). Because each bird's DHR area differed, this proportion is derived from the sum of corresponding bins in DHRs of all 37 male birds. To determine if roost commute correlates with DHR area, we examined if the coefficient of linear regression between roost distance from peak relative use and matching DHR area was greater than zero. To test the hypothesis that younger males commute greater distances to roosts, we used a t -test on log-transformed data. We report back-transformed means and confidence intervals wherever we ran tests on transformed datasets. A paired t -test was used to check for mean difference in vegetation density between roost locations and paired random sites within DHR. In Wood Thrush pair analyses, we used a t -test to test the hypothesis that roosting pattern in pairs without active nests differed from pairs with females incubating eggs or brooding nestlings. Lastly, we applied a Wilcoxon signed rank test to examine whether roost positions within DHRs differed by sex and nest stage. All analyses were conducted

in R (R Core Team 2014), with package “boot” to generate 95% confidence intervals for medians for results of Wilcoxon signed rank test by resampling datasets with 1,000 bootstrapping iterations. We report 95% confidence intervals (CIs) throughout. To report sensible CIs for analysis results of log-transformed data, we present back-transformed CIs representing mean $\pm 1.96SE$ of transformed, normal dataset. Where appropriate, we report means $\pm SE$. All tests are two-tailed and set to $\alpha < 0.05$ significance level.

Results

Male Data

We obtained visual observations in 39% of 74 male roosting locations. Males observed roosting were frequently concealed by vegetation from dorsal and most side views, but the feathers of their abdomens were often visible in the headlamp beam. Birds appeared undisturbed by light and usually did not appear to awaken (feathers fluffed, head tucked in, regularly perching on one leg). Of roosts where birds were detected visually ($n = 29$), average roost height was 6.8 ± 1.0 m (range 2.0 – 26.5 m). Most (69%) of roosting birds were seen in American holly (*Ilex opaca*, 21%), American beech (*Fagus grandifolia*, 17%), red maple (*Acer rubrum*, 17%), and pawpaw (*Asimina triloba*, 14%). Anecdotally, it appeared that the common attribute of the roosting locations was a high degree of concealment rather than similar plant species.

Males usually used different roosting areas on the different nights that we found them. Average temporal separation between consecutive roosting locations was 12 ± 1 days, which yielded a mean distance between the two roosts of 158 ± 25 m (range 2 – 607 m), excluding an outlier of 1,301 m where a male relocated to a new DHR. Only 8%

of males roosted in the same spot, defined as within 20 m of previous roost, on the two nights. Because we recorded roost positions at ≤ 10 m GPS accuracy, 20 m constitutes twice the maximum position error. Accordingly, we designated individual roosts as sampling units, rather than individual birds (Jirinec et al. 2011).

Roost positions did not match diurnal activity patterns and differed with bird age. Roosting locations were distributed throughout DHR, and 23 (31%) were placed outside DHR entirely (Figure 2). Mean distance to respective DHR edge for external roosts was 91 ± 20 m (range 9 – 322 m). Within-DHR roost positioning ($n = 51$) did not follow relative diurnal use as the number of observed roosts within the five DHR partitions (relative use bins) did not differ from corresponding area-based expected proportions ($\chi^2_4 = 2.5, P = 0.64$). DHR area did not explain roost distance to peak relative diurnal use ($F_{1,72} = 0.01, P = 0.91$), but mean commute from peak use was 100% longer for SY males (140.4 m, CI = 81.4 – 242.1, $n = 16$) than in AHY males (70.2 m, CI = 49.1 – 100.5, $n = 18$; two-sample t -test: $t_{32} = 2.1, P = 0.04$).

Roosts were located in areas with higher canopy density (Figure 3). Mean difference in vegetation density within a 10-m neighborhood was 6.5% higher at roost sites than at random points within DHR (CI = 2.0 – 11.1, $n = 74$; paired t -test: $t_{73} = 2.8, P = 0.006$).

Pair Data

Distance between mates in roosting pairs differed with nesting status (Figure 4). Females with nests in incubation and early nestling stage (“active” nest) roosted exclusively in the nest cup, while males were an average of 121.8 m (CI = 72.6 – 204.2, $n = 11$) away on

equivalent nights. However, once nests failed or fledged (“inactive” nest), mean distance between pair members was 91% shorter (10.6 m, CI = 2.2 – 51.9, $n = 7$, two-sample t -test: $t_{16} = 3.4$, $P = 0.004$). Most of these cases ($n = 5$) were “duo-roosts,” with male and female roosting side by side, inside the DHR.

Mate roost positions compared to relative diurnal use differed by sex and nest status (Figure 5). Females with active nests roosted on nests (see above), which were located in peak diurnal use areas. Median percent relative diurnal use (97%, CI = 94 – 98, $n = 11$) at roosts of actively-nesting females was 70% higher than at same-night male roosts (57%, CI = 0 – 73, $n = 11$, Wilcoxon signed rank test: $V = 66$, $P = 0.004$). When a nests failed or fledged, female roosting positions did not differ from male roosts ($n = 7$, Wilcoxon signed rank test: $V = 9$, $P = 0.89$).

Discussion

Our results suggest frequent disparity between Wood Thrush daytime home ranges and corresponding roost sites. We used telemetry-derived utilization distribution to relative percent space use within each DHR. If activity is assumed to, throughout each day, follow the probability of use represented by the DHR, thrushes were most likely to be located near peak relative diurnal use immediately before roosting commences.

Accordingly, we were surprised to find that the mean distance between peak use and male nocturnal roosts to be 115.7 m (CI = 92.2 – 145.1, $n = 74$), with longest distance observed being 702 m. One-third of male roosts were located completely outside DHR. Some birds therefore traveled significant distances to roosting sites.

Long commutes to roosts, especially to areas outside DHRs, require an explanation. Breeding is energetically taxing for passerines (Merila and Wiggins 1997), with birds expending much of their energy on mate acquisition, nest building and feeding young, as well as territory defense. Energetic costs associated with commutes to nocturnal roosts would be expected to decrease, however slightly, individual reproductive output and therefore should not be favored by natural selection. Moreover, individuals wandering outside their territories risk losing paternity or territory ownership to rival males, as well as agonistic encounters with other males whose territories they pass through.

Roosting and Habitat

We did not reject the hypothesis that birds roost in areas with higher vegetation cover. Roosting in dense areas may decrease chances of depredation as individuals are camouflaged by surrounding vegetation from visual predators such as the Barred Owl (*Strix varia*). Predation pressure has been shown to guide sleeping site selection in primates (Qihai et al. 2009, Ramakrishnan and Coss 2001). For birds, the preference for roosts in areas with high vegetation cover has been suggested to be an anti-predation strategy for the Capercaillie (*Tetrao urogallus*; Finne et al. 2000), and Sichuan Hill-partridge (*Arborophila rufipectus*; Liao et al. 2008). In some species, such as the Black-throated Blue Warbler, long commutes to roosts are necessitated by diurnal use of agricultural habitat likely lacking suitable roost sites (Jirinec et al. 2011). Wood Thrush, in contrast, appeared to occupy DHRs in continuous forested areas that did not differ dramatically from roost habitat, yet they often made commutes nonetheless. It was this

observation that led to the hypothesis that vegetation cover would be denser in selected roost sites than at random points within DHR.

While differences in vegetation density between roost sites and DHR were statistically significant, they were not biologically large (~7%). Thus, further research will be necessary to understand what Wood Thrush gains from commuting to nocturnal roosts. One possibility is that optimal roost microclimate or maximum camouflage requires a rare habitat attribute, and only the best territories contain this attribute. Our observation that SY males commuted farther to nocturnal roosts than older males is consistent with the idea that the best DHRs, presumably occupied by older males (Holmes et al. 1996), may contain better roost sites within them. An alternative hypothesis is that males roost far from active nests to avoid attracting attention to it. This is consistent with our observation that when nests were not active, both pair members often roosted together, inside the DHR. Another alternative hypothesis is that males choose distant roost sites to improve their chances at obtaining extra-pair copulations.

Roosting and Extra-pair Behavior

Roosting pattern in bird pairs varied with nest stage. Only female Wood Thrushes incubate eggs, and we were therefore not surprised to find all females with active nests roosting in the nest cup. We were surprised, however, to find so many of their male mates roosting far away on equivalent nights (Figure 4A). Once a nest was terminated, either through depredation or nestling independence, pairs were found sleeping side by side (Figure 4B), inside the DHR. We observed this phenomenon in 5 of 7 cases where we obtained pair roost locations for pairs without an active nest. The 7 cases included two

observations (intra-pair distance 136 and 191 m) where we suspected divorce as these pairs diverged their diurnal use regions in subsequent tracking days.

The switch in roost pattern after a change in nest status was reflected in roost positions within relative diurnal use areas (Figure 5). When pairs had active nests, we observed females on nests (see above), which were located in peak relative diurnal use areas, while male roosts were located at sites where corresponding relative diurnal use values were significantly lower.

We propose the above pattern is at least partly driven by extra-pair sexual behavior of this socially-monogamous bird. A well-supported hypothesis for close proximity of pair members is mate guarding conducted by males to ensure paternity during female fertile periods, especially in egg pre-laying and laying (Birkhead and Moller 1992). Alatalo et al. (1987) demonstrated a linear relationship in distance between pair members and extra-pair copulation (EPC) rate in the Pied Flycatcher (*Ficedula hypoleuca*). Furthermore, Birkhead et al. (1987) found the greatest number (54%) of avian genera examined copulated most frequently in the mornings, followed by 25% of genera with peaks both in the morning and evening. An equally bimodal pattern described by Briskie (1992) closely matched peaks of mate guarding behavior for males of Smith's Longspurs (*Calcarius pictus*). The existence of corresponding physiologically mediated female "insemination windows" is discussed by Birkhead et al. (1996). Extra-pair paternity has been documented in as many as 40% of Wood Thrush nestlings (Evans et al. 2009), while Evans et al. (2008) found social mates were present at 74% of off-territory forays conducted by fertile females, suggesting mate guarding is a strategy to ensure paternity employed by Wood Thrush males. The roosting period, abutted by at

least one insemination window, is thus implicated as a critical period for mate guarding efforts and for taking advantage of the insemination window of neighboring females.

Solicitation of extra-pair copulations (EPCs) is consistent with roosting patterns observed in this study. Males with females in pre-laying and laying periods (i.e. without “active” nests), and thus susceptible to EPCs, roosted immediately adjacent to their mates. Once females were securely incubating or brooding young nestlings, however, males often roosted far from their mates. A similar pattern was documented in gallinaceous birds that roosted within home ranges (Liao et al. 2008), although the authors proposed this as a nest predation reduction strategy. Our observation of 31% of male roosts outside DHRs could be the consequence of males soliciting EPCs from neighboring females in optimal morning and evening hours. The “sleeping around” hypothesis was not explicitly tested in this study, but is consistent with our observations. This possibility is corroborated by the fact that none of female roosts, including roosts alongside males, occurred outside corresponding DHRs. In Pennsylvania, female Wood Thrushes made more frequent off-territory forays in the fertile period accompanied by guarding mates, while solo males forayed frequently when females were incubating (Evans et al. 2008). In our study, either females roosted on active nests without males nearby (males often outside DHR), or they were guarded by males while fertile. Roost commutes for EPC solicitation with guarding males thwarting EPCs might thus be futile for females, making movement uneconomic.

Several potentially-confounding factors are worth noting. Observers flushed roosting birds from their perches in 12% (9 of 74) of cases, often in densely-vegetated areas or when transmitter antenna position resulted in weaker-than-expected signal.

Interrupted birds generally moved a short distance before settling back down and subsequent roost did not appear to differ from roosts associated with birds that were never disturbed. Also, we would like to emphasize that the roost observations are not completely independent as same birds were sampled repeatedly. However, we found 92% of 37 males roosted ≥ 20 m of previous roost, indicating that roost selection occurs nightly (Jirinec et al. 2011). Furthermore, having truly independent observations for our pair analysis would necessitate impractically large sample sizes.

Lastly, we would like to report that radio-tag signal detection was considerably better at night, when the generally ground-dwelling Wood Thrush roosts higher up in the trees of the subcanopy and canopy. As Lang et al. (2002) noted, the species regularly moves long distances between nesting attempts (up to 17,388 m). While we struggled to relocate the 56% of our males who shifted their DHR within the tracking period (longest movement > 4 km), we found detection radius greatly expanded at night.

Conclusion

To our knowledge, we provide the first broad description of roosting ecology for a Nearctic-Neotropical migratory passerine during the breeding season. Unexpectedly, many male Wood Thrush roosts were located outside of their diurnal home ranges. This study found that the species tended to roost in areas with higher canopy density than that of randomly selected points in their daytime range, but we suggest caution before concluding roost commute is driven by roosting habitat availability. Observed patterns in both male-only and pair roosts are consistent with the notion that opportunities for extra-

pair copulations may play a role in bird movement to roosting areas. This hypothesis deserves more attention in subsequent research.

Advances in tracking technology and battery life allow for transmitter attachment on ever smaller birds for longer periods, which stimulated research on avian movement patterns across a broad taxonomic extent. Despite abundant research utilizing individually radio-tagged, diurnal birds, few researchers have extended the tracking interval into the nighttime hours. This is a missed opportunity to gain valuable information on avian roosting behavior, which includes an increasing number of reports quantifying commutes to disjunct roosting areas. Such knowledge is critical for comprehensive understanding of habitat requirements for migratory birds, many of which are declining rapidly.

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Figure Captions

Figure 1. Sample diurnal home range (DHR) with corresponding roost locations for a single Wood Thrush (*Hylocichla mustelina*) pair in southeastern Virginia.

DHR represents 95% kernel density estimation, which employed male diurnal telemetry locations (black dots, $n \geq 50$), to derive relative percent diurnal use (black isopleths, outside = 0% diurnal use, DHR boundary = 5%, DHR center = 100%). Two roost for each male (circles) were identified on separate nights throughout the diurnal tracking period. For radio-tagged pairs, we located female roosts (triangles) on the same nights as we located male roosts. With nests in incubation and nestling stages, females roosted on nests (cross) located near peak relative diurnal use while males were away, often outside DHR boundary.

Figure 2. Wood Thrush male roost positions (dashed bins) in relation to their diurnal home ranges.

Out of 74 roost locations, 23 (31%) were located outside the respective diurnal home ranges (in the 0% diurnal use bin). Within-home range roost ($n = 51$) positioning did not follow the diurnal use pattern as the number of observed roosts inside the five diurnal home range partitions (relative use bins) did not differ from area-based expected proportions (gray bins; $\chi^2_4 = 2.5$, $P = 0.64$).

Figure 3. Mean difference in vegetation density between roost sites and paired random points within Wood Thrush diurnal home ranges derived from LiDAR data.

Positive differences indicate higher vegetation density at roost sites. Mean vegetation density within a 10-m neighborhood was significantly higher at roost sites than at

random points within diurnal home ranges (mean difference 6.5%, CI = 2.0 – 11.1, $n = 74$; paired t -test: $t_{73} = 2.8$, $P = 0.006$).

Figure 4. Distance to active nest (A) and pair separation based on nest status (B).

(A) Females with nests in incubation and early nestling stage (“active” nest) roosted exclusively in nest cup, with males an average of 121.8 m (CI = 72.6 – 204.2, $n = 11$) away on the same nights. (B) Separation of male and female roost sites was significantly higher with active nest compared to inactive nests – when nests failed or fledged (10.6 m, CI = 2.2 – 51.9, $n = 7$, two-sample t -test: $t_{16} = 3.4$, $P = 0.004$).

Figure 5. Roosts within Wood Thrush diurnal home range (relative percent diurnal use) by sex and nest status for the Wood Thrush.

Females with active nests (gray bars) roosted on nests located near peak diurnal activity areas. Median diurnal use (97%, CI = 94 – 98, $n = 11$) at roosts of actively-nesting females differed significantly from same-night male roosts (57%, CI = 0 – 73, $n = 11$, Wilcoxon signed rank test: $V = 66$, $P = 0.004$). When a nests failed or fledged (white bars), female roosting positions did not differ from male roosts ($n = 7$, Wilcoxon signed rank test: $V = 9$, $P = 0.89$). Error bars represent 95% confidence intervals derived from 1000 bootstrap samples.

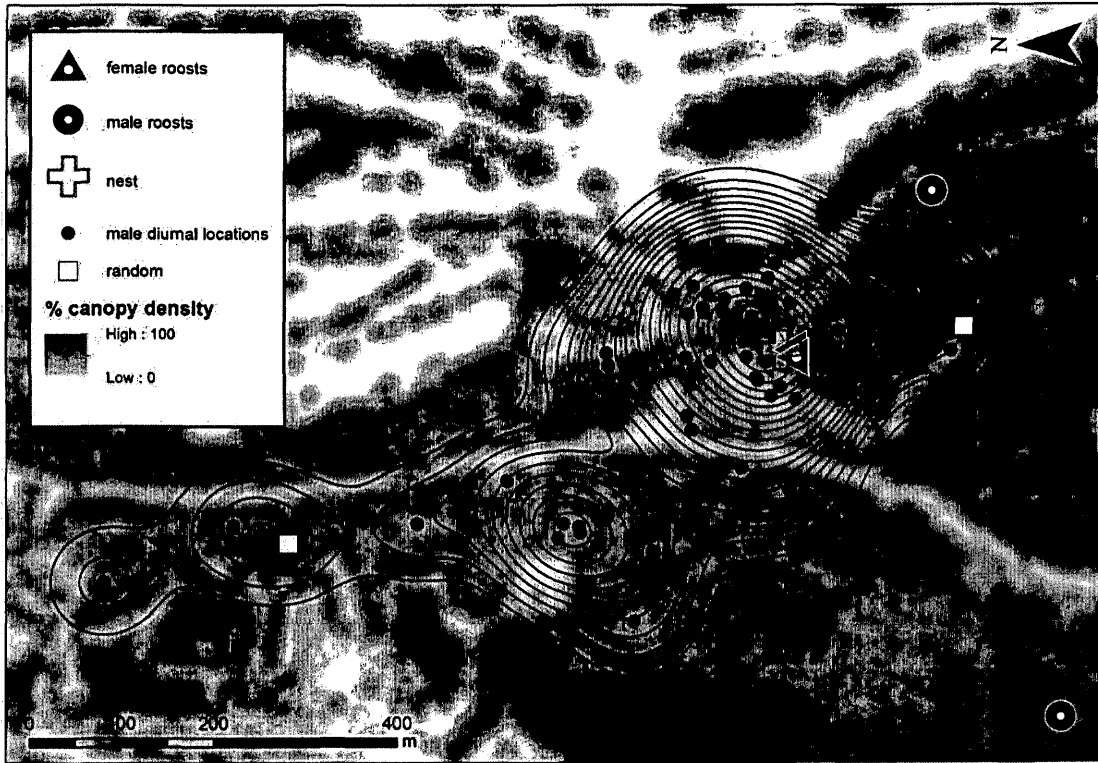


Figure 1

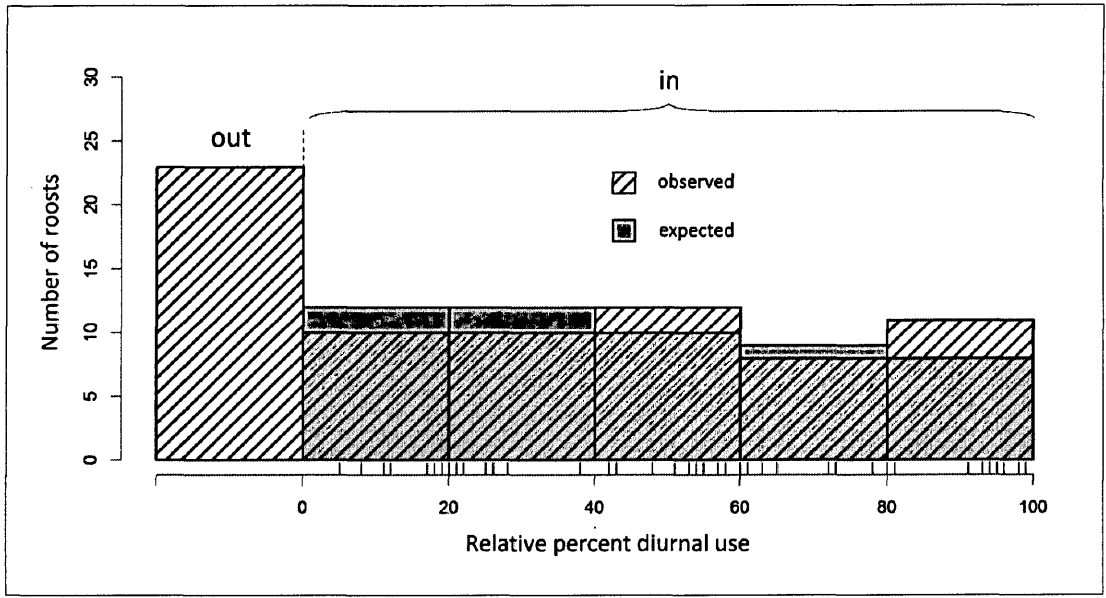


Figure 2

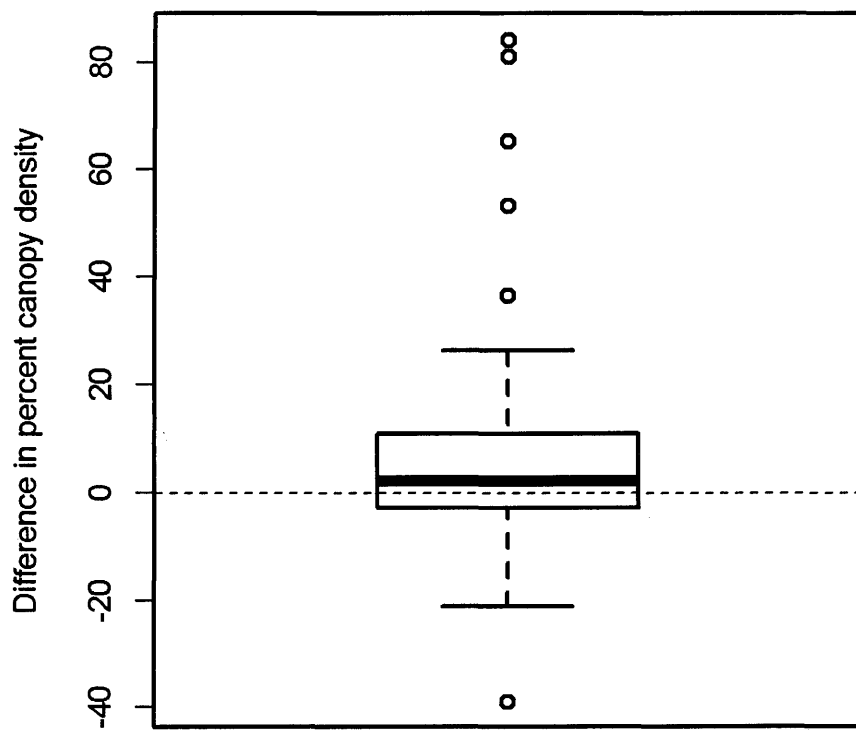


Figure 3

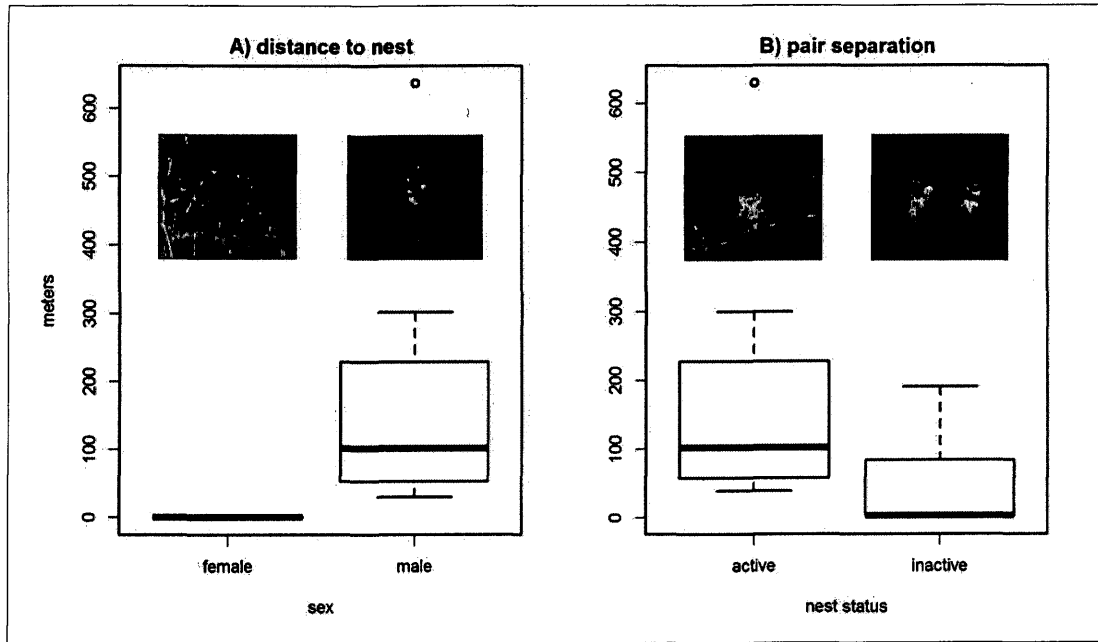


Figure 4

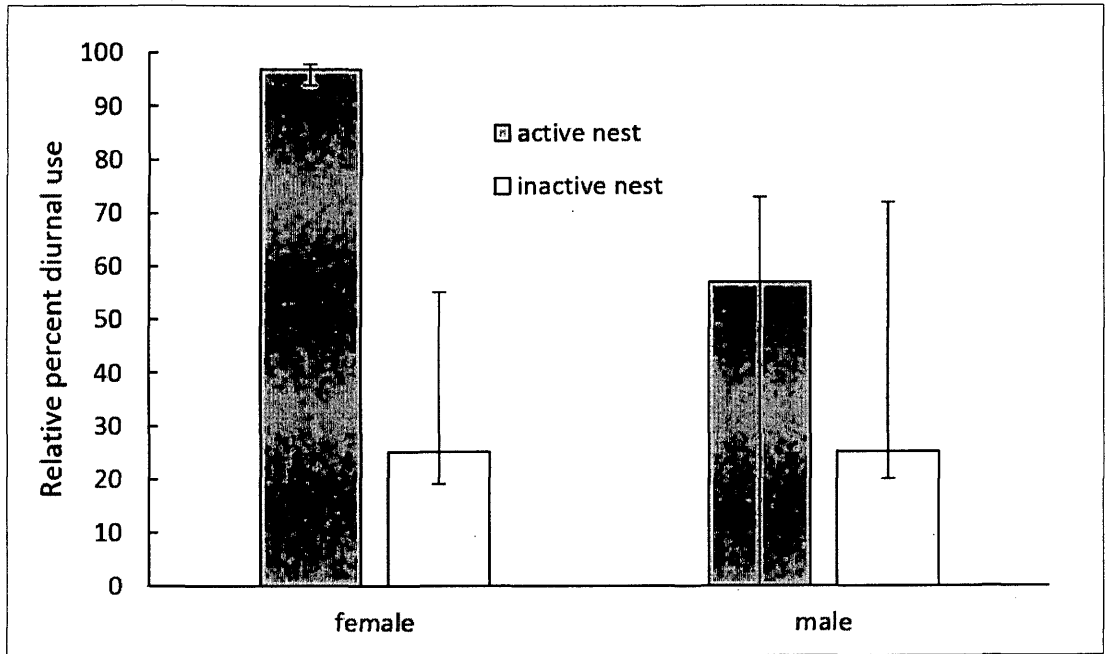


Figure 5

CHAPTER 2

Do food availability and habitat structure explain space-use patterns in breeding home ranges of Wood Thrushes?

Abstract

Researchers have long recognized the importance of understanding habitat requirements, yet breeding bird habitat selection remains one of the central questions in ornithology. We examined microhabitat associations of the declining Wood Thrush (*Hylocichla mustelina*) on its breeding grounds in Virginia. Using radio telemetry locations, we constructed 95% kernel home ranges for 37 male birds and related utilization distribution isopleths (relative percent use) to habitat structure and invertebrate biomass collected within home ranges. To assess the relative effectiveness of food availability and habitat structure in explaining space use patterns, we constructed both a prey model, including only invertebrate prey predictors, and a habitat model, including both prey and habitat structure predictors. Both habitat structure and prey biomass variables explained variation in space use, although prey predictors performed well in our prey model and most survived variable selection into the top habitat model. However, performance of individual invertebrate guilds changed with inclusion of habitat variables. We validated the habitat model by comparing data collected in bird home range cores to data collected at point count sites without Wood Thrush detections over the previous five years. Out of the 11 well-performing habitat model variables, three demonstrated significant differences in the direction predicted by the habitat model. Our research suggests the importance of food availability in driving space use patterns within Wood Thrush home

ranges, but highlights the importance of considering both prey and habitat structure variables.

Introduction

Loss and degradation of habitat is the chief threat to birds (Johnson 2007). Long-term demographic analyses indicate populations of many Nearctic-Neotropical migratory birds are declining (Ballard et al. 2003). Migratory songbird declines have been connected with events occurring on the breeding grounds (Rodenhouse and Holmes 1992), wintering regions (Holmes and Sherry 2001, Norris et al. 2004), and migratory stopover areas (Leu and Thompson 2002, Packett and Dunning 2009), and are often associated with local habitat quality. Preservation of bird habitat is thus crucial for the conservation of avifauna. However, this effort hinges on proper understanding of habitat requirements that would enable identification of quality habitat for protection.

How do we identify quality habitat? Van Horne (1983) warned that animal density does not necessarily equal quality habitat, prompting current metrics widely recognized to be optimal predictors of habitat quality to include information on survival and reproduction, as well as density of each target species (Johnson 2007). However, obtaining these measures of habitat quality often requires multi-year, species-specific monitoring efforts that are of considerable costs to ecologists and land managers alike. With limited funding, managers are often interested in prioritizing quality habitat for focal species based on its value for particular management objectives (Johnson 2007).

Because of frequent confusion in definitions of habitat quality (Hall et al. 1997), we use Johnson's (1980) definition of habitat preference and assume it gives a practical

index of habitat quality. Variation in resource availability generates strong selective pressure for recognition of high-quality habitat that maximizes the survival and reproduction of individual birds (Clark and Shutler 1999). Species-specific habitat preference patterns should therefore coincide with local habitat quality, and although measures relating animal density to habitat quality can be confounded with factors such as conspecific attraction (Reed and Dobson 1993), and ecological traps (Schlaepfer et al. 2002), space-use patterns of individuals may not be. Researchers have utilized a coarse-grained version of this approach to study habitat use, delineating animal home ranges (entire area occupied, Burt 1943) or territories (actively defended areas only, Noble 1939), and identifying differences between these and surrounding areas to classify habitat requirements (Anich et al. 2012). Assuming homogenous use of all areas within a territory has often been necessary for logistical reasons (Barg et al. 2006). However, with recent advances in animal tracking techniques and the recognition that habitat heterogeneity occurs at even small scales, some investigators have examined fine-scale habitat associations within home ranges and territories. To our knowledge, such microhabitat associations have been examined only for two migratory species of concern. Barg (2006) found that high-use areas of Cerulean Warbler (*Setophaga cerulea*) territories were predominately composed of Bitternut Hickory (*Carya cordiformis*), which was a preferred song-post tree. Highly-used segments within home ranges of Swainson's Warblers (*Limnothlypis swainsonii*) were associated with a consistent set of microhabitat features, such as more stems, leaf litter, and canopy cover (Anich et al. 2012).

Here, we examine microhabitat associations of the Wood Thrush (*Hylocichla mustelina*), a reclusive passerine found in wooded environments. Following the trend of many migratory birds, populations of this species show a long-term, range-wide population declines of $-2.12\% \text{ yr}^{-1}$ from 1966 to 2012 (Sauer et al. 2014). Because of its prestige with the public and rapid decline along with other migratory birds, this songbird is often cited as a symbol of declining Nearctic-Neotropical birds and is the focus of conservation and management plans in many areas (Driscoll et al. 2005, Roth et al. 2011). A number of studies document the detrimental effect of nest parasitism on Wood Thrush demography in smaller forest fragments (Lloyd et al. 2005, Trine 1998). However, aspects of fine-scale habitat preference are poorly understood for this species. On the breeding grounds, frequently-occupied areas have been qualitatively related to upland deciduous and mixed forests with moderate subcanopy, semi-open floor with decaying litter, and a high diversity of tall deciduous tree species (Roth et al. 2011).

The effects of habitat structure and food availability on bird habitat use has been evaluated by a number of studies (e.g., Banko et al. 2002, Garcia et al. 2011, Vickery et al. 2001). Much of this research focuses on landscape-scale associations between bird demographic patterns and habitat attributes, rather than direct observations of individual birds. To our knowledge, no study of a forest songbird has related fine-scale space use patterns derived from individually-tracked birds to both habitat structure and food availability resources.

The main goal for this study was to model Wood Thrush space use with both invertebrate prey availability and habitat structure predictors to (a) determine microhabitat associations and (b) assess the relative importance of prey availability

versus habitat structure in driving use patterns for this species. Specifically, our objectives were to develop (1) a food availability model and (2) a prey-habitat model, and (3) to assess model variable validity using an independent dataset of Wood Thrush absence.

Methods

Study Area

For broader land cover representation of this wide-ranging species, we captured and tracked individual birds at eight parks and one military installation located in the Coastal Plain of southeastern Virginia (centroid: 37° 15' N, 76° 40' W). Birds were tracked on property managed by the National Park Service, College of William and Mary, Colonial Williamsburg, City of Newport News, City of Williamsburg, York County, James City County, Kingsmill Resort, York River State Park, and the US Navy.

Encroaching urbanization fragments many of the study sites and the region is moderately covered with eastern deciduous and mixed forest (Monette and Ware 1983). We surveyed vegetation at six circular plots (15 m radius) within each study bird's home range (222 plots total). On average, highest tree density was represented by Tulip Poplar (*Liriodendron tulipifera*; $51.6 \pm \text{SE} = 4.6$ trees/ha), American Beech (*Fagus grandifolia*; 49.6 ± 3.9 trees/ha), American Holly (*Ilex opaca*; 45.2 ± 4.5 trees/ha), with mean diameter at breast-height (cm) at 39.7 ± 0.8 , 25.5 ± 0.6 , 13.8 ± 0.2 , respectively. Ground was generally open with broad leaf-litter carpeting most of the forest floor ($61.8 \pm 1.5\%$). Pawpaw (*Asimina triloba*), along with saplings of *I. opaca* and *F. grandifolia* comprised the highest counts of understory woody vegetation.

Bird Capture and Marking

We tracked 37 male birds using radio telemetry over two breeding seasons (2013, 2014). Results of a concurrent study suggest pair home ranges overlap highly (A. Deverakonda, *unpub. data*). Birds were captured May 15 – June 3 of both years using 30-mm mist nets with conspecific song playback (Angelier et al. 2010). Target netting allowed us to capture individuals with established territories and to avoid floaters which could quickly depart the survey area. For each bird, we affixed a USGS aluminum band along with a unique set of three color bands for identification in case of premature transmitter detachment.

We used a figure-eight leg harness (Rappole and Tipton 1991) to attach a 1.3 g VHF transmitter (BD-2, Holohil Systems Ltd., Carp, ON, Canada) to each bird. Transmitters attached with this technique are standard for medium-sized birds (Powell et al. 1998; Evans et al. 2008; Gow et al. 2011), and ensure secure fitting for the duration of radio life with no evidence for behavioral or physiological effects for the Wood Thrush during breeding and molt (Gow et al. 2011), and little influence on migratory range in case transmitters fail to detach prior to departure for wintering grounds (Powell et al. 1998). We used 0.7 mm Stretch Magic jewelry cord for the harness (intraloop distance = 57.5 mm), and observed no injurious rubbing on individuals recaptured following initial transmitter deployment ($n = 6$) up to 46 days later. Two birds were recaptured in order to re-attach a lost transmitter due to fractured harness, suggesting birds eventually lose tags during normal wear. All federal, state, and local permits were secured prior to field work, and the project was approved by the College of William and Mary Animal Use and Care Committee (IACUC-2013-02-15-8462-mleu).

Home Range Estimation

Home ranges were derived from diurnal radio telemetry locations (Marzluff et al. 2004). Birds were tracked from May 16 through July 25 of both years (mean 11.9 ± 0.8 unique days) between 06:30 and 20:30 EDT until transmitter battery depletion (average battery life = 60 days). We attempted to obtain at least one location per bird each hour between 08:00 – 20:00 to account for variation in temporal space use (Anich et al. 2012); otherwise locations were distributed throughout daytime hours. To ensure biological independence between locations [defined as interval long enough to reach any point within home range, (Barg et al. 2005)], points were recorded ≥ 20 min apart. This interval is equal or larger than in similar studies with three warbler species (Anich et al. 2012), and we believe it is adequate as birds often moved substantially between relocations, easily traversing their home ranges. Final bird location was determined by observers carrying 3-element Yagi antennas and receivers from Wildlife Materials (TRX-1000S, TRX-3000S). To avoid telemetry bias due to observer disturbance, we homed in to within ≤ 50 m of target, then projected bird position in GPS units (Garmin GPSMap 62) using compass bearing and distance with a laser range finder (Opti-Logic 400LH). In cases where birds moved beyond detection radius (Lang et al. 2002), we performed extensive ground searches with twin truck-mounted antennas along with aerial telemetry using a fixed-wing aircraft.

We base home ranges on utilization distributions generated from 95% kernel density estimations (Barg et al. 2005, Marzluff et al. 2004, Worton 1989). The traditionally-popular minimum convex polygon (MCP) approach to delineating activity regions is susceptible to influence of outliers, may contain never-used areas, and does not

provide frequency of use within the home range (Harris et al. 1990). Resource selection functions based on utilization distributions have been used in telemetry studies to link frequency of use with habitat attributes (Marzluff et al. 2004, Millspaugh et al. 2006). Utilization distribution is a representation of an individual's relative space use as a function of telemetry location density, thus portraying the probability of individual occurrence (hereafter % use) within each pixel of its activity area (Horne and Garton 2006, Marzluff et al. 2004). Using utilization distribution in contrast to direct animal locations dilutes intrinsic telemetry error (e.g. GPS accuracy and error during triangulation), allows for occurrence prediction in regions where animals were never directly observed due to discontinuous monitoring, and is therefore considered the best available activity region estimator (Kernohan et al. 2001).

We used inverse isopleths (i.e. quantiles of kernel estimates) of the utilization distribution to represent % use (Figure 1). Home range edge thus corresponds to 5% diurnal use for conservative area estimate (Pechacek and Nelson 2004), whereas the most-used sections within home range were classified as 100% use. Although the least-squares cross-validation (LSCVh) is commonly used as the kernel bandwidth selection method (Gitzen and Millspaugh 2003), we found this approach did not perform well for individual birds with multiple frequently-used regions. An alternative to LSCVh is the likelihood cross-validation (CVh), which has been shown to generally yield estimates with better fit and less variability than LSCVh, and to perform better with smaller sample sizes (Horne and Garton 2006). Barg et al. (2005) recommended 50 locations as the lower limit for LSCVh kernels. We used on average 53.9 ± 1.3 locations (range 50 – 80) to

construct home ranges. Kernel density estimation and subsequent home ranges were constructed in Geospatial Modeling Environment (Beyer 2011).

Invertebrate Prey Sampling

We collected 10 food availability samples within the home range of each bird. Distribution of sampling sites was based on stratified random sampling to retain the ability for analysis with both a continuous (% use) and binary (high and low use) response, as well as for balanced sampling of low-use and high-use (core) sections of home range. Following Anich (2012), we considered the 55% KDE (45% use) as the home range core. Similarly, this quantile appeared to contain discrete clusters of telemetry locations, and fell within the core range used in other studies (Anich et al. 2012). The Wood Thrush is known to forage on invertebrates mainly in forest leaf litter during the breeding season (Roth et al. 2011), and we therefore collected forest litter samples for subsequent invertebrate extraction. We did not encounter substantial variation in litter depth, and firm soil layer was present often underneath a defined layer of decomposing leaves and twigs (~2 cm). We gathered this layer at a 50 x 50 cm plot at each of the 10 sampling sites, removed larger leaves and stems without letting mobile invertebrates escape, and froze the resulting sample at -80°C for processing during the offseason. If no litter was found at the exact GPS location, we collected litter at the closest location within 5 m with $\geq 50\%$ litter cover. We recorded zero leaf litter invertebrates at sites with no litter within 5 m, such as in thick grass, forbs, and bare ground, although such cases comprised only 5.7% of total plots. On a few occasions (1.9%), we encountered small vertebrates such as frogs, salamanders, and snakes (mostly

Carphophis amoenus); these were released unharmed and not considered in analyses. In 2014, we took three soil moisture readings per plot, 3.8 cm deep, using a digital moisture sensor (FieldScout TDR 300) to evaluate effect of soil moisture (% volumetric water content, %VWC) on invertebrate biomass. Moisture readings were spaced evenly along a diagonal transect of the plot frame following litter collection.

Samples were processed by manual sorting of invertebrates from plant matter immediately after defrosting. Assuming that birds respond more to prey morphology than taxonomy, we assigned invertebrates to one of five guilds based on common body types (Table 1). For simplicity, we refer to guilds without regard to their true taxonomic classifications. The “worms” guild, for example, includes soft, worm-like invertebrates such as earthworms (Oligochaeta) and beetle larvae (Coleoptera), which although not closely related, might be treated similarly by prey-seeking birds. After obtaining counts per guild in each sample, we dried invertebrates at 60°C for at least 48 hours prior to obtaining weight in grams to 0.0001 g (Thomas Scientific TSXB120A). Food availability dataset therefore consisted of 370 samples containing both count and biomass for each of the five invertebrate guilds.

Habitat Structure Assessment

Habitat structure predictors were derived from remote sensing datasets and field-based vegetation surveys. We collected field-based habitat structure data in circular plots with 15-m radius at six of the ten food availability sites within bird home ranges (Figure 1). Vegetation site assignment was random insofar as stratified design was retained and plots did not overlap. We gathered data for 67 variables suspected *a priori* as potentially

important predictors of bird presence (Table 5), of which six were derived from remotely-sensed data. Within 15 m of plot center, we recorded counted and identified all large trees (≥ 10 cm DBH) and measured diameter at breast height (DBH). We also measured volume of all downed woody debris ≥ 10 cm in diameter. Trees were assigned into either canopy or subcanopy height strata based on their predominant crown positions. Within 7.5 m of plot center, we identified to species and counted all woody stems (“saplings,” 1 – 10 cm DBH). Lastly, we estimated percent ground cover of seven categories comprising the average of 13 Daubenmire plots [50 x 50 cm, Daubenmire (1959)], spaced evenly along two 15-m transects crossing perpendicularly at vegetation plot center. Only deciduous leaf litter and pine needles were selected as ground cover predictors to augment their independence.

Six habitat structure variables, measured at vegetation plot center, were derived from remote sensing data. We calculated minimum distance of vegetation plot to stream and forest edge in Geographic Information System (GIS, ArcMap 10.1), using Euclidean distance to streams (TIGER, US Census Bureau 2014) and forest boundary. We delineated forest boundary, forest density (1 m and above), understory density (0 – 3 m), canopy height, and terrain ruggedness index (Riley et al. 1999), using discrete return Light Detection and Ranging (LiDAR) data collected in 22 April – 10 May, 2010, and 21 – 31 March, 2013. LiDAR has been used to quantify three-dimensional terrain structure at relatively high resolutions (Lefsky et al. 2002), including detailed vertical biomass distribution (Vierling et al. 2008). We used LAStools software (version 150202) to process LiDAR data and derived vegetation density rasters within desired height strata. Vegetation density was calculated as the number of returns within designated height bin

divided by the number of all returns inside each raster cell. We removed low-lying LiDAR points (< 0.3 m) to avoid noise from floor vegetation. Forest boundary was delineated by tree canopy above 10 m while disallowing for gaps < 25 m². Forest density, understory density, and maximum canopy values represent the average within a 10-m circular neighborhood using focal statistics (ArcMap 10.1) to accommodate GPS accuracy errors.

Bird Surveys for Model Validation

We selected sites where Wood Thrush were known to be absent during the preceding years of another study to validate predictors selected for the final habitat model. Bird absence was based on detection history spanning five years (2010 – 2014) at 131 point count stations. We randomly distributed point count stations in forested tracts embedded in suburban and low-development areas before surveying breeding avifauna in June of each year using variable circular point counts. Every survey station was sampled with three 8-minute consecutive surveys each summer. Stations ($n = 32$) without visual and auditory evidence of Wood Thrush presence (naïve occupancy = 0) over survey period (total 120 min of surveys per site) have been designated as absence sites. We collected food availability and habitat structure samples at absence sites (one plot/site) at the center of each point count location following an identical protocol as described above for occupied bird home ranges.

Analysis

We modeled Wood Thrush utilization distribution using a prey availability model and a habitat structure prey availability model (hereafter “prey” and “habitat” models, respectively). Both models employ % use (0 – 100) as the continuous response variable in a mixed-model framework where observations are nested within individual birds designated as random effects in the “nlme” package in R software (R Core Team 2014). Before analysis, we scaled and centered all predictors using respective means and standard deviations. We selected model predictors based on performance in relation to null model in a univariate analysis. Predictors with lower Akaike’s Information Criterion (AIC) scores than null were brought forward for bivariate tests of collinearity using Pearson’s correlation coefficient. We removed highly correlated variables (correlation coefficient $> |0.7|$) that were either more ambiguous or had a weaker hypothesized relationship with modeled response. Before multivariate analysis, we plotted response and predictor variables to check for nonlinear associations (Zuur et al. 2010). To reduce number of predictors for inclusion in the final model, we built models representing all possible variable combinations of total predictor pool after univariate modeling and checking for collinearity, keeping the maximum number of model terms to six to allow for a sensible computation interval. Variables whose sign remained constant (either always negative or always positive), indicating predictor strength and suggesting lack of interactions, were included in the global model. We subsequently built models representing all possible combinations of the statistically independent predictors from the global model (Doherty et al. 2012), and model-averaged the partial regression coefficients of all models whose cumulative AIC weight summed up to 0.95 (Burnham

and Anderson 2013). Additionally, we evaluated effect of soil moisture and Euclidean distance to streams using Spearman's rank correlation test, and tested our hypothesis that home ranges will have higher %VWC than sites from which birds were absent over the previous five years (hereafter, absence sites), with a two-sample *t*-test. We transformed moisture data using natural log to meet the normality assumption, and checked for homogeneity of variance using Levene's test (Levene 1960). Lastly, we tested for differences in medians between bird home range cores and bird absence areas using a Wilcoxon rank sum test to evaluate variables selected for the habitat model. All tests were two-tailed with analyses conducted in R software.

Results

Prey Model

We counted 4,456 invertebrates comprising a total of 85.33 g of dry biomass across five invertebrate guilds in the 370 plots within bird home ranges. In the 32 bird absence plots, we counted 323 invertebrates totaling 1.78 g. Invertebrate biomass was a better predictor of bird use than invertebrate count. None of the count predictors performed better than the null model in univariate modeling, while all five variables representing biomass of each of the invertebrate guilds were brought forward into the global model.

Model-averaged partial regression coefficients along with model-averaged standard errors are listed in Table 2. The strongest predictor of bird use was the biomass of the worm guild ($\beta = 3.84 \pm 1.50$), followed by biomass of spiders (2.21 ± 1.30), beetles (2.02 ± 1.27), other (-0.74 ± 0.96), and centipedes (-0.06 ± 0.85).

Soil dampness was correlated with biomass of some invertebrate guilds, as we found while testing for correlations with the three guilds whose standard errors did not overlap zero in the prey model (Tab. 3). Worm guild biomass, composed primarily of Oligochaeta, was strongly correlated with soil volumetric water content ($\rho = 0.35$, $P < 0.0001$), and negatively correlated with distance to streams ($\rho = -0.29$, $P < 0.0001$). Soil moisture (log %VWC) was significantly higher at plots within bird home ranges (2.88 ± 0.04) than at bird absence sites (2.65 ± 0.09 ; two-sample t -test: $t_{190} = 2.3$, $P = 0.02$).

Habitat Model

Most invertebrate biomass predictors also survived into the habitat model (Tab. 4). Out of a total of 67 variables tested with univariate models, 37 performed better than null model (Table 5). We removed 12 collinear predictors and evaluated stability of remaining 25 variables in multivariate models. Analysis of all possible combinations of the 11 surviving predictors resulted in 79 models whose AIC weights summed to 0.95. Four of the five invertebrate biomass guilds from the prey model persisted into the top, model-averaged habitat model including both the prey and habitat structure variables. The strongest predictors of bird use were count of Red Oak (*Quercus rubra*, $\beta = -5.66 \pm 2.00$), beetle biomass (5.63 ± 1.96), canopy height (5.49 ± 1.96), and basal area of snags (4.77 ± 1.99).

To validate the effect of the 11 well-performing variables, we used a subset of the habitat data – plots in the core section of bird home ranges ($n = 111$) – and compared the subset with habitat data collected at bird absence locations ($n = 32$, Figure 2). Following

predicted directions generated by the habitat model, the differences in medians between home range and absence site habitat samples were significant for 3 of 11 top-performing predictors: canopy height ($W = 832, P < 0.001$), red oak count ($W = 2178, P = 0.04$), and worm biomass ($W = 1208, P = 0.004$). Non-significant, trends in many of the remaining variables also followed predicted directions.

Discussion

Our results indicate that availability of invertebrate prey appears to play an important role in explaining within-home range space use of male Wood Thrushes. We built two models: one with prey biomass variables and one with both prey biomass and habitat structure variables. The predictors associated with biomass of invertebrate prey guilds have consistently performed well in both models. In the prey-only model, we found the worm biomass guild to be the strongest predictor of bird use. This guild contained primarily biomass of earthworms (Oligochaeta), but included smaller amounts of Lepidoptera, Coleoptera, and Diptera larvae. Positive coefficients whose standard errors did not overlap zero were also estimated for biomass of the spider and beetle guilds, which were primarily composed of Arachnida, Blattodea, and Coleoptera. Although the relationship with use was weak, both the prey model and habitat model included the “other” invertebrate guild, which was primarily composed of ants (Hymenoptera).

A number of studies highlight the importance of invertebrate biomass to Wood Thrush. Holmes and Robinson (1988) quantified Wood Thrush diet by examining bird stomach contents on the breeding grounds in New Hampshire. Out of 329 identifiable prey items observed in stomach contents of 60 birds, 33.4% were Coleoptera adults

(4.6% larvae), 17.3% Hymenoptera, 15.8% Diptera adults (2.7% larvae), 11.6% Lepidoptera larvae, and 1.8% Arachnida. The authors acknowledged that due to short persistence in bird stomach, soft-bodied invertebrates were underestimated in their assessment. In a West Virginia nest camera study of 56 Wood Thrush nests, “common prey items included lepidopteran and other caterpillar-like larvae, earthworms, and small insects (Williams 2002).” In another West Virginia study, daily nest survival probability of ground-gleaning birds (including Wood Thrush), and Wood Thrush nestling growth rate were both positively associated with invertebrate biomass (Duguay et al. 2000). Ovenbirds (*Seiurus aurocapilla*), which also forage on leaf litter invertebrates, were found to choose territories with significantly higher invertebrate biomass than random points within the woodlot (Burke and Nol 1998). The results of the above research are consistent with the positive associations of our invertebrate predictors and Wood Thrush space use, as well as their good performance in models.

The habitat model implicated the importance of seven habitat structure variables, demonstrating food prey availability as only partially important in Wood Thrush space use. The strongest predictor of space use was count of red oak (*Quercus rubra*, $\beta = -5.66 \pm 2.00$), a variable that was corroborated by the predictor validation (Figure 2). However, we cannot easily explain a negative association of red oak and space use. It is possible that red oak density is negatively correlated with an environmental variable we did not measure (e.g., soil type), but which either directly or indirectly positively affects space use. The second strongest habitat predictor, also endorsed by validation, was canopy height (5.49 ± 1.96). Mean canopy height was the most important predictor of Wood Thrush relative abundance found by Robbins et al. (1989), while Hoover and Brittingham

(1998) found the species selected nest sites with higher canopy than random points within forest tract. This result is consistent with the notion the species prefers well-developed forest, although tree diameter did not come forward in our univariate analyses (Table 5). Snag basal area (4.77 ± 1.99) – the third strongest structure predictor – is also expected to be higher in mature forest, in addition to a likely association with invertebrate biomass. Density of spiders was higher adjacent to coarse woody debris in Swedish temperate forests (Castro and Wise 2010), while sites with leftover decaying wood had significantly higher number and diversity of carabid beetle species (Nittérus et al. 2007). Old trees, logs, and snags have been identified as critical habitat elements for more than 500 forest insect species, including saproxylic beetles (Johansson et al. 2006). Many of these decaying-wood-associated beetles do not feed on wood, but rather on the wood-colonizing fungi (Johansson et al. 2006), which might be promoted by higher soil moisture found within bird home ranges. Tree sapling richness (3.19 ± 1.81), which is a predictor of Wood Thrush abundance (Robbins et al. 1989), could also be associated with invertebrate biomass as niche availability increases with number of tree species. The last three structure predictors in our habitat model are linked with red maple (*Acer rubrum*) and American holly (*Ilex opaca*), which are both locally common understory trees and a frequent nesting substrate observed for our study birds. Bakermans et al. (2012) suspected nest site availability explained the positive relationship of Wood Thrush density and number of small trees.

Prey availability predictors, albeit well-represented, had different strengths in the two models. While spider biomass had approximately equal effect in both models, biomass of worms, the strongest prey model predictor (3.84 ± 1.50), was the weakest

variable in the habitat model (1.12 ± 1.37). Inversely, beetle biomass was the strongest prey availability variable in the habitat model (5.63 ± 1.96) while of marginal importance in the prey model (2.02 ± 1.27). It is possible that this discrepancy results from the difference in sample size between the prey model ($n = 370$), and the habitat model ($n = 222$). However, we propose that the more inclusive habitat model ties bird use to its environment with improved accuracy, which reflects utilization of foraging opportunities as well as resources for other activities, such as nesting. Nest positions of birds tracked in this study suggest a strong positive relationship with bird use isopleths (A. Deverakonda, *unpub. data*), indicating variables identified in this study are important predictors of nest site selection.

We point out two drawbacks of our variable validation. First, model validation was done with only a partially-independent dataset (Figure 2). We related data collected within home range cores to bird absence sites, but home range data were used to construct both models. Thus canopy height, for example, could be higher at occupied sites due to a chance positive relationship with bird use which brought the variable forward in the analyses in the first place. Conversely, the same logic does not explain the high worm biomass at bird core sites while the same variable was the poorest predictor of bird use in the habitat model. Similarly, there was no difference in beetle biomass between core and absence sites while beetle performance was among the best two in the entire model. Second, predictors of space use within home ranges might be different from predictors of home range location. One of central tenets in migrant habitat selection is that birds choose habitat hierarchically, from coarse to fine scale (Battin and Lawler 2006). Importance of predictors across scales is likely, but probably not for all variables.

Canopy height, for example, can be assessed by a bird flying over, while evaluation of beetle prey biomass requires more information. Nevertheless, we believe our model validation lends additional legitimacy to the three significant relationships that follow hypotheses generated by the habitat model.

In summary, our models suggest the importance of specific food prey and habitat structure variables as being important predictors of within-home range use patterns for the Wood Thrush. Invertebrate prey guilds performed consistently well in both models. However, the interplay of both prey and habitat structure variables probably provides the best representation of the fine-scale factors needed by this quickly-declining species.

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Table Headings

Table 1. Invertebrate guild assignment.

Table 2. Model-averaged partial regression coefficients and standard errors of the prey availability model. We averaged 12 models whose Akaike's Information Criterion weights summed to 0.95. Predictors were centered to make β -values directly comparable.

Table 3. Spearman's rank correlation test results for two variables suspected to affect invertebrate biomass. Out of the three guilds with measured relationship to bird use, biomass of worm-like invertebrates demonstrated a strong affinity to wet areas.

Table 4. Model-averaged partial regression coefficients and standard errors of the habitat model. We averaged 79 models whose Akaike's Information Criterion weights summed to 0.95. Predictors were centered to make β -values directly comparable.

Table 5. All variables considered in the habitat model and their description. The predictors were first examined in univariate models (AICc), followed checks for collinearity and slope stability (in multivariate models). Top predictors were included in the global model.

Table 1

guild	taxon examples	guild description
“worms”	Oligochaeta; larvae of Lepidoptera, Diptera, and Coleoptera	soft-bodied, worm-like invertebrates
“beetles”	Coleoptera; Hemiptera, Blattodea	insects with hard exoskeletons
“centipedes”	Chilopoda; Diplopoda; terrestrial Isopoda	many-segmented arthropods
“spiders”	Arachnida; Isoptera; Orthoptera, Dermaptera	arthropods with soft abdomen
“other”	Hymenoptera; Diptera; Lepidoptera	all others, no Gastropoda

Table 2

predictor	β	SE	AICc cumulative weight
intercept	43.64	1.49	
worm biomass	3.84	1.50	1.00
spider biomass	2.21	1.30	0.87
beetle biomass	2.02	1.27	0.85
other biomass	-0.74	0.96	0.64
centipede biomass	-0.06	0.85	0.57

Table 3

guild	distance to streams		soil dampness (%VWC)	
	rho	<i>P</i>	rho	<i>P</i>
worm biomass	-0.29	< 0.0001	0.35	< 0.0001
spider biomass	-0.04	0.52	0.13	0.09
beetle biomass	-0.04	0.60	-0.18	0.02

Table 4

predictor	β	SE	AICc cumulative
			weight
intercept	45.12	1.91	
red oak count	-5.66	2.00	0.998
beetle biomass	5.63	1.96	0.997
canopy height	5.49	1.96	0.994
snag basal area	4.77	1.99	0.973
maple basal area	3.85	1.86	0.943
sapling richness	3.19	1.81	0.894
maple sapling count	2.35	1.68	0.822
holly sapling count	2.32	1.70	0.818
spider biomass	2.16	1.57	0.811
other biomass	1.35	1.39	0.721
worm biomass	1.12	1.37	0.696

Table 5

AICc	ID	status	predictor description & notes
2139	ba_snag	global model	basal area of snags – upright dead trees
2139	beetle_g	global model	beetle guild biomass (food prey)
2140	spider_g	global model	spider guild biomass (food prey)
2141	other_g	global model	other guild biomass (food prey)
2144	ba_ah	unstable in mult.	basal area of American holly
2145	can_rich	unstable in mult.	number of species of trees in the canopy stratum
2146	can_sdi	removed, corr > 0.7	canopy trees Shannon diversity index; correlated with can_rich, and rich is more easily explained
2146	ba_ma	global model	basal area of red maple
2146	canopy_ht	global model	LiDAR, mean maximum canopy height in 10 m neighborhood in 1 m raster cell size
2146	sap_sdi	removed, corr > 0.7	saplings Shannon diversity index; correlated with sap_rich, which is easier to explain
2147	total_w	removed, corr > 0.7	sum of biomass of all guilds; correlated with worms, and although worms have higher AIC, take this out for comparison with invert-only model
2147	ba_m2	removed, corr > 0.7	basal area of all trees; correlated with max_canopy_m, which is a better predictor
2147	sapl_rich	global model	# of sapling species (>10 cm dbh)
2147	centipede_g	unstable in mult.	centipede guild biomass (food prey)
2147	cov_dbh	unstable in mult.	coefficient of variation of all large trees
2147	ba_can	removed, corr > 0.7	basal area of canopy trees; correlated with ba_m2, which has lower AIC
2148	worm_g	global model	worm guild biomass (food prey)
2148	tree_sdi	unstable in mult.	all trees Shannon diversity index
2148	ba_haw	unstable in mult.	basal area of hickory, ash, walnut
2149	ba_sg	unstable in mult.	basal area of sweetgum
2149	ba_b	unstable in mult.	basal area of beech
2149	spider_n	removed, corr > 0.7	spider guild count (food prey), correlated with spider_g
2149	ba_sub	unstable in mult.	basal area of subcanopy trees
2150	ba_pi	unstable in mult.	basal area of pine trees
2150	sub_sdi	removed, corr > 0.7	Shannon diversity index of subcanopy trees, correlated with tree_sdi, which is a better predictor, and subcanopy designation is subjective
2150	ba_tp	unstable in mult.	basal area of tulip poplar
2150	ba_o	unstable in mult.	basal area of all oaks
2150	veg_dens	unstable in mult.	fractional density of LiDAR returns 1 m and above
2150	tree_rich	removed, corr > 0.7	tree richness - number of species >10cm dbh; correlated with tree_sdi AND sub_sdi
2150	snag_ct	removed, corr > 0.7	snag count, correlated with ba_snag, which is the top predictor
2150	ro_ct	global model	red oak count
2151	ah_sap_ct	global model	American holly sapling count

2151	haw_ct	removed, corr > 0.7	count of hickory, ash, walnut; correlated with ba_haw, which is better predictor
2152	beetle_n	removed, corr > 0.7	beetle guild count (food prey); correlated with beetle_g
2152	dwd_m3	unstable in mult.	volume (cubic meters) of downed woody debris
2152	ma_sap_ct	global model	red maple sapling count
2153	pi_ct	removed, corr > 0.7	pine trees count; correlated with ba_pi, which is better predictor
2153	null		
2153	av_dbh_s	removed, AIC > null	mean DBH of subcanopy trees
2153	sub_rich	removed, AIC > null	number of species in subcanopy
2153	wo_ct	removed, AIC > null	white oak count
2153	o_ct	removed, AIC > null	count of all oak trees
2153	av_dbh	removed, AIC > null	mean DBH of all trees
2154	unders_dens	removed, AIC > null	fractional density of LiDAR returns 12 cm to 3 m
2154	conif_sap_ct	removed, AIC > null	count of coniferous saplings
2154	centipede_n	removed, AIC > null	centipede guild count (food prey)
2154	ah_ct	removed, AIC > null	American holly count
2154	b_ct	removed, AIC > null	beech count
2154	tp_ct	removed, AIC > null	tulip poplar count
2154	canop_ct	removed, AIC > null	count of canopy trees
2154	sg_ct	removed, AIC > null	sweetgum count
2154	ma_ct	removed, AIC > null	red maple count
2154	b_sap_ct	removed, AIC > null	beech saplings count
2155	percov_ll	removed, AIC > null	% cover of deciduous leaf litter
2155	tri	removed, AIC > null	terrain ruggedness, as described by Riley et al. (1999)
2156	percov_pl	removed, AIC > null	% cover pine needles
2156	subcan_ct	removed, AIC > null	count of subcanopy trees
2156	sapl_ct	removed, AIC > null	all saplings count
2156	percov_f	removed, AIC > null	% cover forbs
2156	tree_ct	removed, AIC > null	total tree count
2157	other_n	removed, AIC > null	other guild count (food prey)
2157	av_dbh_c	removed, AIC > null	mean DBH of canopy trees
2157	pp_ct	removed, AIC > null	pawpaw count
2157	worm_n	removed, AIC > null	worm guild count (food prey)
2158	total_n	removed, AIC > null	sum of all invertebrates (food prey)
2159	edge_dist_m	removed, AIC > null	Euclidean distance to forest edge, forest constructed as follows: LiDAR, maximum above 10 m canopy within 5 m neighborhood, holes below 5m ² removed
2162	dist_stream_m	removed, AIC > null	Euclidean distance to streams (tiger streams)

Figure Captions

Figure 1. Example home range of one of 37 Wood Thrush (*Hylocichla mustelina*) males tracked in this study.

Home ranges were constructed using 95% kernel density estimation (KDE), which employed male telemetry locations (black dots, $n \geq 50$), to derive percent diurnal use (grey isopleths, boundary = 5% use, home range centers = 100% relative use). We delineated home range core area (bold isopleth, 55% KDE) to facilitate stratified random placement of leaf-litter invertebrate sampling locations (triangles, $n = 10$) and 30-m-wide habitat structure plots (grey circles, $n = 6$).

Figure 2. Validation of habitat model predictors.

We used habitat data collected in plots ($n = 111$) from Wood Thrush home range cores and compared them to plots collected at bird absence locations ($n = 32$) using Wilcoxon rank sum test. Absence was defined as no Wood Thrush detections over 120 min of point count surveys spanning 5 breeding seasons. All tests were two-tailed. The differences in medians between core and absence habitat samples were significant for 3 of 11 top-performing predictors: canopy height ($W = 832$, $P < 0.001$), red oak count ($W = 2178$, $P = 0.04$), and worm biomass ($W = 1208$, $P = 0.004$). Albeit insignificant, trends in many of the remaining variables followed predicted directions.

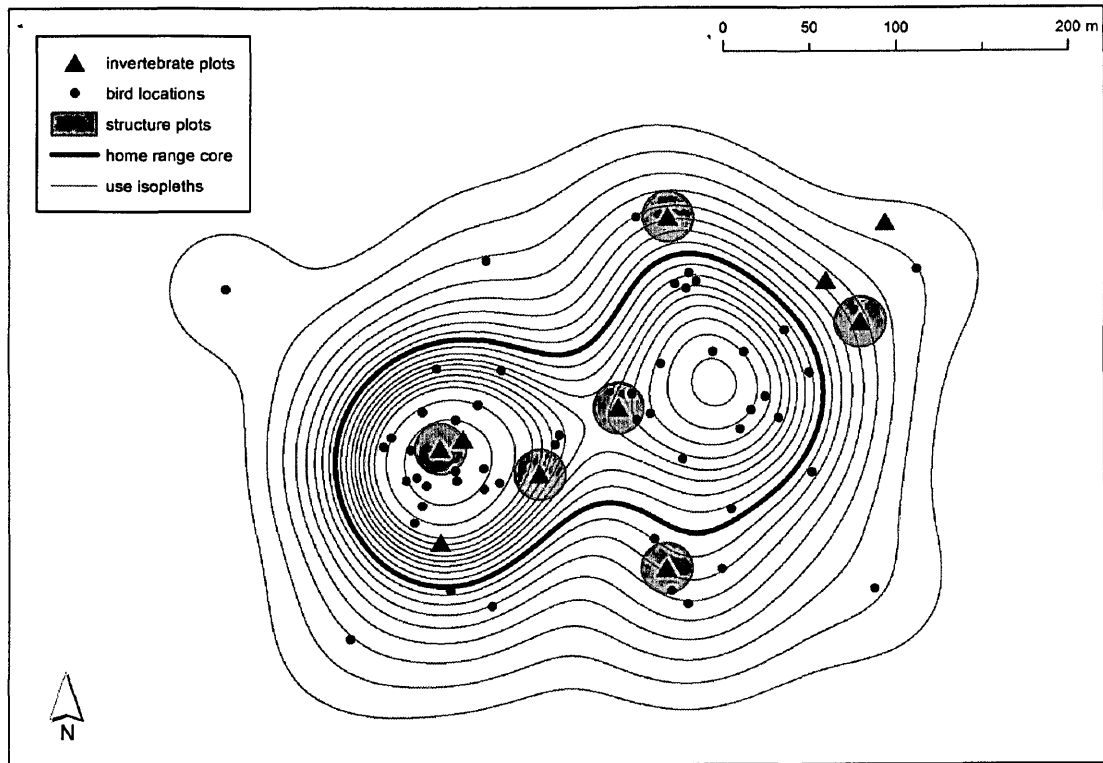


Figure 1

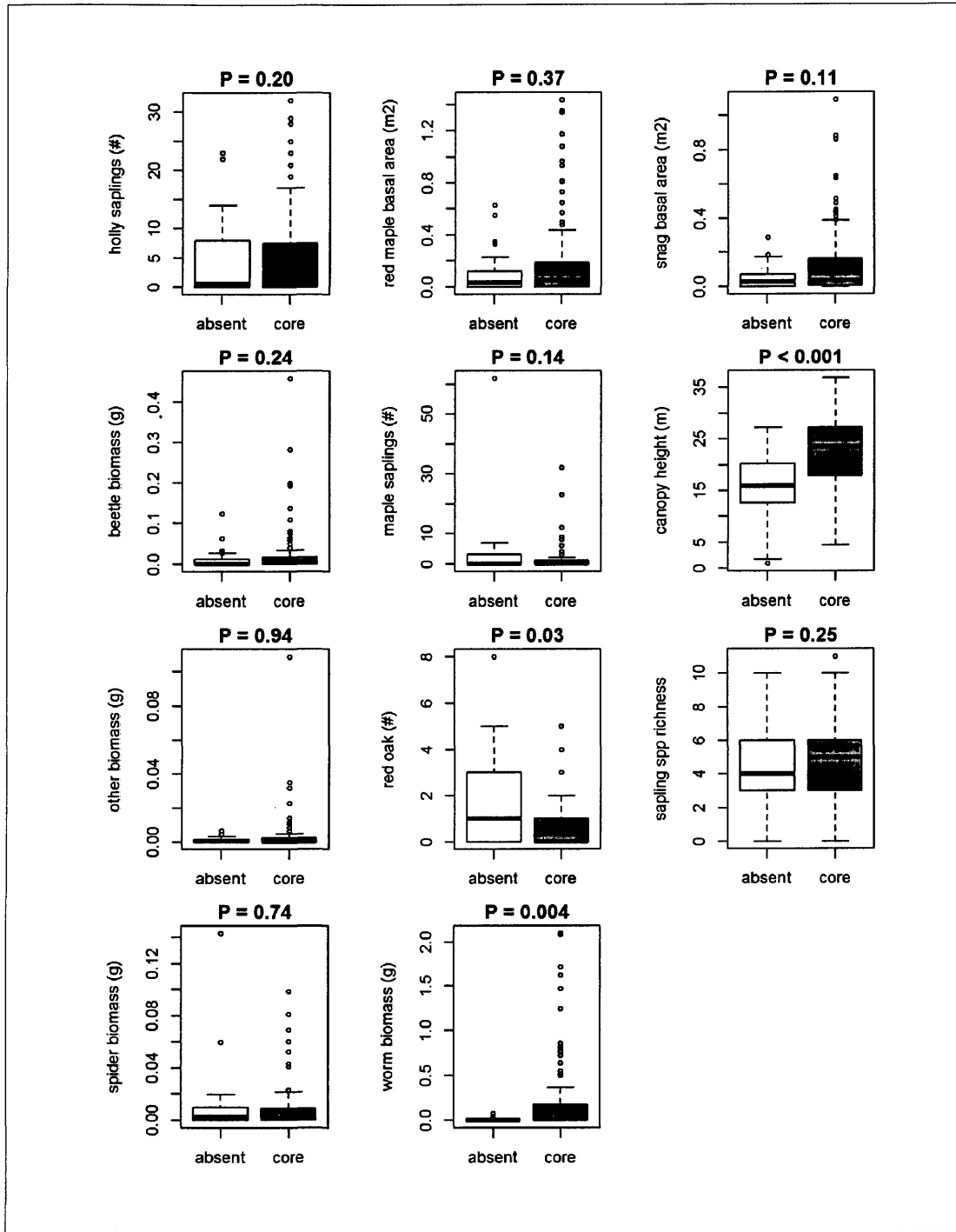


Figure 2