



RESEARCH ARTICLE

## Prey availability and habitat structure explain breeding space use of a migratory songbird

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### ABSTRACT

Researchers have long recognized that the spatial distribution of animals relates to habitat requirements. In birds, despite recent advances in tracking techniques, knowledge of habitat needs remains incomplete for most species. Using radio telemetry, we quantified the relative space use of 37 Wood Thrush (*Hylocichla mustelina*) males, captured over 2 years (2013, 2014) on their breeding grounds in coastal Virginia. Following tracking, we collected data on prey availability ( $n = 370$  plots) and habitat structure ( $n = 222$  plots) within bird home ranges, and modeled bird utilization distribution with both sets of variables using mixed models. Our objectives were to (a) determine the relative importance of habitat structure and prey availability for bird use, (b) identify specific resources that related to bird utilization distribution, (c) test the hypothesis that soil moisture explained prey availability, and (d) evaluate models by determining whether model-identified conditions agreed with data at sites where Wood Thrushes were absent over the preceding 5 years. Of prey variables, high-use areas within bird home ranges were linked to higher biomass of spiders and worm-like invertebrates, which were strongly correlated with soil moisture. Of habitat structure variables, bird use related negatively to red oak (*Quercus* spp.) count and pine (*Pinus* spp.) basal area, and positively to forest canopy height, snag basal area, and number and species richness of trees, among others. Evaluation of 12 covariates in our best model revealed that 5 were significant, with conditions at bird absence sites congruent with our models. Goodness-of-fit tests revealed poor fit of the prey-only model, whereas the habitat-only model explained nearly 8 times the variation in bird use. The model utilizing both prey and structure covariates yielded only marginal improvement over the habitat-only model. Consequently, management objectives aimed at habitat improvement for the declining Wood Thrush should particularly consider habitat structure resources.

**Keywords:** Wood Thrush, *Hylocichla mustelina*, habitat, habitat structure, food availability, LiDAR, home range, habitat quality, space use

### La disponibilidad de las presas y la estructura del hábitat explican el uso del espacio reproductivo en un ave canora migratoria

#### RESUMEN

Los investigadores han reconocido hace tiempo que la distribución de los animales se relaciona con sus requerimientos de hábitat. A pesar de avances recientes en las técnicas de rastreo, el conocimiento de los requerimientos del hábitat aún es incompleto en la mayoría de especies de aves. Usando telemetría de radio cuantificamos el uso relativo del espacio de 37 machos de la especie *Hylocichla mustelina* capturados a lo largo de dos años (2013, 2014) en sus territorios de reproducción en la costa de Virginia. Luego de los seguimientos recolectamos datos sobre la disponibilidad de presas ( $n = 370$  cuadrantes) y la estructura del hábitat ( $n = 222$  cuadrantes) en el ámbito hogareño de las aves y modelamos la distribución del uso de hábitat de las aves con ambos conjuntos de variables empleando modelos mixtos. Nuestros objetivos fueron (a) determinar la importancia relativa de la estructura del hábitat y la disponibilidad de presas para el uso de las aves, (b) identificar recursos específicos que se relacionan con la distribución del uso de hábitat de las aves, (c) poner a prueba la hipótesis de que la humedad del suelo explica la disponibilidad de presas y (d) evaluar los modelos determinando si las condiciones identificadas por éstos concuerdan con datos en sitios donde *H. mustelina* estuvo ausente durante los 5 años anteriores. En cuanto a las variables relacionadas con las presas, las áreas de alto uso dentro del ámbito hogareño de las aves se relacionaron con mayor biomasa de arañas y de invertebrados vermiformes, y también estuvieron altamente correlacionadas con la humedad del suelo. En cuanto a las variables de estructura de hábitat, el uso de las aves se relacionó negativamente con el número de *Quercus* spp. y el área basal de *Pinus* spp., y positivamente con la altura del dosel, el área basal de tocones y el número y riqueza de especies de árboles, entre otras. La evaluación de 12 covariables en nuestro mejor modelo indicó que cinco fueron significativas y las condiciones en los sitios con ausencia de aves fueron congruentes

con nuestros modelos. La prueba de bondad de ajuste determinó que el modelo que considera sólo las presas se ajusta pobremente, mientras que el modelo que considera sólo las variables del hábitat explica casi ocho veces más la variación en el uso de hábitat de las aves. El modelo que usaba las variables de presas y de hábitat como covariables fue solo marginalmente mejor que el modelo que solo consideraba las variables de hábitat. En consecuencia, las estrategias de manejo destinadas al mejoramiento del hábitat de las poblaciones en declive de *H. mustelina* deberían considerar particularmente las características de la estructura del hábitat.

*Palabras clave:* ámbito hogareño, calidad del hábitat, disponibilidad de alimento, estructura del hábitat, hábitat, *Hylocichla mustelina*, LiDAR, uso del espacio.

## INTRODUCTION

Loss and degradation of habitat is the leading threat to birds (Johnson 2007). Long-term demographic analyses indicate populations of many Nearctic–Neotropical migrants are decreasing (Ballard et al. 2003). These 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 and management of bird habitat is thus crucial for the conservation of avifauna. However, conservation efforts hinge on a proper understanding of habitat requirements and identification of high-quality habitat.

Habitat quality is difficult to measure. Robust assessment of habitat quality generally follows quantification of survival and reproduction (Johnson 2007), which often requires multi-year, population-specific monitoring efforts that are of considerable costs (e.g., Sim et al. 2011). Furthermore, demographic parameters are inextricably tied to endogenous and exogenous factors that frequently vary in time and space (Yang et al. 2008). Although Van Horne (1983) warned that animal density does not necessarily relate to habitat quality, Bock and Jones's (2004) synthesis of 109 cases involving 67 bird species from North America and Europe found that higher-density sites produced greater recruitment per capita and per unit area in 72% and 85% cases, respectively. The above result suggests that habitat use may be related to habitat quality because birds, in general, have the capability to recognize high-quality habitat. This assumption follows ecological theory that habitat use should be adaptive as variation in resource availability generates strong selective pressure for recognition of high-quality habitat that maximizes survival and reproduction (Jaenike and Holt 1991, Clark and Shutler 1999). In fact, responses to territory intrusions by conspecifics indicated that aggression level varied by habitat type and food availability in a wintering migratory warbler (Smith et al. 2012), suggesting habitat quality recognition. Increased nest success at preferred than at nonpreferred sites for 7 coexisting songbirds indicates that recognition of proper habitat is adaptive (Martin 1998).

However, correct evaluation of habitat quality may vary with spatial scale and fitness metrics (Orians and Wittenberger 1991, Chalfoun and Martin 2007).

Quantification of habitat use can be employed to identify important habitat attributes at the home range scale. Researchers have delineated animal home ranges (entire area occupied; Burt 1943) or territories (actively defended areas only; Noble 1939), and employed differences between used and unoccupied areas to classify habitat requirements (Anich et al. 2012). With recent advances in animal tracking techniques and the recognition that habitat heterogeneity occurs even at small scales (Marzluff et al. 2004), some investigators have examined fine-scale habitat associations using utilization distributions within home ranges and territories derived from remote tracking of individually tagged birds. To our knowledge, such space use quantification has been conducted for 2 migratory species of concern. Barg et al. (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 higher stem density, deeper leaf litter, and higher canopy cover (Anich et al. 2012). Available literature indicates that knowledge of space use patterns and underlying mechanisms is limited for most species. Importantly, publications where utilization distribution was estimated and related to habitat largely focused on structural attributes and appeared to not separate effects of food availability—presumably a critical component in habitat use. Not surprisingly, studies have linked available food supply to migratory songbird body condition (Brown and Sherry 2006) as well as distribution (Johnson and Sherry 2001).

In this study, we quantified space use of individually marked Wood Thrush (*Hylocichla mustelina*), a passerine found in eastern deciduous forest ecosystems, and modeled bird utilization distribution with a broad range of habitat structure and food availability variables. Following the trend in many migratory birds, Wood Thrush populations indicate a long-term, range-wide population decline of  $\sim 2\% \text{ yr}^{-1}$  (1966 to 2012; Sauer et al. 2014). Because of its perception as a charismatic species and rapid decline, 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, Evans et al. 2011). A number of studies document a harmful effect of nest parasitism on Wood Thrush demography in smaller forest fragments (Trine 1998, Lloyd et al. 2005). On the breeding grounds, frequently occupied areas have been qualitatively related to upland deciduous and mixed forests with moderate subcanopy, semi-open forest floor with decaying litter, and a high diversity of tall deciduous tree species (Evans et al. 2011). Overall, Wood Thrush habitat requirements are still poorly understood and questions about which variables are important within bird home ranges and their relative contributions to habitat use have not yet been answered. This knowledge gap prevents effective conservation of this declining songbird.

We had 4 objectives in this study. The first objective was to determine the relative effect of habitat structure and prey availability on space use, whereas the second objective was to identify which specific variables explained utilization distribution within bird home ranges. To achieve the first 2 objectives, we developed (i) a prey availability model, (ii) a habitat structure model, and (iii) a composite model that included both prey availability and habitat structure variables. Because preliminary analyses suggested prey availability was related to space use, we collected soil moisture data to test the hypothesis that soil water content affects prey biomass as our third objective. Lastly, we evaluated the models by determining whether model-identified conditions agreed with data collected at sites where Wood Thrushes were absent over the preceding 5 years.

## METHODS

### Study Area

We used radio telemetry to track 37 Wood Thrush males captured within 8 parks and one military installation located in southeastern Virginia (37°15'N, 76°40'W). Birds were tracked on property managed by the College of William & Mary ( $n = 11$ ), U.S. National Park Service ( $n = 10$ ), Colonial Williamsburg ( $n = 5$ ), City of Newport News ( $n = 3$ ), City of Williamsburg ( $n = 3$ ), York County ( $n = 1$ ), James City County ( $n = 1$ ), Kingsmill Resort ( $n = 1$ ), York River State Park ( $n = 1$ ), and the U.S. Navy ( $n = 1$ ). Area of the minimum convex polygon delineated by bird capture sites was 255 km<sup>2</sup>. Although the region is moderately covered with eastern deciduous and mixed forests (Monette and Ware 1983), infringing urbanization has fragmented many of the study sites.

### Bird Capture and Marking

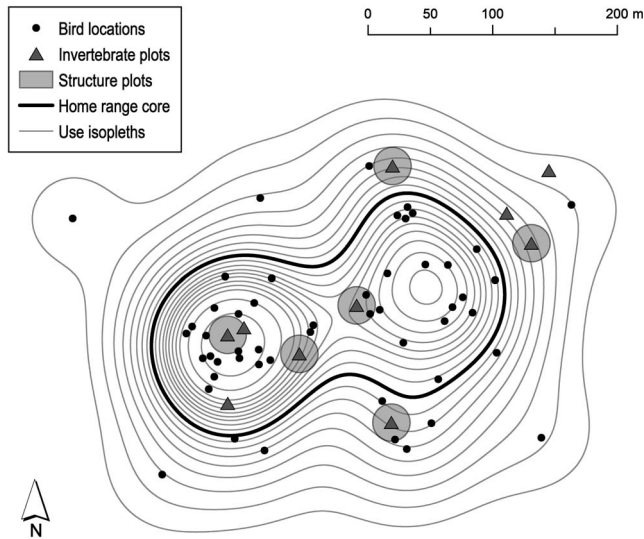
We captured 37 Wood Thrush males during the 2013 and 2014 breeding seasons. Males were used because, unlike

females, they maintain territories and can be trapped easily using conspecific song playback (Angelier et al. 2010). Moreover, results of a parallel study suggested female home ranges overlap substantially with their mate's home range (A. Deverakonda personal observation). Birds were captured from May 15 to June 3 of both years using mist nets with song playback to avoid floaters without established territories that could quickly depart our study area. To standardize capture locations, we trapped birds  $\leq 200$  m from existing point-count stations placed randomly in wooded tracts with stratification by forest land cover (coniferous, upland, riparian) and a rural to urban land use gradient in a Geographic Information System (GIS; ArcMap 10.1, ESRI, Redlands, California, USA).

We aged and sexed each bird, and collected standard morphometric data (weight, wing chord) following Pyle (1997), and attached a USGS aluminum band, a unique set of 3 color bands, and a VHF radio transmitter (1.3 g, BD-2, Holohil Systems Ltd., Carp, Ontario, Canada). The radio transmitter was affixed via a figure-eight leg harness (Rappole and Tipton 1991). Transmitters fastened 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 of behavioral or physiological effects for the Wood Thrush during breeding and molting (Gow et al. 2011), and little influence during migration in case radio-tags fail to detach prior to departure for wintering grounds (Powell et al. 1998). We used 0.7 mm Stretch Magic jewelry cord (Pepperell Braiding, Pepperell, Massachusetts, USA) 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 reattach a lost transmitter due to fractured harness.

### Home Range Estimation

Home ranges were based on daytime radio telemetry locations as described in Jirinec et al. (2015). We followed birds from May 16 through July 25 of both years (mean  $11.9 \pm 0.8$  unique days per bird; mean  $\pm$  SE) between 0630 and 2030 hr EDT for the duration of transmitter life (average battery life = 60 days). To account for possible variation in space use throughout the day, we recorded at least one location within each daylight hour (0800–2000 hr) over radio-tag functionality period (Anich et al. 2012); otherwise locations were distributed throughout the day. We acquired  $\sim 5$  locations per bird per day for most individuals. In some cases, however, when birds went missing for extended periods (Lang et al. 2002), we increased daily tracking efforts to achieve location targets. Points were recorded at least 20 min apart to ensure biological independence between successive bird positions,



**FIGURE 1.** Example home range of one of 37 Wood Thrush males tracked in this study. Home ranges were constructed using 95% fixed-kernel density estimation (KDE), which employed male telemetry locations (black dots,  $n \geq 50$ ), to derive percent relative diurnal use (gray contours, boundary = 5% relative use, home range centers = 100% relative use). We delineated home range core area (bold contour, 55% KDE) to facilitate stratified random placement of leaf litter invertebrate sampling locations (triangles,  $n = 10$ ) and 30-m-diameter habitat structure plots (gray circles,  $n = 6$ ).

which we defined as a period long enough to visit any point within a respective home range (Barg et al. 2005). This interval matches or is longer than in comparable studies on 3 other songbirds (Anich et al. 2012), and we believe it was sufficient for the Wood Thrush as birds often moved considerably between consecutive locations, easily traversing their entire home ranges. We tracked birds with 3-element antennas and Wildlife Materials receivers (TRX-1000S and TRX-3000S; Wildlife Materials, Murphysboro, Illinois, USA). To avoid disturbance to birds and thus degraded spatial data quality, observers homed-in to within  $\leq 50$  m of target, then located bird either visually ( $\sim 16\%$  of cases), or by reading signal source from multiple locations until bird position was narrowed down to a small area ( $\sim 5$  m<sup>2</sup>). This approach was necessary due to understory vegetation obstructing bird view and the elusive behavior of this species. After we determined bird locations, we obtained projected coordinates using a GPS (GPSMAP 62; Garmin, Olathe, Kansas, USA), compass azimuth, and distance estimated with a laser range finder (400LH; Opti-Logic, Tullahoma, Tennessee, USA). When birds moved beyond detection radius as documented by Lang et al. (2002), we conducted widespread road-based searches with twin antennas mounted on trucks. To survey regions without access permits and larger roadless areas, we utilized aerial telemetry from a fixed-wing aircraft, as

well as omnidirectional antennas fastened to mountain bikes.

We employed telemetry locations to create space utilization distributions generated from 95% fixed-kernel density estimations (Worton 1989, Marzluff et al. 2004, Barg et al. 2005). 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). A utilization distribution is a representation of an individual's space use as a function of telemetry location density, thus portraying the probability of individual occurrence (hereafter relative percent use, relative use, space or habitat use) within each section of its activity area (Marzluff et al. 2004, Horne and Garton 2006). Using such space use distribution in contrast to direct animal locations dilutes intrinsic telemetry error (e.g., GPS accuracy), 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). Furthermore, telemetry error in most studies is not high enough to affect fixed-kernel estimates (Moser and Garton 2007).

We used inverse isopleths of the utilization distribution to denote relative percent use contours (Figure 1). In this approach, 5% relative use corresponds to home range edge for a conservative estimate of home range footprint (Pechacek and Nelson 2004), whereas core areas representing peak relative use are classified as 100% use. Despite the common application of least-squares cross-validation (LSCVh) as the kernel bandwidth selection method (Gitzen and Millspaugh 2003), we experienced poor LSCVh performance in instances where birds had disconnected home range sections. Instead, we used the likelihood cross-validation (CVh) method, which has been shown to perform better with smaller sample sizes, as well as to produce estimates with better fit and less variability than LSCVh overall (Horne and Garton 2006). Barg et al. (2005) suggested at least 50 locations for LSCVh kernels, and we therefore obtained  $53.9 \pm 1.3$  locations (mean  $\pm$  SE; range: 50–80) per bird to construct 95% CVh-based fixed-kernel home ranges in Geospatial Modeling Environment (Beyer 2011).

### Invertebrate Prey Sampling

To estimate prey availability, 10 invertebrate prey samples were taken at randomly placed plots within the home range of each bird. We used ArcMap 10.1 to place sampling plots within home ranges such that half of plots ( $n = 5$ ) were positioned within the high-use areas of each home range. Following Anich et al. (2012), we considered the 55% KDE isopleth (45% relative use) as the home range core because it appeared to contain discrete clusters of

**TABLE 1.** Invertebrate guild assignments.

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 adults; Lepidoptera	All others, no Gastropoda

telemetry locations, and fell within the core range used in other studies (e.g., Ginter and Desmond 2005).

The Wood Thrush is known to forage on invertebrates mainly in forest leaf litter during the breeding season (Holmes and Robinson 1988, Ladin et al. 2015), and hence we collected forest litter samples for invertebrate prey extraction. Samples were collected shortly after bird tracking completion in each of the 2 years: July 23–27, 2013, and July 31 to August 4, 2014, such that all samples associated with a home range were collected on the same day. We did not encounter substantial variation in litter depth, and a firm soil layer was present often underneath a defined layer of decomposing leaves and twigs (~2 cm depth). We gathered forest leaf litter in a 50 × 50 cm plot at each of the 10 sampling sites within each home range, removed larger leaves and stems without letting fast-moving invertebrates escape, and froze the resulting sample at –80°C for processing during the off-season. If no litter was found at the exact GPS position, we collected litter at the closest spot within 5 m where downed leaves covered at least half of the sampling plot. We recorded zero leaf litter invertebrates at sites with no leaf litter within 5 m, such as in thick grass, forbs, and bare ground, although such cases comprised only 6% of all plots. After sampling soil, leaf litter, and understory vegetation, Ladin et al. (2015) found 92% of invertebrate individuals in leaf litter, lending justification to our assumption of no food availability at plots without leaf litter. On a few occasions (2%), we encountered small vertebrates such as frogs, salamanders, and snakes (mostly *Carphophis amoenus*); these were released unharmed and not considered in analyses.

Samples were processed by manual separation of invertebrates from plant matter immediately after defrosting. Assuming that birds respond to prey morphology rather than taxonomy, we assigned invertebrates to one of 5 guilds based on common body types: worms, beetles, centipedes, spiders, other (Table 1). For practical reasons, we refer to guilds without regard to their true taxonomic assignments. The “worms” guild, for example, included soft, worm-like invertebrates such as earthworms (Oligochaeta) and beetle larvae (Coleoptera), which although not closely related, we assumed were treated similarly by prey-seeking birds. After acquiring count per guild in each sample, we dried invertebrates at 60°C for at least 48 hr prior to obtaining weight in grams to 0.0001 g with an

analytical balance (TSXB120A; Thomas Scientific, Swedesboro, New Jersey, USA). Food availability dataset therefore consisted of 370 samples containing both count and biomass for each of the 5 invertebrate guilds.

Preliminary analyses of 2013 data suggested an association between invertebrate biomass and bird use, and we therefore explored what affected invertebrate availability per se. In 2014, we tested the hypothesis that invertebrate biomass was positively correlated with soil water content and took soil moisture readings at invertebrate plots within home ranges of the 17 birds captured that season. Three soil moisture readings were taken per plot, 3.8 cm deep, using a digital moisture sensor (FieldScout TDR 300; Spectrum Technologies, Aurora, Illinois, USA) to obtain percent volumetric water content (VWC) estimates. Sensor readings were spaced evenly along a diagonal transect of the plot frame following leaf litter collection. Plots without leaf litter were excluded from analyses involving soil moisture.

### Habitat Structure Assessment

We examined 54 habitat structure variables in our models (Appendix Table 3). Variables that we could link a priori to bird breeding, foraging, and roosting requirements, based on published studies and our observations, were incorporated into the analysis. In order to select the best-performing predictors of bird use, we often included multiple variables that were purposely related to one mechanism. For example, we collected data on tree species richness because higher richness will likely support more invertebrate species (Crisp et al. 1998), and therefore higher prey availability. Although richness of subcanopy and canopy trees is clearly correlated, we considered both variables in order to determine which related more strongly to bird use based on predictor performance. Wood Thrush presence has been associated with a more mature forest (Robbins et al. 1989), and we therefore added variables which reflect tree size: mean diameter at breast height (DBH), tree basal area, and maximum canopy height. Habitat structure elements connected to invertebrate biomass were represented by variables measuring dead and decaying wood (volume of downed-woody debris, snag basal area, snag count; Johansson et al. 2006) and soil wetness (distance to streams, terrain ruggedness index; Levings and Windsor 1984). Wood

Thrushes tend to nest in understory trees (Farnsworth and Simons 1999), which in our study area were dominated by American holly (*Ilex opaca*), red maple (*Acer rubrum*), pawpaw (*Asimina triloba*), and American beech (*Fagus grandifolia*) saplings, and hence we included variables associated with these trees along with covariates quantifying sapling availability. In a parallel study examining Wood Thrush roosting, we often detected birds sleeping in areas with high vegetation density and the understory trees mentioned above (Jirinec et al. 2015). Furthermore, we examined a number of other tree species because of their abundance in local woodland tracts known for frequent Wood Thrush occurrence. Coniferous forest, in contrast to deciduous woodland, has been suggested as unsuitable for the species (Robbins et al. 1989), prompting us to incorporate basal area of pine trees (*Pinus* spp.), pine count, coniferous sapling count, and ground cover of pine needles. In summary, we believe the suite of variables, albeit sizable, was justified for consideration in the composite model.

Habitat structure predictors were derived from field-based vegetation surveys and remotely sensed data. Whereas invertebrate samples were frozen and hence processing was not subject to field time constraints, we had to reduce the number of vegetation structure plots to accommodate field schedule. The resulting difference in data sets, however, diminished our ability to directly compare results of habitat structure and prey analyses. We collected field-based habitat structure data in circular plots (15-m radius) at 6 of the 10 random invertebrate prey availability sites within bird home ranges (Figure 1). Vegetation site assignment was randomly assigned to 3 of 5 invertebrate prey plots in high- and low-use areas within a home range ( $n = 222$ ) while ensuring that plots did not overlap. We collected vegetation data at the end of the breeding season in both years: August 21 to September 6, 2013, and August 17 to September 5, 2014. Within 15 m of plot center, we recorded, counted and identified all large trees  $\geq 10$  cm DBH. We also measured volume of all downed woody debris  $\geq 10$  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 7 categories comprising the average of 13 Daubenmire plots (50 × 50 cm; Daubenmire 1959), spaced evenly along two 30-m transects crossing perpendicularly at vegetation plot center. Only deciduous leaf litter, pine needles, and forbs were selected as ground cover covariates for final analyses.

Six habitat structure variables, measured at vegetation plot center, were derived from remotely sensed data. We calculated the minimum distance of vegetation plot to stream and forest edge in ArcMap 10.1, using Euclidean

distance to streams (Topologically Integrated Geographic Encoding and Referencing data, US Census Bureau 2014) and forest boundary. We delineated forest boundary, forest density (1 m above ground to canopy), understory density (0.3–3 m), canopy height, and terrain ruggedness index (Riley et al. 1999), using discrete return light detection and ranging (LiDAR) data collected in April 22 to May 10, 2010, and March 21–31, 2013, which we acquired from a public-access repository (Virginia Lidar; <http://virginalidar.com/>). 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; <http://lastools.org>) to process LiDAR data and derive vegetation density rasters within desired height strata. Vegetation density was calculated as the number of returns within a designated height bin divided by the number of all returns inside each raster cell (Morsdorf et al. 2006). We removed low-lying LiDAR points ( $< 0.3$  m) to avoid noise from forest floor vegetation. Forest boundary was delineated by tree canopy above 10 m while disallowing for gaps  $< 25$  m<sup>2</sup>, which we found produced a much more accurate edge than could be possible with readily available land-cover datasets. Forest density, understory density, and maximum canopy values represent the average within a 10-m circular neighborhood using focal statistics in ArcMap 10.1 to account for GPS accuracy errors (maximum  $\pm 10$  m).

### Model Evaluation

In addition to examining the goodness-of-fit (GOF) of all models, we tested the output of our composite model with vegetation and invertebrate data collected on bird point count survey stations. Rykiel (1996) pointed out the frequent confusion about the meaning of model evaluation in ecology and called for stating evaluation criteria whenever it is undertaken. Here, we attempted to meet Rykiel's "credible model" criterion, which is a "sufficient degree of belief in the validity of a model to justify its use for research and decision making." Because our main goal was to identify resources that related to bird use, rather than to build predictive models of bird utilization distribution, the evaluation procedure involved checking whether the model-identified predictors of bird use agreed with independent data collected at sites not utilized by the Wood Thrush (hereafter "absence" sites).

We built a validation dataset consisting of bird absence (i.e. no-use sites) from 131 point count stations in the study area. Survey stations were randomly placed in forested tracts stratified by forest type along an urban to rural gradient, and breeding avifauna was surveyed in June over 5 years (2010–2014) with variable circular point counts. Every survey station was sampled with four 8-min consecutive surveys each summer. Stations without visual

or auditory evidence of Wood Thrush presence (naïve occupancy = 0) over the survey period (total 160 min of surveys per station) were assumed to be absence sites ( $n = 32$ ).

We chose to employ absence point count stations, rather than both presence and absence stations, for 2 reasons. First, the decision about what constitutes a “presence” at a station where bird detections could range between 1 and 20 (where 20 equates to a Wood Thrush detection during every 4 surveys each year), was ambiguous. Although this caveat could be ameliorated with a clearly defined occupancy modeling procedure, the second issue was that point count data do not indicate where within a detection radius a bird was heard or seen. If, for instance, we assume a 200-m detection radius, a bird could have been anywhere within 13 ha. With patchily distributed resources, this would likely result in a mismatch between plot-derived sample and the factors associated with local bird presence. Using absence sites precluded these issues.

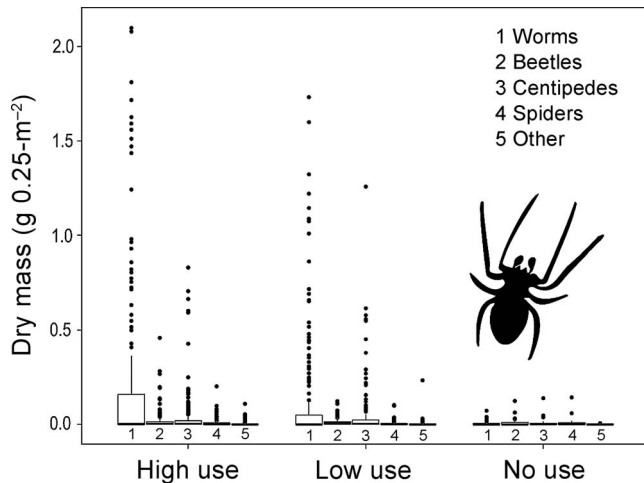
We collected invertebrate prey and habitat structure data at absence sites (one plot per site) at the center of each point count station following the same protocol as described above for bird home ranges. Evaluation samples were collected in 2014 between July 26 and July 30 (prey availability) and May 23 and July 31 (habitat structure). We compared data corresponding to model-identified variables at bird absence plots to plots placed within home range cores (high-use sites). Variables with significantly lower (or higher) medians following model-derived sign were considered more credible. Medians were chosen because the mean is a poor estimate of central tendency when data are not normally distributed (Zar 1984), which was the case here in most instances. For example, if our model produced canopy height with a positive coefficient, we would expect a significantly lower median canopy height at no-use sites than at sites corresponding to high-use. Although survey effort differed between absence sites and home ranges ( $n = 1$  station<sup>-1</sup> vs.  $n = 3$  bird<sup>-1</sup>), we were unable to equate survey effort due to time constraints.

### Analysis

We modeled Wood Thrush space use with 3 models. The prey availability model (“prey model”) was composed solely of variables representing invertebrate availability, whereas the habitat-only model (“habitat model”) included variables reflecting structural habitat attributes of bird home ranges. The third model (“composite model”) incorporated both prey availability and habitat structure covariates. All models employed relative percent use (0–100), corresponding to the nearest utilization distribution isopleth to plot center, as the response variable in a mixed model framework. Because data associated with the 5 prey guilds were strongly right-skewed, we log-transformed all prey

variables to achieve normality. Observations were nested within individual birds designated as random effects in package nlme in R software (R Core Team 2014). Before analysis, we scaled and centered all covariates using respective means and standard deviations, and plotted response and predictor variables to check for nonlinear associations (Zuur et al. 2010).

For each model, we removed uninformative variables by employing a three-tiered, data-driven approach. First, we fitted univariate models with each candidate predictor variable (i.e. we modeled relative use with each covariate alone). Predictors associated with univariate models that had lower Akaike’s Information Criterion (AIC<sub>c</sub>, AIC corrected for small sample sizes; Burnham and Anderson 2002) scores than the null (intercept-only) model were brought forward for bivariate tests of collinearity using Pearson’s correlation coefficient ( $r_p$ ). Analyses in ecological studies of complex ecosystems are frequently hindered by multicollinear explanatory variables where even low levels of such inter-correlation can bias statistical and inferential interpretation of the results (Graham 2003, Cade 2015). We therefore attempted to exclude multicollinear variables from final models in 2 steps. First, we removed highly correlated variables ( $r_p > |0.7|$ ) that were either more ambiguous or had a weaker a priori hypothesized relationship with Wood Thrush relative use. Second, we built models representing all possible covariate combinations of the total predictor pool after univariate modeling utilizing package MuMIn in R (R Core Team 2014). However, because this approach is computation-intensive, we kept the maximum number of model terms to 6, which we found to yield a sensible computation interval without the need for cluster computing. Only variables whose regression coefficient direction remained constant (i.e. no change of sign, either always negative or always positive) in all of the models representing the top 95% cumulative AIC<sub>c</sub> weight, indicating predictor strength as well as suggesting lack of collinearity (Graham 2003, Cade 2015), 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 regression coefficients of all models whose cumulative AIC<sub>c</sub> weight summed up to 0.95 (Burnham and Anderson 2002). Although model-averaging has been suggested to suffer from collinearity (Cade 2015), we have taken sufficient steps to minimize correlation among model covariates by the procedure described above. Model GOF was assessed using the adjusted- $r^2$  derived from a linear regression of observed vs. model-predicted relative bird use obtained from the model-averaged output. Moreover, we used the weighted sum of the predicted relative percent use of each model included in the top 95% of AIC<sub>c</sub> weight rather than averaging individual parameters, an alternative to param-



**FIGURE 2.** Histograms of prey availability data across broad Wood Thrush space use categories. We utilized locations of radio-tagged males ( $n = 37$ ) to construct home ranges and derive a utilization distribution for each bird with fixed-kernel estimation. Home ranges were separated into a core section (high-use) and less-utilized section (low-use), and leaf litter invertebrates were collected at 5 randomly placed plots within each home range section per bird. We report prey availability data as dry mass per plot ( $0.25 \text{ m}^2$  of leaf litter). The “no-use” category corresponds to plots placed at point count stations without Wood Thrush detections over 5 breeding seasons (2010–2014;  $n = 32$ ). Sample sizes for the high, low, and no use categories were  $n = 185, 185, 32$  plots, respectively.

eter averaging suggested by Burnham and Anderson (2002).

Additionally, we evaluated the effect of soil moisture and Euclidean distance to streams on leaf litter invertebrate biomass collected in 2014 with a Spearman’s rank correlation test, and tested our hypothesis that home ranges will have higher soil moisture than 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 home range high-use sites (“cores”) and bird absence sites using a Wilcoxon rank sum test to evaluate variables selected for the composite model. All tests were two-tailed with analyses conducted in R software (R Core Team 2014). To generate 95% confidence interval for median home range size, we used R package boot (R Core Team 2014) to resample home range areas with 1,000 bootstrapping iterations. Otherwise, we report means  $\pm$  SE where applicable throughout the paper.

## RESULTS

Overall, bird home ranges were placed within deciduous forest. The median home range size for the 37 males was 10.4 ha (95% CI: 6.4–16.4 ha). Highest average tree density

in the 6 circular plots per bird ( $n = 222$  plots total) was represented by the tulip poplar (*Liriodendron tulipifera*;  $51.6 \pm 4.6$  trees  $\text{ha}^{-1}$ ), American beech ( $49.6 \pm 3.9$  trees  $\text{ha}^{-1}$ ), and American holly ( $45.2 \pm 4.5$  trees  $\text{ha}^{-1}$ ), with mean diameter at breast height (cm) of  $39.7 \pm 0.8, 25.5 \pm 0.6,$  and  $13.8 \pm 0.2$ , respectively. Ground was generally open with broadleaf litter carpeting most of the forest floor ( $62 \pm 2\%$ ). Pawpaw, along with holly and beech saplings comprised the highest counts of understory woody vegetation.

Designating birds as a random effect explained less than 1% of residual sums of squares in all 3 models, indicating little variation among individuals in factors explaining space use. Model GOF procedure revealed that when quantifying model fit to data using model-averaged parameters vs. model-averaged output produced identical predicted values.

## Prey Model

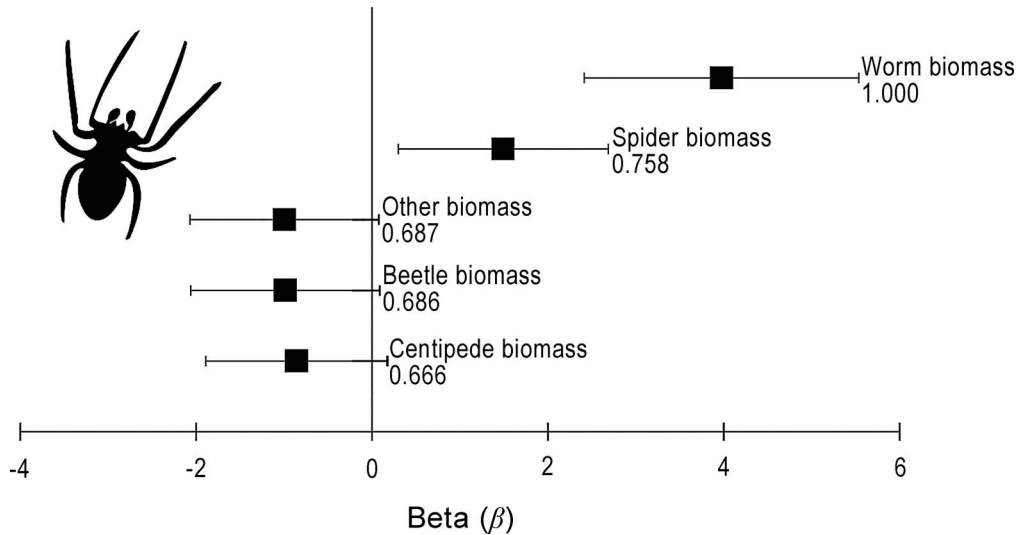
We counted 4,456 invertebrates comprising a total of 85.33 g of dry biomass across the 5 invertebrate guilds in the 370 prey sampling plots within bird home ranges. In the 32 bird absence plots, we counted 323 invertebrates totaling 1.78 g. For a summary of invertebrate biomass across the 3 broad use categories, see Figure 2.

All of the invertebrate predictors performed better than the null model in univariate modeling. Given that each of the count and biomass predictors for each guild (e.g., worm count and worm biomass) were strongly correlated ( $r_p > |0.7|$ ), we selected biomass predictors over count predictors for inclusion in the global model. Analysis of all possible combinations of these variables yielded 15 models whose  $\text{AIC}_c$  weights summed to 0.95 (Appendix Table 4).

Model-averaged regression coefficients along with model-averaged standard errors suggested biomass of 2 guilds was effective in space use models (Figure 3). These variables had positive regression coefficients whose standard errors did not include zero, indicating high-use areas within bird home ranges were associated with higher biomass of these prey guilds. The strongest predictor was biomass of the worm guild ( $\beta = 3.97 \pm 1.56$ ), followed by biomass of spiders ( $1.49 \pm 1.19$ ). Standard errors overlapped zero for the “other” category ( $-1.00 \pm 1.07$ ), beetles ( $-0.99 \pm 1.08$ ), as well as for centipedes ( $-0.86 \pm 1.03$ ), providing little evidence these prey groups were related to bird use.

We found a significant correlation between soil water content and biomass of 2 of the 5 invertebrate guilds representing the predictors in the prey model (Table 2). Biomass of worms, composed primarily of Oligochaeta, displayed a strong positive association with soil moisture ( $r_s = 0.35, P < 0.001, n = 162$ ), and a strong negative relationship with distance to streams ( $r_s = -0.29, P < 0.001, n = 222$ ). We also detected a negative correlation





**FIGURE 3.** Model-averaged regression coefficients and standard errors derived from our model of Wood Thrush relative space use applying invertebrate prey variables only. We used mixed models to explain telemetry-derived bird use with 370 invertebrate samples collected within the home ranges of 37 individuals. Birds were captured in southeastern Virginia over 2 breeding seasons (2013, 2014). We averaged 15 models whose Akaike’s Information Criterion (AIC<sub>c</sub>) weights ( $w_i$ ) summed to 0.95 and found 5 variables to be useful predictors of bird space use. We report the predictor, its model-averaged regression coefficient ( $\beta$ -value), error bars representing  $\pm 1$  model-averaged SE, and predictor AIC<sub>c</sub> weight ( $w_i$ ). Predictors were centered to make  $\beta$ -values directly comparable. A variable with AIC<sub>c</sub> cumulative weight of 1 was included in all 15 models.

between distance to streams and centipede biomass ( $r_s = -0.21, P = 0.006, n = 222$ ). Soil moisture (log %VWC) was 9% higher at plots within bird home ranges ( $2.88 \pm 0.04, n = 162$ ) than at bird absence sites ( $2.65 \pm 0.09, n = 30$ , two-sample  $t$ -test:  $t_{190} = 2.3, P = 0.02$ ). Overall GOF of the model-averaged prey model was low ( $\text{adj-}r^2 = 0.02, P < 0.001$ ; see Appendix Figure 7A).

**Habitat Model**

Nine variables representing habitat structure were selected into the top habitat model (Figure 4). We started with a total of 54 habitat variables, out of which 29 performed better than the null model based on AIC<sub>c</sub> (Appendix Table 3). We eliminated 9 predictors due to high collinearity ( $r_p > |0.7|$ ), leaving 20 predictors for evaluation of variable sign stability with multivariate models. Nine variables persisted through

this step into model building with all possible variable combinations, which yielded 49 models whose AIC<sub>c</sub> weights summed to 0.95 (Appendix Table 5). The top predictors of relative space use were count of the red oak guild ( $\beta = -5.74 \pm 2.12$ ), canopy height ( $5.15 \pm 2.09$ ), and snag basal area ( $4.08 \pm 1.99$ ). GOF of the model-averaged habitat model ( $\text{adj-}r^2 = 0.15, P < 0.001$ ; see Appendix Figure 7B) was much higher than the prey model.

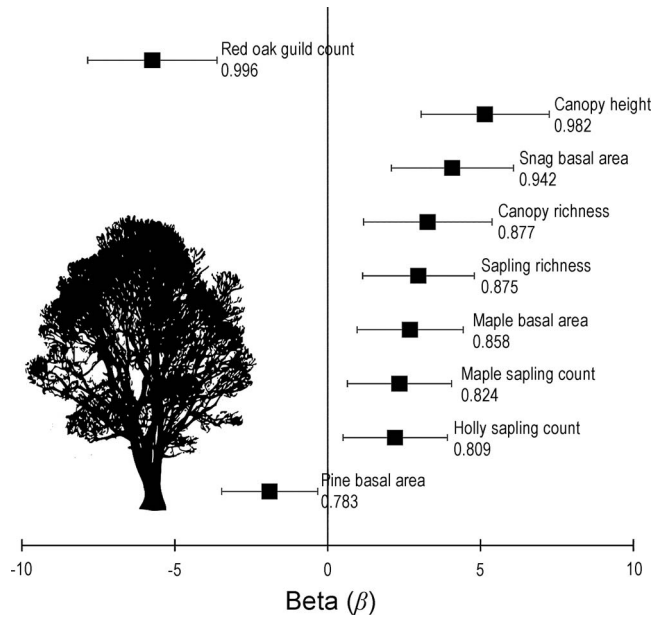
**Composite Model**

Both invertebrate prey and habitat structure covariates were important in the composite model (Figure 5). Out of a total of 66 variables tested with univariate models, 37 performed better than null model (Appendix Table 3). We removed 12 collinear predictors and evaluated stability of the remaining 25 variables with multivariate models. Analysis of all possible combinations of the 12 surviving covariates yielded 307 models whose AIC<sub>c</sub> weights summed to 0.95 (Supplemental Material Appendix Table 6). The strongest model-averaged predictors of bird use were count of the red oak guild ( $\beta = -5.82 \pm 2.11$ ), canopy height ( $5.00 \pm 2.08$ ), and snag basal area ( $4.10 \pm 2.00$ ), which were all about equally important in the model. Overall GOF of the model-averaged composite model improved nearly nine-fold over the prey model ( $\text{adj-}r^2 = 0.17, P < 0.001$ ; see Appendix Figure 7C).

The predictors selected into the final composite model were all present either in the prey or habitat models. Three of 5 invertebrate biomass guilds from the prey model

**TABLE 2.** Results of Spearman’s rank correlation test between prey model variables and 2 variables representing measures of habitat wetness. All  $P$ -values have been adjusted using Bonferroni correction; asterisk denotes statistical significance.

Guild	Distance to streams		Soil moisture	
	$r_s$	$P$	$r_s$	$P$
Worm biomass	-0.29	<0.001*	0.35	<0.001*
Spider biomass	-0.04	1.00	0.13	0.46
Other biomass	-0.15	0.13	0.00	1.00
Beetle biomass	-0.04	1.00	-0.18	0.10
Centipede biomass	-0.21	0.006*	0.12	0.71

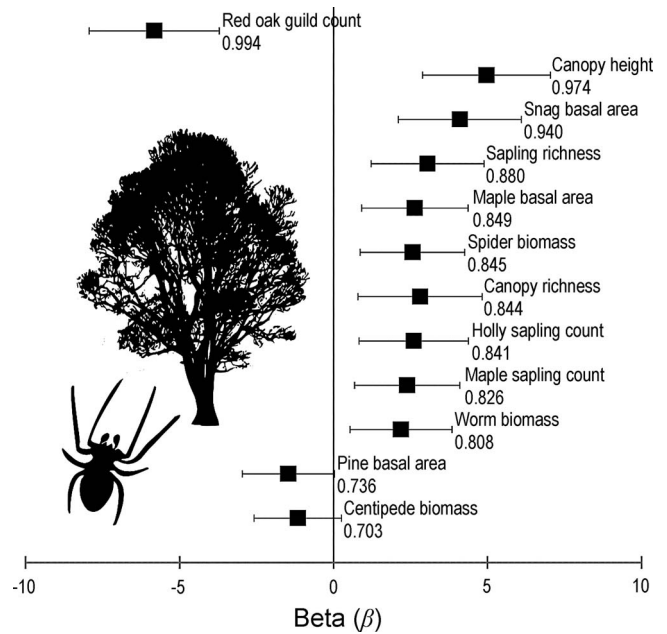


**FIGURE 4.** Model-averaged regression coefficients and standard errors derived from our model of Wood Thrush relative space use applying habitat structure variables only. We used mixed models to explain telemetry-derived bird use with data from 222 plots placed within home ranges of 37 individuals. Birds were captured in southeastern Virginia over 2 breeding seasons (2013, 2014). We averaged 49 models whose Akaike's Information Criterion ( $AIC_c$ ) weights ( $w_i$ ) summed to 0.95 and found 9 variables to be useful predictors of bird space use. We report the predictor, its model-averaged regression coefficient ( $\beta$ -value), error bars representing  $\pm 1$  model-averaged SE, and predictor  $AIC_c$  weight ( $w_i$ ). Predictors were centered to make  $\beta$ -values directly comparable. A variable with  $AIC_c$  cumulative weight of 1 was included in all 49 models.

survived variable selection into the final composite model, while all 9 habitat model variables persisted into the composite model.

### Predictor Evaluation

In predictor credibility evaluation, 5 composite model covariates agreed with bird absence data (Figure 6). Following predicted directions generated by the model, the differences in medians between home range core data and data collected at bird absence sites were significant in 5 of 12 tests: red oak guild count, canopy height, canopy richness, worm biomass, and pine basal area. The median red oak guild count at absence sites (1 tree plot<sup>-1</sup>,  $n = 32$ ), was significantly higher than within core plots (0 trees plot<sup>-1</sup>,  $n = 111$ , Wilcoxon rank sum test:  $W = 2178$ ,  $P = 0.03$ ), whereas the median canopy height was significantly lower at absence sites (15.9 m,  $n = 32$ ) than at core sites (23.6 m,  $n = 111$ , Wilcoxon rank sum test:  $W = 832$ ,  $P < 0.001$ ). Similarly, median number of canopy tree species was lower at absence sites (3 species plot<sup>-1</sup>,  $n = 32$ ) than

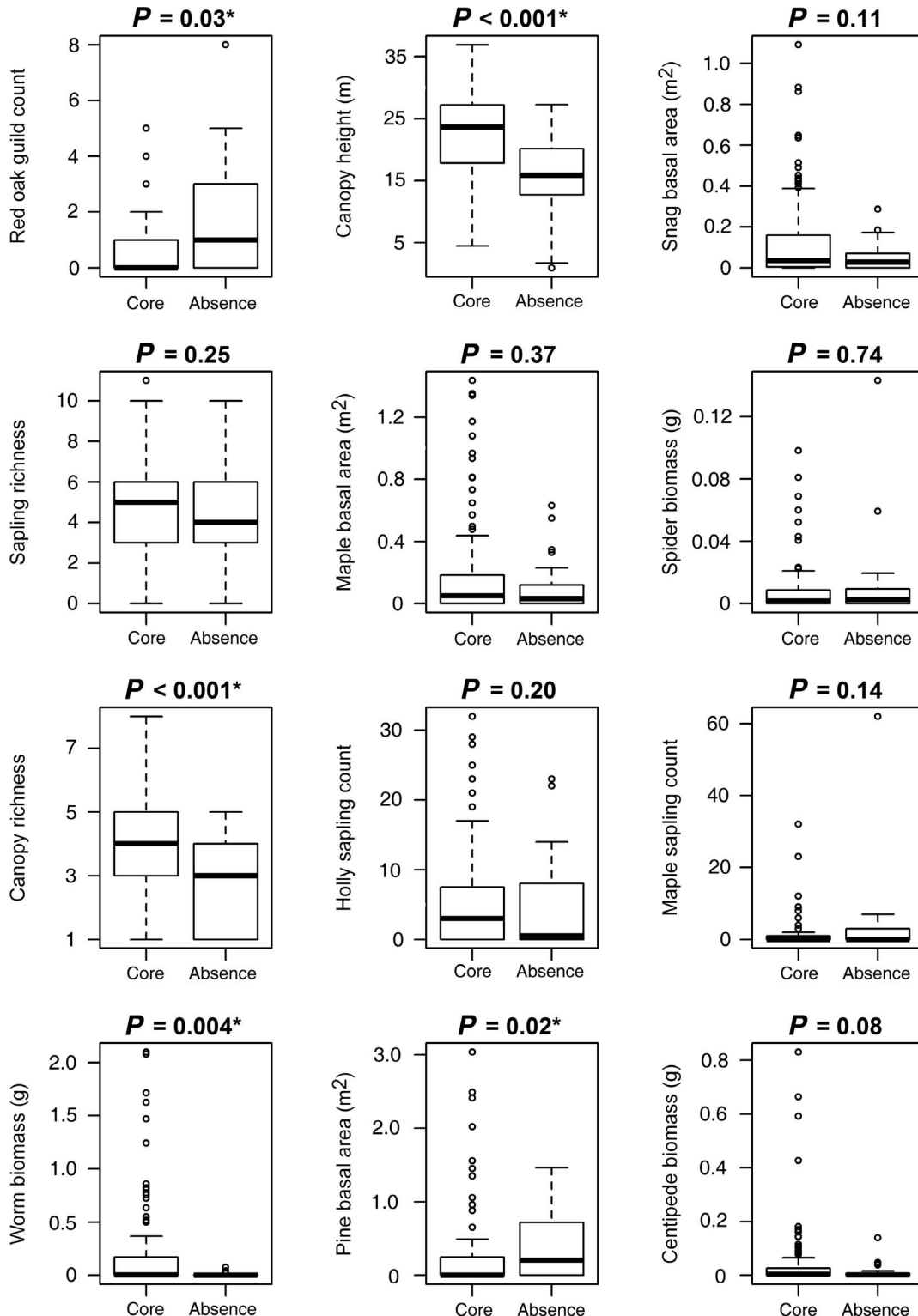


**FIGURE 5.** Model-averaged regression coefficients and standard errors derived from our model of Wood Thrush relative space use applying both habitat structure and invertebrate prey variables. We used mixed models to explain telemetry-derived bird use with data from 222 plots placed within home ranges of 37 individuals. Birds were captured in southeastern Virginia over 2 breeding seasons (2013, 2014). We averaged 307 models whose Akaike's Information Criterion ( $AIC_c$ ) weights ( $w_i$ ) summed to 0.95 and found 12 variables to be useful predictors of bird space use. We report the predictor, its model-averaged regression coefficient ( $\beta$ -value), error bars representing  $\pm 1$  model-averaged SE, and predictor  $AIC_c$  weight ( $w_i$ ). Predictors were centered to make  $\beta$ -values directly comparable. A variable with  $AIC_c$  cumulative weight of 1 was included in all 307 models.

within home range centers (4 species plot<sup>-1</sup>,  $n = 111$ ; Wilcoxon rank sum test:  $W = 971$ ,  $P < 0.001$ ), median worm guild biomass was lower at absence plots (0 g,  $n = 32$ ) than within home range centers (0.0034 g,  $n = 111$ ; Wilcoxon rank sum test:  $W = 1208$ ,  $P = 0.004$ ), and lastly, median pine basal area was higher at absence sites (0.21 m<sup>2</sup>,  $n = 32$ ) than within home range cores (0 m<sup>2</sup>,  $n = 111$ ; Wilcoxon rank sum test:  $W = 2226$ ,  $P = 0.02$ ).

### DISCUSSION

Our results indicate that the availability of invertebrate biomass did explain some of the space utilization within breeding home ranges of Wood Thrush males, but habitat variables were clearly driving our models. We built 3 models: prey-only, habitat-only, and prey-habitat. The predictors associated with biomass of invertebrate prey guilds were selected into both the prey and composite models. In the prey model (Figure 3), we found the worm biomass guild to be the strongest predictor of bird use. This



**FIGURE 6.** Evaluation of composite model predictors. We used habitat data collected in plots ( $n = 111$ ) from Wood Thrush home range high-use areas (cores) and compared them to plots collected at bird absence locations ( $n = 32$ ) with Wilcoxon rank sum test. Absence was defined as no Wood Thrush detections over 160 min of point count surveys spanning 5 breeding seasons. All tests were two-tailed. Following predicted directions generated by the model, the differences in medians between home range core and absence data were significant (\*) in 5 of 12 tests: red oak guild count, canopy height, canopy richness, worm biomass, and pine basal area. Albeit insignificant, trends in many of the remaining variables followed model predictions.

guild contained primarily biomass of earthworms (Oligochaeta), but included smaller amounts of Lepidoptera, Coleoptera, and Diptera larvae as well. Positive regression coefficient whose standard error did not overlap zero was also associated with biomass of spider guild, which was primarily composed of Arachnida and Orthoptera.

A number of studies suggested 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% were Coleoptera adults (5% larvae), 17% Hymenoptera, 16% Diptera adults (3% larvae), 12% Lepidoptera larvae, and 2% Arachnida. The authors acknowledged that due to short persistence in bird stomachs, soft-bodied invertebrates were underestimated in their assessment. In a West Virginia nest camera study of 56 Wood Thrush nests (Williams 2002), “common prey items included lepidopteran and other caterpillar-like larvae, earthworms, and small insects.” In a comprehensive study of Wood Thrush diet utilizing stable isotope analysis of bird blood, Ladin et al. (2015) found that food sources in Delaware were composed mainly of snails and spiders, with smaller amounts of isopods and earthworms. Snails and spiders were consumed in higher proportions than expected based on availability, indicating the importance of high-calcium and high-protein diets during the breeding season (Ladin et al. 2015). In another West Virginia study, daily nest survival probability of ground-gleaning birds (including the 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 a forest patch (Burke and Nol 1998). The results of the above research are consistent with the positive association of invertebrate predictors and Wood Thrush space use in this study, as well as their good performance in the 2 models that included them.

Although Ladin et al. (2015) suggest snails were an important Wood Thrush staple in Delaware, we largely ignored snails in this study. We did not collect snails and slugs (Gastropoda) the first season (2013) because snails were often sizable and it was unclear when they were too large for birds to consume. We did account for gastropods in 2014 and found snails or slugs to be present in 49% of invertebrate plots, comprising a mean dry mass of  $0.029 \pm 0.007$  g per plot. However, we did not detect a relationship with bird space use, possibly due to lack of adequate sample.

The habitat model indicated the importance of 9 habitat structure variables for where birds concentrate space use.

One of the top predictors of bird use was count of the red oak guild, a variable that was corroborated by the predictor evaluation (Figure 6). Locally, the red oak guild was primarily composed of the southern red oak (*Quercus falcata*), which is associated with xeric areas (S. Ware personal observation). To examine the relationship between soil moisture and the red oak guild count, we ran a post-hoc Spearman's rank correlation test on the 2 variables. This analysis revealed a negative correlation between soil moisture and the red oak guild ( $r_s = -0.28$ ,  $P < 0.005$ ,  $n = 99$ ), lending more support to our earlier results: worm guild biomass, the best positive predictor of relative bird use in the prey model, was positively correlated with soil moisture and negatively correlated with distance to streams. Moreover, we found significantly higher mean soil moisture within bird home ranges than at sites with no Wood Thrush detections over 5 years. It thus appears that birds were selecting mesic areas that were unsuitable for the dry-associated members of the red oak guild. Another of the top habitat model predictors was canopy height, which was also endorsed by variable evaluation. Mean canopy height was the most important predictor of Wood Thrush relative abundance found by Robbins et al. (1989), whereas Hoover and Brittingham (1998) found this species to select nest sites with higher canopy than random points within forest tracts. Combined with these observations, our results are consistent with the notion that the species prefers a well-developed forest, although tree diameter did not come forward in our univariate analyses (Appendix Table 3). It is plausible that a more mature forest contains better microhabitat for soil-dwelling invertebrates, such as higher soil moisture. Snag basal area—also a well-performing habitat predictor—is expected to associate with invertebrate biomass. Density of spiders was higher adjacent to coarse woody debris in Swedish temperate forests (Castro and Wise 2010), whereas 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 insects, including saproxylic beetles (Johansson et al. 2006). Many of these decaying-wood-associated invertebrates 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 richness, associated with 2 variables (canopy and sapling richness) in our top habitat model, has been observed as a positive predictor of Wood Thrush abundance by Robbins et al. (1989)—perhaps because invertebrate richness increases with niche availability that is provided by additional tree species (Crisp et al. 1998). Three habitat structure predictors are linked with the red maple and American holly, which were both locally common understory trees and a frequent nesting substrate observed in our study birds. Bakermans et al. (2012) suspected nest site availability explained the

positive relationship between Wood Thrush density and the number of small trees. Nest positions of birds tracked in this study suggested a strong positive relationship with bird use (A. Deverakonda personal observation), indicating variables identified by the habitat model might be important predictors of nest site selection. The last variable in the habitat model was pine basal area, a predictor that related negatively to space use. This result is in line with other research suggesting Wood Thrushes avoid coniferous forest (e.g., Robbins et al. 1989). The weak performance of pine basal area in the habitat model could be a consequence of our sampling scale. Samples were taken within home ranges, and birds might avoid placing home ranges in coniferous forest altogether. Such a scenario is supported by our observations of significantly more pine at bird absence sites than within bird home ranges (Figure 6).

The composite model was composed of 3 prey and 9 habitat structure variables, indicating that either prey availability or habitat alone is not sufficient to explain bird utilization distribution. When compared with the prey or habitat models, the more inclusive composite model should tie bird use to its environment with improved accuracy, which reflects utilization of foraging habitat as well as resources for other activities, such as nesting. However, the GOF procedure revealed that while the composite model's explanatory ability was nearly 9 times the prey model, the composite model provided only a marginal improvement over the habitat model.

Whereas all habitat structure variables had just about identical strengths in the models that contained them, prey predictors, albeit well-represented in the composite model, had different coefficients. Spider biomass had a greater effect in the composite model, whereas biomass of worms, the strongest prey model predictor, was only marginally important in the composite model. A possible reason for the discrepancy between the 2 models is that some of the habitat structure variables were a proxy for food availability. As discussed earlier, such was probably the reason for the strong performance of red oak counts in both the habitat and composite models, and a link to invertebrates could be made with canopy height, snag basal area, as well as sapling richness. Even though we did not detect collinearity between variables included in the final models, the vegetation plots might have still represented food availability better. This could be the case if invertebrate biomass exhibited a clumped distribution and the vegetation plots sampled a larger area than invertebrate plots. Although the prey model had a larger sample size ( $n = 370$ ) than the habitat and composite models ( $n = 222$ ), the habitat structure data, due to plot size, represented a much higher proportion of bird home range area. The invertebrate biomass data were strongly right-skewed (Figure 2), indicating that invertebrates were indeed distributed patchily. The "clumped invertebrates" hypothesis was

supported by our observation that running the prey model with a reduced dataset matching samples included in the composite model (60% of original prey model data) produced regression coefficients that closely followed prey coefficients in the final composite model.

Alternatively, prey availability most likely fluctuates within home ranges over the breeding season. McKinnon et al. (2015) found that seasonal habitat drying within areas used by Wood Thrush on the wintering grounds was related to a significant reduction of invertebrate prey. If bird prey is tied to soil moisture, as our study suggests, and soil moisture varies temporally with weather, our approach to sample invertebrates over a 5-day window at the end of the tracking period might inadequately reflect invertebrate availability at the time when birds foraged. Regrettably, we were unable to assess food availability in real time due to the cryptic habit of litter invertebrates and the fact that telemetry had to be completed before home range extent was known. However, our results indicate that at least some prey groups are related to physical features in bird home ranges that are static at the breeding season scale, such as decomposing wood. Soil moisture, for instance, is related to home range topography (Grayson et al. 1997, Western et al. 1999). We therefore believe that some places within home ranges will consistently produce higher prey biomass than others.

Another factor that could result in a failure to properly capture food availability is if birds foraged according to the marginal value theorem (Charnov 1976). With patch regeneration rate sufficiently low, birds could deplete a food patch and move on, which would affect space use patterns over time. Regardless of the reason behind the contrast in model regression coefficients, the composite model explained space use much better than the prey model, and only slightly better than the habitat model (Appendix Figure 7), highlighting the importance of habitat structure variables for within-home range space use. However, because of the difficulty of disentangling complex ecological relationships and the fact that this analysis is correlative in principle, we cannot attribute cause and effect with confidence.

We recommend caution when interpreting the results of both models and variable evaluation. Model-averaging of beta coefficients in mixed models can be problematic (Cade 2015). Nevertheless, a number of points suggest we minimized this issue here: (1) we removed collinear variables from the analysis, (2) GOF procedure indicated no difference between model-averaged parameter vs. model-averaged output results, and (3) we found that little variation was explained by model random effects (individual bird). Still, the relative strength of model beta coefficients can be distorted slightly. In our separate predictor evaluation with bird absence sites, predictors of bird use within home ranges, which is what we modeled,

might be different from predictors of home range location, which is what our bird absence sites were more closely related to. In other words, during variable evaluation, we have mixed scales at least partly. One of the central tenets of migratory bird habitat selection is that birds choose habitat hierarchically, from large to fine scale (Battin and Lawler 2006). Forest canopy height, for example, can be assessed by a bird flying over. However, the quantity of spider prey might require a closer inspection after a potential breeding site has met requirements at a larger scale, such as a minimum forest patch area. Nevertheless, we believe our model evaluation lends additional credibility to 5 predictors: number of red oaks, which is an inverse proxy for humid soils and associated prey; canopy height, which is related to forest maturity; canopy richness, which might support more prey species; worm biomass, which is prey availability itself; and pine trees, which reinforces the notion that the Wood Thrush is a species associated with deciduous forest.

To our knowledge, no previous study of a forest songbird has related within-home range utilization distribution derived from individually tracked birds to both habitat structure and food availability predictors. Moreover, to evaluate variable credibility, we conducted multi-year point count surveys and compared model-derived predictors of bird utilization at high-use locations within bird home ranges with sites where birds were never detected over 5 breeding seasons. Results from our mixed models indicate that habitat structure was especially important in explaining differential use within Wood Thrush home ranges, as these variables performed consistently well in models representing both food availability and habitat structure resources. Although many of the important structure covariates could be ultimately linked to prey availability, our results highlight the possibility that habitat structure resources might ultimately drive diurnal space use patterns in many birds. However, research into causes of bird utilization distribution ought to assess both habitat structure and food availability, especially where complex ecological interactions preclude proper attribution to causal mechanisms.

This study implies that high-quality Wood Thrush habitat involves access to a sufficient quantity of prey biomass, particularly spiders and worm-like invertebrates associated with mesic areas, as well as a suite of habitat structure resources. Management objectives aimed at habitat improvement for this declining species should therefore consider a deciduous forest that contains a well-developed canopy, sites with humid soils, snags, and higher numbers and species richness of understory trees.

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**Author contributions:** Vitek Jirinec and Matthias Leu conceived the idea, design, and experiment. Vitek Jirinec collected the data and conducted the research. Vitek Jirinec and Matthias Leu wrote the paper. Vitek Jirinec, Matthias Leu, and Robert Isdell developed and designed the methods. Vitek Jirinec, Matthias Leu, and Robert Isdell analyzed the data. Matthias Leu contributed substantial materials, resources, or funding.

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[and\\_nesting\\_success\\_of\\_wood\\_thrushes\\_Hylocichla\\_mustelina\\_to\\_habitat\\_characteristics\\_at\\_multiple\\_scales](#)

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**APPENDIX TABLE 3.** Predictor variables considered for the composite model ( $n = 66$ ), sorted from lowest to highest  $\Delta AIC_c$  obtained during univariate modeling. A priori-hypothesized relationship with space use is included in the hypothesis column. Covariates were either brought forward into the global model ( $n = 12$ ; Status = global model) or removed. We removed variables if  $AIC_c >$  the null model ( $n = 29$ ; Status =  $AIC_c >$  null), Pearson's correlation coefficient ( $r_p$ )  $> |0.7|$  ( $n = 12$ ; Status = correlated), or a covariate was unstable during multivariate modeling ( $n = 13$ ; Status = unstable).

$\Delta AIC_c$	ID	Hypothesis	Status	Predictor description and notes
0 <sup>a</sup>	ba_snag**	+	global model	basal area of snags (upright dead trees)
0 <sup>a</sup>	beetle_g*	+	unstable	beetle guild biomass
1	spider_g*	+	global model	spider guild biomass
2	other_g*	+	unstable	other guild biomass
5	ba_ah	+	unstable	basal area of American holly ( <i>Ilex opaca</i> )
6	can_rich**	+	global model	number of tree species in the canopy stratum
7	can_sdi	+	correlated	canopy tree Shannon diversity index; correlated with can_rich, and richness is more easily interpreted
7	ba_ma**	+	global model	basal area of the red maple ( <i>Acer rubrum</i> )
7	max_canopy_m**	+	global model	LiDAR, mean maximum canopy height within a 10-m neighborhood using raster grid with a 1-m resolution
7	sap_sdi	+	correlated	sapling (<10 cm DBH) Shannon diversity index; correlated with sap_rich, which is more easily interpreted
8	total_w	+	correlated	sum of the biomass of all guilds; correlated with worms_g
8	ba_m2	+	correlated	basal area of all trees; correlated with max_canopy_m
8	sapl_rich**	+	global model	number of sapling species
8	centipede_g*	+	global model	centipede guild biomass
8	cov_dbh	-	unstable	coefficient of variation of all trees (>10 cm DBH)
8	ba_can	+	correlated	basal area of canopy trees; correlated with ba_m2
9	worm_g*	+	global model	worm guild biomass
9	tree_sdi	+	unstable	all trees (>10 cm DBH) Shannon diversity index
9	ba_haw	+	unstable	basal area of the tree guild comprised of hickory, ash, and walnut
10	ba_sg	+	unstable	basal area of sweetgum ( <i>Liquidambar styraciflua</i> )
10	ba_b	+	unstable	basal area of American beech ( <i>Fagus grandifolia</i> )
10	spider_n	+	correlated	spider invertebrate guild count, correlated with spider_g
10	ba_sub	+	unstable	basal area of subcanopy trees
11	ba_pi**	-	global model	basal area of pine trees ( <i>Pinus</i> spp.)
11	sub_sdi	+	correlated	Shannon diversity index of subcanopy trees, correlated with tree_sdi
11	ba_tp	+	unstable	basal area of tulip poplar ( <i>Liriodendron tulipifera</i> )
11	ba_o	+	unstable	basal area of oaks ( <i>Quercus</i> spp.)
11	veg_dens	-	unstable	fractional cover/density of LiDAR returns 1 m and above
11	tree_rich	+	correlated	number of species (>10 cm DBH), correlated with tree_sdi and sub_sdi
11	snag_ct	+	correlated	snag count, correlated with ba_snag, which is a better predictor
11	ro_ct**	+	global model	red oak ( <i>Quercus rubra</i> ) count
12	ah_sap_ct**	+	global model	American holly ( <i>Ilex opaca</i> ) sapling count
12	haw_ct	+	correlated	count of the tree guild comprised of hickory, ash, and walnut, correlated with ba_haw, which is a better predictor
13	beetle_n	+	correlated	beetle invertebrate guild count, correlated with beetle_g, which is a better predictor
13	dwd_m3	+	unstable	volume (cubic meters) of downed woody debris
13	ma_sap_ct**	+	global model	red maple ( <i>Acer rubrum</i> ) sapling count

## APPENDIX Continued.

$\Delta AIC_c$	ID	Hypothesis	Status	Predictor description and notes
13	pi_ct	-	correlated	pine tree ( <i>Pinus</i> spp.) count, correlated with ba_pi, which is a better predictor
<b>14</b>	<b>null</b>			
14	av_dbh_s	+	AICc > null	mean DBH of subcanopy trees
14	sub_rich	+	AICc > null	number of species in the subcanopy
14	wo_ct	+	AICc > null	white oak ( <i>Quercus alba</i> ) count
14	o_ct	+	AICc > null	count of all oak trees ( <i>Quercus</i> spp.)
14	av_dbh	+	AICc > null	mean DBH of all trees (>10 cm DBH)
15	unders_dens	-	AICc > null	fractional cover/density of LiDAR returns 30 cm to 3 m above ground
15	conif_sap_ct	-	AICc > null	count of coniferous saplings
15	centipede_n	+	AICc > null	centipede invertebrate guild count
15	ah_ct	+	AICc > null	American holly ( <i>Ilex opaca</i> ) count
15	b_ct	+	AICc > null	American beech ( <i>Fagus grandifolia</i> ) count
15	tp_ct	+	AICc > null	tulip poplar ( <i>Liriodendron tulipifera</i> ) count
15	canop_ct	+	AICc > null	count of canopy trees
15	sg_ct	+	AICc > null	sweetgum ( <i>Liquidambar styraciflua</i> ) count
15	ma_ct	+	AICc > null	red maple ( <i>Acer rubrum</i> ) count
15	b_sap_ct	+	AICc > null	American beech ( <i>Fagus grandifolia</i> ) saplings count
16	percov_ll	+	AICc > null	% cover of deciduous leaf litter
16	tri	+	AICc > null	terrain ruggedness index, as described by Riley et al. (1999)
17	percov_pl	-	AICc > null	% cover pine ( <i>Pinus</i> spp.) needles
17	subcan_ct	-	AICc > null	count of subcanopy trees
17	sapl_ct	+	AICc > null	count of all saplings
17	percov_f	-	AICc > null	% cover of forbs (herbaceous flowering plants)
17	tree_ct	+	AICc > null	count of all trees (>10 cm DBH)
17	other_n	+	AICc > null	count of "other" invertebrate guild
18	av_dbh_c	+	AICc > null	mean DBH of canopy trees
18	pp_ct	+	AICc > null	count of pawpaw ( <i>Asimina triloba</i> )
18	worm_n	+	AICc > null	count of worm invertebrate guild
19	total_n	+	AICc > null	sum of all invertebrate individuals
20	edge_dist_m	+	AICc > null	Euclidean distance to forest edge (forest constructed as follows: LiDAR, at least one tree $\geq 10$ m tall within a 5-m neighborhood, while disallowing for gaps below 25 m <sup>2</sup> )
23	dist_stream_m	-	AICc > null	Euclidean distance to streams (TIGER)

<sup>a</sup>  $AIC_c = 2139$ .

\* variable selected into the global prey model.

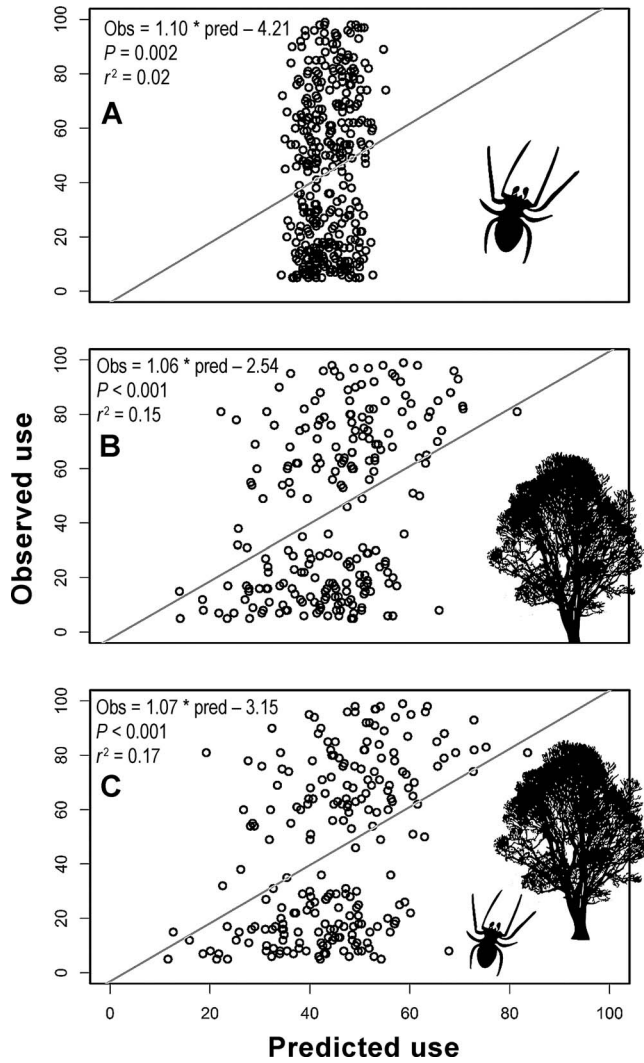
\*\* variable selected into the global habitat model.

APPENDIX TABLE 4. Prey model: top models ( $n = 15$ ) for model averaging.

Model	Intercept	beetle_g	centipede_g	other_g	spider_g	worm_g	df	logLik	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
1	43.64	-1.47	-1.19	-1.37	2.12	4.04	8	-1757.21	3530.82	0.00	0.2225
2	43.64	-1.60		-1.51	2.10	3.85	7	-1758.87	3532.04	1.22	0.1207
3	43.64	-1.62	-1.36		2.06	3.78	7	-1758.96	3532.23	1.41	0.1099
4	43.64		-1.35	-1.53	1.73	4.07	7	-1759.02	3532.35	1.53	0.1037
5	43.64	-0.90	-1.15	-1.28		4.38	7	-1759.48	3533.28	2.45	0.0652
6	43.64	-1.80			2.03	3.53	6	-1760.70	3533.63	2.81	0.0545
7	43.64			-1.72	1.66	3.85	6	-1760.76	3533.75	2.92	0.0516
8	43.64		-1.56		1.62	3.78	6	-1760.87	3533.96	3.14	0.0462
9	43.64		-1.26	-1.40		4.36	6	-1761.00	3534.24	3.42	0.0403
10	43.64	-1.04		-1.42		4.19	6	-1761.12	3534.47	3.65	0.0359
11	43.64	-1.07	-1.31			4.13	6	-1761.19	3534.60	3.78	0.0336
12	43.64			-1.58		4.14	5	-1762.69	3535.55	4.73	0.0210
13	43.64				1.52	3.48	5	-1762.73	3535.62	4.80	0.0202
14	43.64		-1.46			4.07	5	-1762.77	3535.70	4.88	0.0194
15	43.64	-1.24				3.88	5	-1762.90	3535.96	5.14	0.0170

**APPENDIX TABLE 5.** Habitat model: top models ( $n = 49$ ) for model averaging.

Model	Intercept	ah_sap_ct	ba_ma	ba_pi	ba_snaq	can_rich	ma_sap_ct	max_canopy_m	ro_ct	sapl_rich	df	logLik	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
1	45.12	2.64	2.98	-2.42	4.08	3.49	2.77	5.19	-5.96	3.18	12	-1040.48	2106.45	0.00	0.2692
2	45.12	2.84	3.15	-2.62	4.26	3.43	2.61	4.83	-5.99	2.92	11	-1042.83	2108.91	2.45	0.0789
3	45.12		2.85	-2.25	4.88	3.25	2.54	5.53	-5.65	3.47	11	-1042.93	2109.11	2.65	0.0714
4	45.12	2.39	3.38	-2.25	3.80	3.69		4.99	-5.78	3.79	11	-1043.02	2109.29	2.84	0.0652
5	45.12	2.48		-2.63	3.93	4.13	3.22	4.84	-6.09	3.38	11	-1043.18	2109.62	3.16	0.0554
6	45.12	2.99	3.18	-2.11	4.27	3.94	3.46	5.33	-5.76		11	-1043.29	2109.83	3.38	0.0498
7	45.12	2.39	3.51	-2.36	4.87		2.95	6.31	-4.85	3.55	11	-1043.33	2109.91	3.46	0.0478
8	45.12	3.85	2.80	-2.69		4.66	2.38	4.97	-6.35	3.41	11	-1043.96	2111.18	4.72	0.0254
9	45.12	2.60	3.52		3.98	3.62		4.67	-5.82	3.51	10	-1045.26	2111.57	5.11	0.0209
10	45.12		3.24	-2.45	4.56	3.45		5.32	-5.51	4.01	10	-1045.33	2111.69	5.24	0.0196
11	45.12		3.03		5.15	3.16	2.35	5.17	-5.66	3.21	10	-1045.40	2111.84	5.38	0.0183
12	45.12	3.15	3.31		4.41	3.85	3.26	5.00	-5.79		10	-1045.46	2111.95	5.50	0.0172
13	45.12			-2.81	4.70	3.87		5.17	-5.79	3.64	10	-1045.54	2112.12	5.66	0.0159
14	45.12		3.36	-2.55	5.55		2.74	6.54	-4.64	3.79	10	-1045.63	2112.31	5.85	0.0144
15	45.12	2.59	3.67		5.03	3.85	2.79	5.94	-4.89	3.29	10	-1045.63	2112.31	5.86	0.0144
16	45.12	2.70			4.12	4.10	3.07	4.43	-6.13	3.10	10	-1045.66	2112.35	5.90	0.0141
17	45.12		3.05	-2.31	5.21	3.70	3.27	5.73	-5.38		10	-1045.96	2112.96	6.50	0.0104
18	45.12	2.11	3.97	-2.17	4.62			6.17	-4.59	4.23	10	-1045.98	2113.01	6.56	0.0101
19	45.12	2.17		-2.46	3.57	4.46		4.55	-5.90	4.14	10	-1046.04	2113.13	6.67	0.0096
20	45.12	2.85		-2.31	4.12	4.64	3.99	4.96	-5.88		10	-1046.13	2113.30	6.85	0.0088
21	45.12	3.27	2.44	-1.76	3.80	5.58	2.43		-6.29	3.39	11	-1045.04	2113.33	6.88	0.0086
22	45.12	3.56	3.16	-2.52		4.76		4.81	-6.17	3.93	10	-1046.27	2113.58	7.12	0.0076
23	45.12	2.76	3.76	-1.80	3.95	4.30		5.11	-5.47		10	-1046.36	2113.75	7.30	0.0070
24	45.12	2.75	3.81	-2.00	5.20			6.63	-4.45		10	-1046.42	2113.89	7.43	0.0066
25	45.12	2.15		-2.60	4.86			6.13	-4.75		10	-1046.47	2113.97	7.52	0.0063
26	45.12	4.13	2.98				3.76	5.11	-4.45	3.87	10	-1046.47	2113.98	7.53	0.0062
27	45.12	3.66		-2.88			3.55	6.63	-6.40		10	-1046.53	2114.10	7.64	0.0059
28	45.12		3.38		4.83		2.83	4.99	-5.53	3.73	9	-1047.68	2114.22	7.76	0.0055
29	45.12	4.29	3.00	-2.36		5.19	3.11	5.11	-6.15		10	-1046.93	2114.91	8.45	0.0039
30	45.12		3.52		5.79		2.54	6.17	-4.66	3.53	9	-1048.05	2114.96	8.50	0.0038
31	45.12				4.97	3.82	2.81	4.76	-5.81	3.37	9	-1048.14	2115.12	8.67	0.0035
32	45.12	3.39	2.60	-2.35	3.95	5.42	2.32		-6.30	3.19	10	-1047.04	2115.12	8.67	0.0035
33	45.12		3.81		5.24			6.39	-4.41	4.40	9	-1048.15	2115.15	8.69	0.0035
34	45.12	2.31	4.10		4.78			5.84	-4.64	3.95	9	-1048.18	2115.22	8.76	0.0034
35	45.12	1.95	3.21	-2.48	4.65	1.07	2.40	5.58	-5.51	2.81	11	-1045.99	2115.23	8.78	0.0033
36	45.12		3.20		4.27	3.59	3.05	5.40	-5.40		9	-1048.23	2115.32	8.86	0.0032
37	45.12			-2.63	4.27	4.22		4.86	-5.65	4.32	9	-1048.24	2115.32	8.87	0.0032
38	45.12	2.90	3.85		4.09	4.21		4.84	-5.51		9	-1048.37	2115.60	9.14	0.0028
39	45.12	2.38			3.77	4.42		4.18	-5.94	3.85	9	-1048.41	2115.66	9.21	0.0027
40	45.12	3.01			4.27	4.58	3.80	4.59	-5.93		9	-1048.41	2115.67	9.22	0.0027
41	45.12	3.04	2.81	-1.63	3.57	5.68			-6.12	3.93	10	-1047.37	2115.78	9.32	0.0025
42	45.12		2.54	-3.09	5.43	4.63	1.90	5.44	-5.98	3.95	10	-1047.38	2115.80	9.34	0.0025
43	45.12	3.11		-1.97	3.69	5.99	2.83		-6.38	3.55	10	-1047.38	2115.81	9.36	0.0025
44	45.12	2.90	3.93		5.31	3.57	3.57	6.29	-4.51		9	-1048.53	2115.91	9.46	0.0024
45	45.12		3.30	-2.76	5.48		3.33	6.35	-4.57	4.08	9	-1048.65	2116.15	9.69	0.0021
46	45.12	3.85			5.03	4.74		4.44	-6.23	3.63	9	-1048.67	2116.19	9.74	0.0021
47	45.12		3.50	-2.49	5.03	4.39	3.79	5.36	-5.51		9	-1048.71	2116.27	9.81	0.0020
48	45.12	3.82		-2.68			2.54	6.51	-4.86	4.00	10	-1047.69	2116.43	9.97	0.0018
49	45.12		3.61	-2.00	4.84	4.07		5.49	-5.13		9	-1048.87	2116.60	10.14	0.0017



**APPENDIX FIGURE 7.** Model goodness-of-fit (GOF) results for (A) the prey model, (B) habitat model, and (C) composite model.