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# Are Occupancy Models Feasible Alternatives to Collecting Breeding Data?

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# Are Occupancy Models Feasible Alternatives to Collecting Breeding Data?

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Master of Science

Department of Biology

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# APPROVAL PAGE

This Thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Science

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Approved by the Committee, April, 2013

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# COMPLIANCE PAGE

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# ABSTRACT

Biologists must find ways to maximize biodiversity while minimizing impacts on human social and economic needs. Tools such as Geographic Information Systems (GIS) and satellite imagery allow researchers to identify and delineate land cover types most important for conservation. Important land cover types can be identified by developing species distribution models (SDMs), which relate species occurrence against land cover and environmental variables. SDMs can be spatially applied to create a predictive map that land managers can then use to delineate habitat best suitable for long-term conservation. An occupancy model is a type of SDM that is commonly used to estimate probability of occupancy of bird species across large-scales. However, to my knowledge, no study has directly examined whether probability of occupancy correlates with breeding success. The objectives of this study were to 1) create single-season occupancy model for a Neotropical migrant species, the Wood Thrush *(Hylocichla mustelina)* and 2) correlate probability of occupancy with breeding success for Wood Thrushes breeding on the Virginia Peninsula, an area consisting of urban-rural and agricultural areas. I selected a priori seven site-specific covariates that were predicted to be important for Wood Thrush occupancy and reproductive success. Although Wood Thrushes are an extremely well-studied species, my findings indicate that Wood Thrush habitat use differs in this study area compared with previous literature. Wood Thrush occupancy related positively to anthropogenic variables such as road density and edge density of forest-to-low urban development, which contradicts previous literature that claimed Wood Thrushes are an interior forest species. However, all site-specific covariates had confidence intervals that overlapped with zero, indicating that the occupancy model had low predictive power. Additionally, no relationship was found between Wood Thrush probability of occupancy and breeding success. It is possible that the Wood Thrush in this area may have a large turn-over within season, which violates the closure assumption of occupancy models. Although this study found no relationship between Wood Thrush occupancy and breeding success, it did demonstrate the need to evaluate which variables are important for a species' habitat use, even a well-studied species such as the Wood Thrush, when studying a species in a new landscape.

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# INTRODUCTION

One of the most prominent and rapidly expanding anthropogenic land uses influencing habitat loss in the United States is urbanization (Czech 2005, Robinson et al. 2005). As the human population continues to grow, urban areas will become the dominant land cover type in many landscapes. Urbanization of wild land (i.e. land cover types not overlapping with human development [Marzluff et al. 2001]), has direct implications on avian fitness and population dynamics (Borgmann et al. 2004).

Because urbanization results in habitat loss (Robinson et al. 2005) and because continued land development by humans is inevitable, conservationists and land managers must find ways to maximize biodiversity while having the least impact on human social and economic needs. Tools such as Geographic Information Systems (GIS) and satellite imagery allow researchers to delineate areas of high conservation priority by identifying land cover types most important for long-term conservation of birds. Habitat important for conservation can be identified by developing species distribution models (SDMs). SDMs are statistical models relating species occurrence against environmental variables and human stressors (MacKenzie et al. 2006, Franklin 2009).

Bird species distribution modeling has become a readily implemented conservation tool because field data needed to develop these models are inexpensive to collect and allow researchers to identify factors that determine distribution patterns for a species within a larger geographical range. A critical assumption of SDMs is that areas overlapping with high-occupancy probabilities or densities equate with areas of high quality habitat. When investigating density as a surrogate for habitat quality, Van Horne (1983) was first to point out that species density cannot necessarily be equated with habitat quality, and proposed that habitat quality be defined as “the product of density, mean individual survival probability, and mean expectation of future offspring” (Van Horne 1983:896). Other studies have examined the relationship between habitat quality and density (Vickery et al. 1992, Bock & Jones 2004, Perot & Villard 2009) and have found mixed results, indicating that although a positive density-productivity relationship is typically found among bird species, additional factors, such as reproductive success and survival data, are needed to determine habitat quality for some species. To my knowledge, no study has evaluated whether probability of occupancy relates positively to reproductive success.

An occupancy model is a type of species distribution model that accounts for imperfect detection to derive unbiased estimates of occupancy (MacKenzie et al. 2002). Occupancy models are based on logistic regressions to estimate both occupancy ($\psi$) and detection ($\rho$) probabilities simultaneously (MacKenzie et al. 2006). Covariates can be included to assess heterogeneity in $\psi$ and $\rho$. Final models can then be spatially applied to create a predictive map showing where a species is more or less likely to occur. Land managers can use this predictive map to delineate habitat most suitable for long-term species conservation based on areas where occupancy is predicted to be highest.

It is important to examine whether probability of occupancy correlates positively with breeding success in birds. Presence/absence data used in occupancy modeling are typically determined via aural detections (Bibby et al. 2000). However, because most male songbirds tend to sing for a longer duration when they are attempting to attract a mate or defend a territory (Beckett & Ritchison 2010, Hennin et al. 2009, Watson 1987), it is possible that lower quality, unpaired males, may be detected more often than paired males who sing less frequently. Thus, occupancy models may predict higher probabilities of occupancy in habitat where pairing success is low. This potential shortfall could result in misguided long-term conservation efforts.

The objective of this study was to evaluate whether breeding success correlated with probability of occupancy. Specifically, I had the following two objectives: 1) develop a spatially explicit single-season occupancy model for a Neotropical migrant and 2) correlate probability of occupancy with breeding success. I selected a Neotropical migrant species because many Neotropical migrants are species of concern (Sherry & Holmes 1996, Norris et al. 2004, Holmes 2007) and occupancy modeling can be used to study their habitat associations. I chose the Wood Thrush *(Hylocichla mustelina)* because it commonly breeds in eastern deciduous forests in Virginia. Wood Thrushes nest in mid-successional hardwood forests and use early-successional hardwood forests during the post-fledgling period (Anders et al. 1998, Vega Rivera et al. 1998). Although these land-cover types are abundant in Virginia (Monette et al. 1983, Westervelt et al. 2006), this species is declining by 2.2% annually (Sauer et al. 2008). One potential mechanism of population decline has been attributed to edge effects, most often caused by nest predation (Robinson et al. 1995) in fragmented landscapes (Hoover et al. 1995). Thus, I predicted that Wood Thrush probability of occupancy would be higher in larger patches of deciduous forest and lower in developed and fragmented areas. Although the Wood Thrush is a well-studied species, they have mostly been studied in large-contiguous Eastern Deciduous Forests. My research is unique because I studied Wood Thrush habitat use along an urban-to-rural gradient and across a fragmented forest system.

## METHODS

### *Study Area:*

The study area was within the portion of the Chesapeake Bay Lowlands Ecoregion (TNC 2000) between the Rappahannock and the James River and was bounded to the west by the fault line (Fig. 1). Point count surveys and breeding data were collected within Charles City County, City of Williamsburg, James City County, Gloucester County, New Kent County and York County. Much of the study area overlapped with the coastal deciduous forest ecological system and included additional land-cover types such as agriculture, residential, commercial and urban areas.

In the coastal deciduous forest, depending on the successional stage, the canopy consists of *Pinus taeda* (loblolly pine), *Fagus grandifolia* (American beech), *Quercus alba* (white oak), *Liriodendron tulipifera* (tuliptree) and *Liquidambar styraciflua* (sweetgum). The understory is typically dominated by *Acer rubrum* (red maple), *Ilex opaca* (holly) and *Cornus florida* (dogwood), whereas the shrub layer consisted of *Smilax rotundifolia* (roundleaf greenbrier), *Toxicodendron radicans* (eastern poison-ivy), *Parthenocissus quinquefolia* (Virginia creeper), *Leersia oryzoides* (rice cutgrass), *Peltandra virginica* (green arrow-arum), *Myrica cerifera* (wax myrtle) and *Mitchella repens* (patridge berry) (Monette et al. 1983,Westervelt et al. 2006).

*Breeding success data:*

During May through July of 2011 and 2012, I visited 18 (2011 = 8; 2012 = 10) breeding study sites within the study area that were large enough to accommodate at least 10 Wood Thrush territories (average territory ~ 2.1 ha, Evans et al. 2008). In 2011, study sites were chosen through an opportunistic sampling where Wood Thrushes were known to occur based on point counts surveyed in 2010. In 2012, study site locations were randomly selected from a 500m grid overlapping with coniferous, mesic and upland deciduous forest on public land. Prior to the field season in 2012, I visited each breeding study site to determine if it was suitable for collecting breeding data. I had to adjust five sites by either moving or altering the size due to inaccessibility. Study sites were considered inaccessible if I was unable to park in biking distance of the site or if large marshy areas or deep ravines prevented me from walking around the entire study site.

I visited each site every three to six days to delineate male territories. The average sampling effort was greater in 2011 (average days per site = 16.75, range = 7-28, sd = 7.04) then in 2012 (average days per site = 10.4, range = 5-15, sd = 3.53). This was most likely due to observing a greater number of males in 2011 (n = 73) compared to 2012 (n = 26). If I did not detect males within a study site, I continued to survey those study sites throughout the season. During each visit, I observed males for approximately three hours and geo-referenced (UTM coordinates) locations of males exhibiting singing, foraging, or warning behavior using a Garmin GPS unit (Garmin GPSmap 60Cx). To delineate territories, I followed each male while maintaining a distance of at least 20m to avoid flushing. I observed the location where a male was perched, singing, warning, calling, or foraging in the leaf litter and geo-referenced locations once the male vacated the area. During each visit, I attempted to obtain at least five locations for each male; however, this was not always possible because I did not detect each male during each visit. I obtained on average 3.78 observations per territory in 2011(range =1-12, 2.83) and 10.35 observations per territory in 2012 (range = 2-25, sd = 7.67).

Visiting territories every three to six days enabled me to assign pairing status and/or fledgling success to each territory. I assigned a modified Reproductive Index (Vickery et al. 1992a, Christoferson & Morrison 2001, Bonifait et al. 2006) to each territory: 1= territorial male present for < 4 weeks, 2 = territorial male present > 4 weeks, 3 = territorial male and female present > 4 weeks, 4 = evidence of fledgling success. Pairing success was determined if I found a nest or observed a female on the same territory. Males tended to sing less frequently when paired. Females were typically seen foraging near the ground or flying near singing males.

Additionally, when I followed an individual male, I was able to successfully find nests because they generally remained in proximity to their nest. Fledgling success was determined by male behavior and by carefully searching territories for the presence of fledglings. I observed that adult males sang less frequently when their nestlings fledged and instead began to produce warning calls. When this occurred, I followed and observed both parents until I found the fledglings, which were typically begging for food. In order to make sure I did not fail to detect the presence of fledglings, I searched all territories for evidence of fledglings for 5 days once a male stopped singing. If I was unable to find any fledglings and the adults were absent, I concluded that the nest had been depredated and that the pair had abandoned their territory. To calculate an overall reproductive success for each study site, I averaged the Reproductive Index across territories.

### *Presence/Absence Surveys and Survey-specific Covariates:*

In June 2011 and 2012, a total of 140 point count surveys were conducted (2011 = 70; 2012 = 70) (Fig. 1). Point count locations were randomly placed in forest patches along an urban-rural gradient and stratified by public access. Using ArcGIS 10 (ESRI 2011), I reclassified the Southeast Gap (SEGAP) land-cover data set (http://www.basic.ncsu.edu/segap/) to extract coniferous forest, mesic and upland deciduous forest, as well as urban land covers. I then clipped all forest patches to a delineated layer of accessible public land. I placed random point count locations within clipped forest patches ensuring equal sampling of forest types. I then inspected the urban gradient by extracting the proportion of urban area within a 1-km buffer surrounding each point count location.

Following Mitchell and Donovan (2008), each point count location was surveyed for Wood Thrushes for four 8-minute surveys during a single visit between 15 minutes after sunrise and 10:15 a.m. Each survey was separated by a two minute break. For each observation, I estimated the distance to each individual using a laser range finder (Insight 400XL, Opti-Logic) and noted whether individuals were visually or aurally detected. I recorded Wood Thrush presence/absence when individuals were detected within a 130-m threshold distance. For each survey, I also recorded covariates that may have influenced detection probability: Julian Date, start time of the survey, average wind speed (m/s) and temperature ($0^C$), which I measured with a pocket weather meter (Model 2000, Kestrel Meters).

*Site-specific Covariates:*

I created a priori nine GIS layers that represented both environmental factors and human stressors that could impact Wood Thrush occupancy: proportion of dry-mesic forest, proportion of flooded forest, proportion of low-development, road density, distance to forest edge, distance to open water, density of forest-low urban edges, stream density and deer hunting intensity. I first reclassified Southwest Gap Analysis Project (SEGAP) land cover data set (http://www.basic.ncsu.edu/segap/) to include: open water (SEGAP Value = 1, 2 ), developed open space (SEGAP Value = 4, 17, 18), low development (SEGAP Value = 5), medium-to-high-development (SEGAP Value = 6, 7), unconsolidated shore (SEGAP Value = 35, 125, 127, 145, 146), dry-mesic hardwood forest (SEGAP Value = 39, 40, 66, 86, 108), pine forest (SEGAP Value = 71), flooded forest (SEGAP Value = 73, 151, 153, 164, 165, 174, 204), pasture (SEGAP Value = 148), row crop (SEGAP Value = 149) and tidal marsh (SEGAP Value = 215, 248). Because Wood Thrush occupancy may be affected by processes occurring at multiple scales (scale is variably defined as extent and resolution [Turner 1989]; in this study scale equates with extent), I chose to evaluate the effect of each habitat variable on Wood Thrush occupancy at 120-m, 300-m, 1-km, 2-km and 3-km scales. The 120-m scale was based on an average Wood Thrush territory of 45 ha (Evans et al. 2008). I based the 300-m scale on the post-natal territory size. Anders et al. (1998) showed that the Wood Thrush natal home-range can vary between 2.6 to 24.8 ha, thus a 300m extent was selected to represent the larger natal home-range. I used a 1-km scale following Schwenk and Donovan (2011) who found that Wood Thrush occupancy was positively affected by intermediate forest patches within this scale. I chose a 2-km scale because Wood Thrush juveniles have been shown to disperse an average distance of 2.08 ± 1.48 km from their natal home-range to their post-dispersal home-range (Anders et al. 1998). Finally, I chose a 3-km scale in order to explore any landscape-level effects that may impact Wood Thrush occupancy.

Because Wood Thrush reproductive success has been shown to be higher in large deciduous forest patches (Hoover et al. 1995), I evaluated the relationship of proportion of DRY-MESIC FOREST and Wood Thrush occupancy (Anders et al. 1998, Vega Rivera et al. 1998). I first created binary (0, 1) layers for dry-mesic hardwood forest and then performed moving-window analyses using the neighborhood function in Spatial Analyst (ESRI 2011) to estimate proportion of DRY-MESIC FOREST within each of the five scales. Many studies have shown that Wood Thrush reproductive success is negatively impacted by fragmentation (Hoover et al. 1995, Robinson et al. 1995). Because forests in my study area are fragmented by agricultural, residential and urban areas, and because forest cover highly correlated with road density, I used ROAD DENSTIY to investigate how Wood Thrush occupancy is influenced by forest fragmentation. To calculate ROAD DENSITY, I used the TIGER road dataset (U.S. Census 2010) and created a binary layer (0, 1) for roads associated with low-to-medium traffic volume (categorized as local and other in the TIGER road dataset). I calculated ROAD DENSITY within the five scales using the Line Density tool in Spatial Analyst in ArcGIS 10 (ESRI 2011).

I included two predictor variables representing DISTANCE TO WATER and DISTANCE TO FOREST EDGE. Based on field observations, distance to open water (brackish/salt water) seemed to negatively influence Wood Thrush occurrence. Thus, I created a binary layer (1=open water, NoData = all other land cover) and calculated the Euclidean distance of each point count location to the nearest cell of open water using the Euclidean Distance function in Spatial Analyst (ESRI 2011). Previous literature has shown that Wood Thrushes respond negatively to decreasing forest patch size and to increasing edge effects (Hoover et al.1995, Robinson et al. 1992, Robinson et al. 1995b). DISTANCE TO FOREST EDGE was used as a surrogate for forest patch size and edge effects. I calculated DISTANCE TO FOREST EDGE by creating a binary layer (0 = non-forest land covers, 1= all forest land cover) for all forest land cover: dry-hardwood forest, mesic forest, flooded forest and pine forest. I calculated the Euclidean distance to the edge of forest using the Euclidean distance tool in Spatial Analyst in ArcGIS 10 (ESRI 2011). Because Wood Thrushes response to open water and edge of forest may be nonlinear, I expressed the Euclidean DISTANCE TO OPEN WATER and FOREST EDGE as an exponential decay value using the following equation (Nielsen et al. 2005): decay value = exp (Euclidean Distance / -scalar). I used the Raster Calculator in ArcGIS 10 to calculate the decay value for scalars of 90 m, 180 m and 300 m. These scalars were chosen to parallel the scales chosen for evaluating the effects of habitat variables on Wood Thrush occupancy. I then obtained the Decay Distance for each point count for each scalar calculated for both the DISTANCE TO OPEN WATER and FOREST EDGE.

I calculated edge density of FOREST-TO-LOW URBAN DEVELOPMENT as a proxy for forest fragmentation. I first created a binary layer (1 = all forest land cover, 2 = low urban land cover) and then delineated all edges of forest-to-low urban development in Geospatial

Modeling Environment (GME) (Beyer 2011) using the tool Edge. I then calculated edge density within the five scales using the Line Density tool in Spatial Analyst in ArcGIS 10 (ESRI 2011).

Although topographic variables such as elevation and slope have been found to be important in explaining suitable Wood Thrush habitat (Lichstein et al. 2002, Rittenhouse et al. 2007, Simons et al. 2000), the topography of this study area is mostly flat and I therefore did not include any topographic variables. However, I observed that Wood Thrushes seem to use habitat in ravines near small streams. Thus, I developed a STREAM DENSITY layer. I first clipped the TIGER stream dataset (U.S. Census 2010) to the study area. Because Wood Thrushes seemed to prefer small streams exclusively, I eliminated all major streams from the TIGER stream dataset (U.S. Census 2010) by erasing all streams that overlapped with flooded forest. I then calculated STREAM DENSITY within the five scales using the Line Density tool in Spatial Analyst in ArcGIS 10 (ESRI 2011).

### *Deer Browsing Layer:*

I observed that Wood Thrush occupancy seems to be higher in areas with sparse understory. This is most likely due to Wood Thrushes being an understory species foraging through leaf litter (Holmes & Robinson 1988). Unfortunately, forest understory heterogeneity throughout the study area cannot be captured from satellite or aerial imagery. However, colleagues and I have observed that areas where deer hunting is prohibited had sparse understory whereas areas exposed to intensive deer hunting had extremely dense understory. Thus, I developed a categorical DEER HUNTING intensity layer: 0 = no deer hunting, 1 = deer hunting. I first created a raster layer for all areas that prohibited deer hunting by performing the following steps in ArcGIS 10 (ESRI 2011): First, I reclassified the Wildlife-Urban Index (WUI) so that areas categorized as non-vegetated or agriculture with medium to high housing = 1 (Radeloff et al. 2005). Second, I clipped the Protected Area Dataset (PAD-US) (USGS 2011) to the study area (PAD-VA) and reclassified all Protected Areas =1 with the exception of land owned by the Virginia Department of Conservation and Recreation (VDCR) (www.dcr.virginia.gov), the Virginia Department of Forestry (VDOF) (www.dof.virginia.gov), the Virginia Department of Game and Inland Fisheries (VDGIF) (http://www.dgif.virginia.gov/) and public parks that allow seasonal hunting, determined via a survey of each public park. Third, I created a developed land cover layer by creating a binary layer where development (all roads and low-high development) = 1 and all other land cover = NoData. Fourth, I created a layer for the cities of Hampton, Newport News and Richmond because they prohibit deer hunting year round. Last, I combined the WUI layer, the PAD-VA layer, the developed land cover layer and the cities layer into one raster = 0 and all other land cover = NoData.

I then created a raster for all areas that had limited seasonal hunting using ArcGIS 10 (ESRI 2011) by performing the following steps: First, I reclassified the WUI layer to have interface, intermix, non-vegetated or agriculture with low to very low density housing, and non-WUI vegetated with no housing = 2 (Radeloff et al. 2005). Second, land owned by VDCR (www.dcr.virginia.gov), VDF (www.dof.virginia.gov), VDGIF(http://www.dgif.virginia.gov/) and public parks that allow seasonal hunting were reclassified = 1. Third, to account for potential effects of deer hunting on PAD-VA land, I added a -100m buffer with the exception of all land owned by the Department of Defense (DOD). This was due to previous knowledge that property of DOD is heavily fenced which prevents it from being accessible to deer. The 100-m buffer was then reclassified = 1. Lastly, I merged the WUI layer, the layer with VDCR, VDF, VDGIF and public parks, with the 100-m buffer into one raster = 1 and all other land cover = NoData.

Next, I created a raster for intensive seasonal hunting by reclassifying the WUI layer to have the non-WUI vegetated with very low density housing = 2 (Radeloff et al. 2005). Finally, I merged the rasters for no hunting (0), limited seasonal hunting (1) and intensive seasonal hunting (2) using Spatial Analyst in ArcGIS 10 (ESRI 2011) and reclassified intensive seasonal hunting to value =1 to create a final binary deer HUNTING INTENSITY layer. I performed a focal majority in the Neighborhood function in Spatial Analyst (ESRI 2011) for each of the five scales.

## STATISTICAL ANALYSIS

### *Presence/Absence Surveys:*

Because surveys were conducted on the same day, I employed a "capture matrix" to account for potential lack of independence among surveys as a survey-specific variable. The capture matrix adjusts detection probabilities based on when an individual bird is first detected during the four surveys (McKenzie et al. 2006) If a Wood Thrush is detected during survey 1, the capture matrix vector = 0111, for an individual detected during survey 2, the vector = 0011, and so on.

### *Single-Season Occupancy Modeling:*

In addition to modeling linear relationships of the survey- and site-specific covariates, I explored quadratic and/or pseudo-threshold log relationships (Scherer et al. 2012). Quadratic relationships predict maximum effects of the parameter at intermediate levels or at extreme values. The quadratic form is written as:

$$\text{logit}\,(\theta) = \beta_0 + \beta_1(x_1) + \beta_1(x_1^2) + \beta_n(x_n) + \beta_n(x_n^2)$$

where $\theta$ represents the real parameter ($p$ or $\Psi$), and $x_n$ represents the covariate of interest.

The pseudothreshold relationship predicts that effects of the covariate change at some constant rate and then approach but do not reach an asymptote (Franklin et al. 2000). The pseudothreshold form is written as:

$$\text{logit}(\theta) = \beta_0 + \beta_1 \log_e(x_1 + 0.005) + \beta_n \log_e(x_n + 0.005)$$

where $\theta$ represents the real parameter ($p$ or $\Psi$), and $x_n$ represents the covariate of interest.

Prior to modeling, I centered all quadratic site-specific variables to avoid multicollinearity. I also standardized all continuous survey- and site-specific variables in order to be able to interpret magnitude of slopes across all covariates. All covariates were tested for multicollinearity using Spearman's rank correlation coefficient (Quinn and Keough 2009). Covariates with a correlation coefficient $r_s > |0.7|$ were not included within the same model.

I used Akaike's information criterion (AIC) to select models (Burnham and Anderson 2002) and performed all occupancy analyses of the Wood Thrush using the R package Unmarked (Fiske and Chandler 2011, R Core Development Team 2008). I created a single-season occupancy model for the Wood Thrush using 140 point count surveys (2011 = 70, 2012 = 70). I determine the best model for detection probability, by creating multivariate models with all possible combinations of the six survey-specific covariates while keeping the $\Psi$ model [$\Psi(.)$] constant (Appendix 1.a). I determined the best detection model using the top AIC value. I kept the top detection model constant to calculate all occupancy models.

I first used univariate models for each site-specific covariate to determine the best scale based on the top AIC value. Using the best scale for each site-specific covariate, I created multivariate models with all possible combinations of the site-specific covariates. To model average the occupancy probability, I spatially applied the top models whose AIC weights ($w_i$) summed 95% (Burnham and Anderson 2002). I then multiplied each spatially applied occupancy model by its AIC weight ($w_i$) and summed all models to produce a final spatially applied occupancy model. To look at individual site-specific covariate effects on occupancy, I calculated the cumulative AIC weight ($w_i$):

$$\text{CUM } w_j = (\Sigma\ w_i)$$

for each covariate. Values ranged between 0-1; covariates with a CUM $w_j$ closer to 1 indicated a strong association with occupancy probability whereas values close to 0 indicated a weak association.

*Final model performance evaluation:*

I evaluated internal model performance, that is sensitivity (true presence) and specificity (true absence) of final models, using the receiver operating characteristic (ROC) estimating the area under the curve (AUC; Metz 1978) using statistical software R "pROC" package (Xavier et al. 2011; R Core Development Team 2008). Additionally, I evaluated model performance by performing a logistic regression with 31 independent point counts (2011=15; 2012 =16) collected in 2011 and 2012.

*Correlating occupancy estimates with breeding success data:*

I performed a Spearman rank correlation tests on the average occupancy probability and the average reproductive index. Using zonal statistics in ArcGIS (ESRI 2011), I extracted the average occupancy probability within each of the 18 Wood Thrush study sites. I averaged Reproductive Indices across territories within a study site. I assumed Spearman rank correlations to be significant at the $p = 0.05$

## RESULTS

*Demography Data:*

I collected breeding data from 19 May-22 July, 2011, and 21 April-22 July, 2012. I found on average 9.13 males per study site (range=6-17; sd = 3.68) in 2011and 2.6 males per site (range = 0-6; sd = 2.5) in 2012 (Table 1). I found on average of 4.5 paired males per site (range=0-14; sd = 4.31) and 2.63 fledglings (range=0-10; sd = 4.1) in 2011 and an average of 1.5 paired males per site (range = 0-4; sd =1.51) and 0.7 fledglings (range = 0-3; sd = 0.95) in 2012 (Table 1). The reproductive index varied across sites with an average of 2.02 per site (range = 0-3.29; sd =1.1) (Table 1). The average reproductive index in 2011 was 2.21 (range =1.0-1.39; sd = 0.74) and 1.87 (range =0-3.17; sd =1.35) in 2012.

*Survey-specific Covariates:*

Multicollinearity was not present among the survey-specific covariates ($r_s < 0.7$). Linear relationships of all survey-specific covariates out-performed quadratic and pseudothreshold relationships (Appendix 1.a). The most important survey-specific candidate model for the Wood Thrush included Julian Date and a CAPTURE MATRIX, and was better than the constant ρ model [p(.)] (Appendix 1.a). The overall (average) survey-specific detection probability was 0.64 (range=0.46-0.85; sd=0.02).

*Site-specific Covariates:*

For the covariates STREAM DENSITY and FLOODED FOREST quadratic relationships out-performed the linear form. The covariates ROAD DENSITY, proportion of LOW URBAN DEVELOPMENT and edge density of FOREST/LOW URBAN DEVELOPMENT all performed better when included as a pseudo-threshold variable. Edge density of FOREST/LOW URBAN DEVELOPMENT, PROPORTION OF LOW URBAN DEVELOPMENT and ROAD DENSITY were all highly correlated ($r_s = 0.83\text{-}0.98$) and were modeled independently of one another. Smaller scales (120m and/or 300m) were not evaluated for proportion of FLOODED

FOREST, STREAM DENSITY, edge density of FOREST/LOW URBAN DEVELOPMENT, proportion of DRY-MESIC FOREST, proportion of LOW DEVELOPMENT and ROAD DENSITY due to an over-saturation of 0 values ( > 20 zeros), which could result in lack of model convergence. Both covariates distance to OPEN WATER and distance to FOREST EDGE were poor predictors of Wood Thrush occupancy, with AIC values below null occupancy model [$\psi(.)$] and were excluded from modeling (Appendices 1.i and 1.j).

Proportion of FLOODED FOREST at 1km (CUM $w_j = 0.79$), STREAM DENSITY at 3km (CUM $w_j = 0.77$), proportion of DRY-MESIC FOREST at 3km (CUM $w_j = 0.70$) and edge density of FOREST/LOW URBAN DEVELOPMENT at 1km (CUM $w_j = 0.64$) all had a relatively high importance in predicting Wood Thrush occupancy. Deer HUNTING INTENSITY at 1km (CUM $w_j = 0.33$), proportion of LOW URBAN DEVELOPMENT at 1km (CUM $w_j = 0.22$), and ROAD DENSITY at 1km (CUM $w_j = 0.15$) were not strong predictors of Wood Thrush occupancy (Fig. 2). The final averaged 95% AIC-weighted model was comprised of 33 candidate models (Table 2) producing the equation:

$$\psi = -3.07 + 0.66 * (\text{proportion of dry-mesic forest}) - 0.78 * (\text{proportion of flooded forest}) + 0.42 * (\text{proportion of flooded forest}^2) + 0.99 * (\text{road density}) + 0.26 * (\text{edge density of forest/low urban development}) + 0.16 * (\text{proportion of low development}) + 0.34(\text{stream density}) - 0.08(\text{stream density}^2) - 0.13 * (\text{deer hunting intensity})$$

Wood Thrush occupancy varied greatly across the Virginia peninsula (Fig. 3). High occupancy areas were predicted west of the fault line and confined to areas with high stream densities and large proportions of upland forests. Wood Thrush occupancy was highest in residential areas, particular throughout the City of Williamsburg. Low-to-mid occupancy predictions occurred closer to open water and large patches of rural land cover.

*Model Performance:*

Seven out of the 30 independent presence/absence surveys detected Wood Thrush presence. Model performance was not consisted among internal and external validation methods. The Wood Thrush occupancy model performed well (AUC = 0.79) when validated internally. However, the observed data (independent occurrence data not use for model building) did not correlate ($p = 0.98$) with expected $\psi$ values.

*Probability of Occupancy vs. Breeding Success:*

Average probability of occupancy ($\psi$) varied across sites with an average $\psi = 0.26$ (range = 0.1-0.59; sd = 0.19) (Table 1). Average $\psi$ and the average reproductive index did not significantly correlate ($r_s = 0.30$, $p = 0.27$) (Fig. 4).

## DISCUSSION

To my knowledge, this study was the first to attempt to evaluate whether occupancy probabilities correlate positively with reproductive success. I found no relationship between Wood Thrush occupancy and breeding success. My findings were not surprising because the Wood Thrush population within this study area seemed to respond differently across the landscape compared to previous studies. Additionally, although the Wood Thrush occupancy model had an AUC value of 0.79, the model predicted poorly when evaluated with independent presence/absence data not used for model building. This was not unexpected because only seven out of the 30 independent presence/absence surveys detected Wood Thrushes. One possible explanation for the poor predictive power of the occupancy model is that there may be a high turnover among habitat with a high proportion of urban and rural land cover. On several occasions, I observed breeding study sites where Wood Thrushes appeared to be absent during the early part of the breeding season, but then males would end up establishing territories during June/July. This turnover indicates that Wood Thrushes may be responding to the landscape in an unpredictable way, causing this population to be difficult to evaluate with occupancy modeling because of the violation of the closure assumption (MacKenzie et al. 2006).

Wood Thrush occupancy related negatively and nonlinearly with FLOODED FOREST at the 1-km scale with use being restricted to intermediate levels of this land cover. Occupancy related linearly and positively to proportion of DRY-MESIC FOREST at a 3-km scale, which is supported by previous studies that have shown Wood Thrush reliance on large patches of mid-successional hardwood forests during the breeding season (Hoover et al. 1995). Occupancy also related quadratically and positively to intermediate STREAM DENSITY at the 3-km scale. This was expected because Wood Thrushes were observed to consistently breed in deep ravines near small streams but avoided either extreme, such as dry or flooded forests. This is supported by studies that have shown that slope (Rittenhouse et al. 2007) and moisture (Bertin 1977, Rittenhouse et al. 2007) are important variables explaining breeding Wood Thrush habitat use. Although Kaiser and Lindell (2007) showed little-to-no impact of edge effects on Wood Thrush reproductive success and occurrence, the need for core habitat at large scales for Wood Thrush to breed successfully is well supported (Hoover et al. 1995, Driscoll et al. 2005). However, in this study, Wood Thrush occupancy was positively associated with edge density of FOREST-TO-LOW URBAN DEVELOPMENT, ROAD DENSITY and proportion of LOW URBAN DEVELOPMENT. In this study, Wood Thrush occupancy was high in the greater Williamsburg area, specifically in smaller patches of forest near forest edges, where I also found the highest breeding success based on the reproductive index.

To my knowledge, this study area is unique when evaluating Wood Thrush occupancy and breeding success because forest land cover is intermixed with low urban/residential land cover throughout the majority of the area, whereas past studies have been conducted in large, 1995, Simons et al. 2000, Lichstein et al. 2002). Wood Thrushes may use forest patches near low-density urban areas because deer hunting is prohibited, which results in much sparser understory compared with forest patches located in rural landscapes where deer hunting is permitted. Wood Thrushes rely on sparse understory for foraging through leaf litter (Holmes and Robinson 1988), thus, the benefits of breeding in more fragmented forest patches with sparse understory may out weight any negative impact caused from edge effects, such as nest predation and parasitism (Hoover et al. 1995, Robinson et al. 1995).

DEER HUNTING INTENSITY was most important at the 1-km scale, indicating the impacts of deer hunting may extend beyond the local scale. However, DEER HUNTING intensity was not a very strong predictor of Wood Thrush occupancy. This was potentially due because the DEER HUNTING INTENSITY spatial layer did not capture the spatial heterogeneity of deer browsing because as hunting intensity is spatially heterogeneous on private lands and cannot be mapped. It would be ideal to know exactly where and for how long deer hunting is permitted during each season, especially on private lands. The results of my research suggests that deer browsing is a potential mechanism affecting Wood Thrush occupancy and breeding success and further investigation using a more detailed deer browsing layer is warranted.

Although all site-specific covariates were selected a priori based off of findings from previous literature and through my own personal experience, all covariates explaining heterogeneity in occupancy had confidence intervals overlapping with zero, indicating that all site-specific covariates had weak predictive power of Wood Thrush occupancy. In hindsight, this was not surprising because Wood Thrush occupancy across the study area was not consistent during the three years of presence/absence data collected in a parallel study (M. Leu pers.

comm.) causing Wood Thrush occupancy to be difficult to measure. There are several possible reasons for the observed unpredictability among this local Wood Thrush population. First, I personally observed a constant turnover during a single season. This violates the critical closure assumption of occupancy models (MacKenzie et al. 2006). Secondly, there may be mechanisms that impact Wood Thrush occupancy in this study area that I did not model. It was surprising that not one site-specific covariate had predictive power because they were all chosen based off of previous studies. This is important to address for future studies that develop models using covariates shown to be important based on previous findings in the literature. My study demonstrates that when modeling even a well-studied species, such as the Wood Thrush, habitat use may differ across geographic regions.

Occupancy modeling is a method that shows great promises in guiding long-term conservation efforts. The ability of land managers to have tools such as occupancy models to delineate habitat most needed for long-term conservation is crucial as the world becomes increasingly dominated by urban land cover. Although my findings suggest that Wood Thrush occupancy modeling is not a reliable method to use in lieu of collecting breeding data, my findings indicate that researchers and land-managers cannot solely rely on previous literature to inform management and conservation planning, especially when modeling habitat use or occupancy in a new geographical area. Additionally, I recommend evaluating Wood Thrush habitat use instead of occupancy within this study area and further exploring what mechanisms are important for the Wood Thrush population in the Coastal Plains of Virginia and whether or not this population is inhabiting an ecological trap. This is necessary for future long-term land management decisions with conserving the declining Wood Thrush population in Virginia. I suggest radio-tracking Wood Thrush males as they move among territories within a breeding season.

**Table 1** Wood Thrush breeding success data from 18 study sites that were visited in 2011 and 2012. Territories were ranked based on a Reproductive Index (RI). The average RI was calculated across sites. The average probability of occupancy (Psi) was extracted from the final spatially applied Wood Thrush occupancy model.

| Year | Site | # of males | % Pairing Success | % Fledgling Success | RI | Psi |
|---|---|---|---|---|---|---|
| 2011 | New Quarter Park | 11 | 54.55 | 72.73 | 2.85 | 0.46 |
| 2011 | WAM_Compton | 6 | 66.67 | 0.00 | 2.33 | 0.57 |
| 2011 | WAM_Jamestown | 10 | 30.00 | 30.00 | 2.22 | 0.37 |
| 2011 | WAM_Millneck | 17 | 82.35 | 58.82 | 3.29 | 0.51 |
| 2011 | NNP_Campsite | 7 | 71.43 | 0.00 | 2.25 | 0.18 |
| 2011 | NNP_Crawford | 6 | 50.00 | 0.00 | 2.40 | 0.35 |
| 2011 | Wallermill Park | 9 | 11.11 | 0.00 | 1.33 | 0.29 |
| 2011 | York River State Park | 7 | 0.00 | 0.00 | 1.00 | 0.11 |
| 2012 | Newport News Park | 1 | 100.00 | 0.00 | 3.00 | 0.12 |
| 2012 | Harrison Lake National Fish Hatchery | 0 | 0.00 | 0.00 | 0.00 | 0.13 |
| 2012 | VCU Rice Center | 1 | 0.00 | 0.00 | 2.00 | 0.07 |
| 2012 | Chickahominy WMA | 0 | 0.00 | 0.00 | 0.00 | 0.11 |
| 2012 | Noland Park | 0 | 0.00 | 0.00 | 0.00 | 0.08 |
| 2012 | Richmond National Battlefield | 4 | 50.00 | 25.00 | 2.67 | 0.24 |
| 2012 | Beaverdam Park | 6 | 50.00 | 16.67 | 2.50 | 0.09 |
| 2012 | Freedom Park | 5 | 60.00 | 20.00 | 2.33 | 0.10 |
| 2012 | Colonial National Park System | 6 | 66.67 | 50.00 | 3.17 | 0.44 |
| 2012 | Fords Colony | 3 | 66.67 | 33.33 | 3.00 | 0.32 |

**Table 2** Wood Thrush top 95% AIC-weighted site-specific multivariate models AIC table. The number following each covariate's name is associated with the covariate's scale. LN indicates a pseudothreshold relationship.

| Model | AIC | $\Delta_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic)) | 339.85 | 0.00 | 0.09 | 9 | 321.85 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN)) | 340.37 | 0.52 | 0.07 | 8 | 324.37 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic)) | 340.59 | 0.73 | 0.06 | 10 | 320.59 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Proportion of Low-Development at 1km (LN), Stream Density at 3km (quadratic)) | 340.76 | 0.90 | 0.06 | 10 | 320.76 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN), Stream Density at 3km (quadratic)) | 340.83 | 0.98 | 0.06 | 10 | 320.83 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic)) | 340.95 | 1.10 | 0.05 | 9 | 322.95 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN), Deer Hunting Intensity at 1km) | 341.26 | 1.41 | 0.05 | 9 | 323.26 |
| Ψ(Proportion of Dry-Mesic forest at 3km, Road Density at 1km (LN), Stream Density at 3km (quadratic)) | 341.39 | 1.54 | 0.04 | 8 | 325.39 |
| Ψ(Proportion of Dry-Mesic forest at 3km, Road Density at 1km (LN)) | 341.68 | 1.83 | 0.04 | 6 | 329.68 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic forest at 3km, Proportion of Low-Development at 1km (LN)) | 341.75 | 1.90 | 0.04 | 8 | 323.75 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Road Density at 1km (LN), Stream Density at 3km (quadratic)) | 341.80 | 1.95 | 0.04 | 9 | 323.80 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN)) | 341.96 | 2.10 | 0.03 | 8 | 325.96 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 342.00 | 2.14 | 0.03 | 11 | 320.00 |

| | | | | | |
|---|---|---|---|---|---|
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 342.12 | 2.26 | 0.03 | 11 | 320.12 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN), Deer Hunting Intensity at 1km) | 342.35 | 2.50 | 0.03 | 7 | 328.35 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Proportion of Low-Development at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 342.36 | 2.51 | 0.03 | 11 | 320.36 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Proportion of Low-Development at 1km (LN), Stream Density at 3km (quadratic)) | 342.43 | 2.57 | 0.03 | 8 | 326.43 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Road Density at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km)) | 342.49 | 2.64 | 0.03 | 9 | 324.49 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Proportion of Low-Development at 1km (LN), Deer Hunting Intensity at 1km) | 342.93 | 3.08 | 0.02 | 9 | 324.93 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Deer Hunting Intensity at 1km) | 342.95 | 3.09 | 0.02 | 9 | 324.95 |
| Ψ(Proportion of Dry-Mesic forest at 3km, Proportion of Low-Development at 1km (LN)) | 343.05 | 3.20 | 0.02 | 6 | 331.05 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic)) | 343.21 | 3.36 | 0.02 | 8 | 327.21 |
| Ψ(Proportion of Dry-Mesic forest at 3km, Proportion of Low-Development at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 343.92 | 4.07 | 0.01 | 9 | 325.92 |
| Ψ(Proportion of Dry-Mesic forest at 3km, Proportion of Low-Development at 1km (LN), Deer Hunting Intensity at 1km) | 344.12 | 4.27 | 0.01 | 7 | 330.12 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Road Density at 1km (LN)) | 344.25 | 4.40 | 0.01 | 7 | 330.25 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN)) | 344.48 | 4.62 | 0.01 | 6 | 332.48 |
| Ψ(Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 344.50 | 4.65 | 0.01 | 9 | 326.50 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Edge Density of Forest-to-Low Urban Development at 1km (LN)) | 345.71 | 4.86 | 0.01 | 7 | 330.71 |

| | | | | | |
|---|---|---|---|---|---|
| Ψ(Proportion of Dry-Mesic Forest at 3km, Edge Density of Forest-to-Low Urban Development at 1km (LN), Deer Hunting Intensity at 1km) | 345.15 | 5.30 | 0.01 | 7 | 331.15 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic forest at 3km, Stream Density at 3km (quadratic), Deer Hunting Intensity at 1km) | 345.35 | 5.49 | 0.01 | 10 | 325.35 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Road Density at 1km (LN), Deer Hunting Intensity at 1km) | 345.44 | 5.59 | 0.01 | 8 | 329.44 |
| Ψ(Edge Density of Forest-to-Low Urban Development at 1km (LN), Stream Density at 3km (quadratic)) | 345.53 | 5.68 | 0.01 | 7 | 331.53 |
| Ψ(Proportion of Flooded Forest at 1km (quadratic), Proportion of Dry-Mesic forest at 3km, Deer Hunting Intensity at 1km) | 345.71 | 5.86 | 0.01 | 8 | 329.71 |

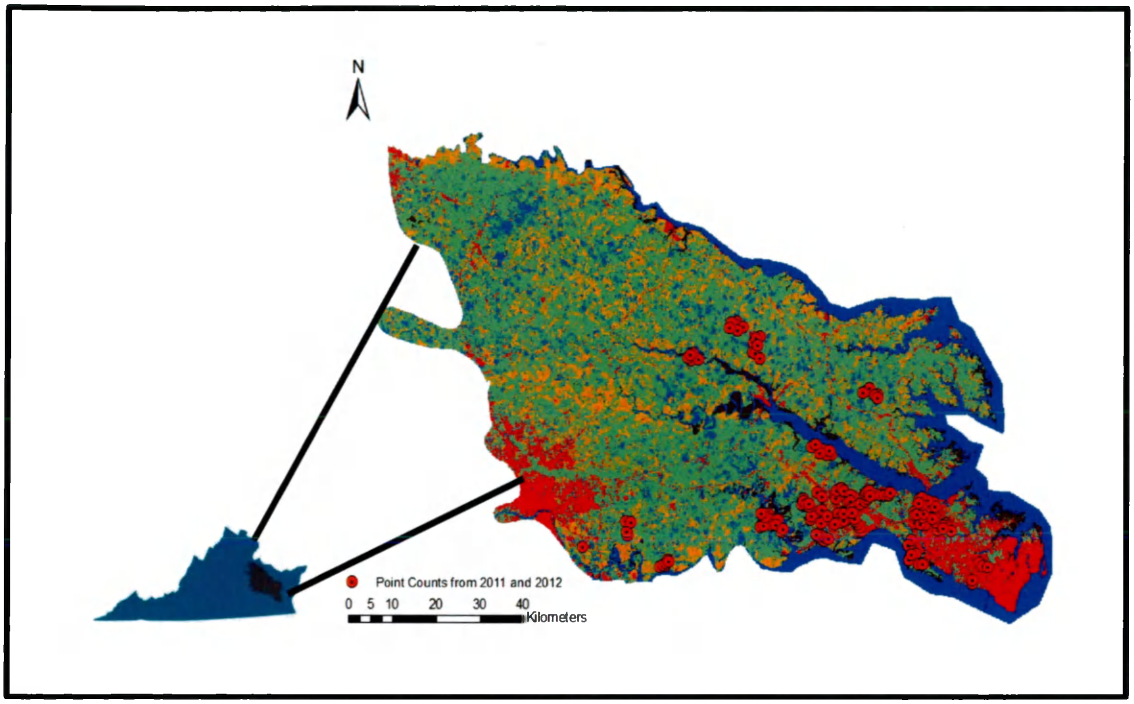

**Figure 1** Map of the study area in the Coastal Plains of Virginia

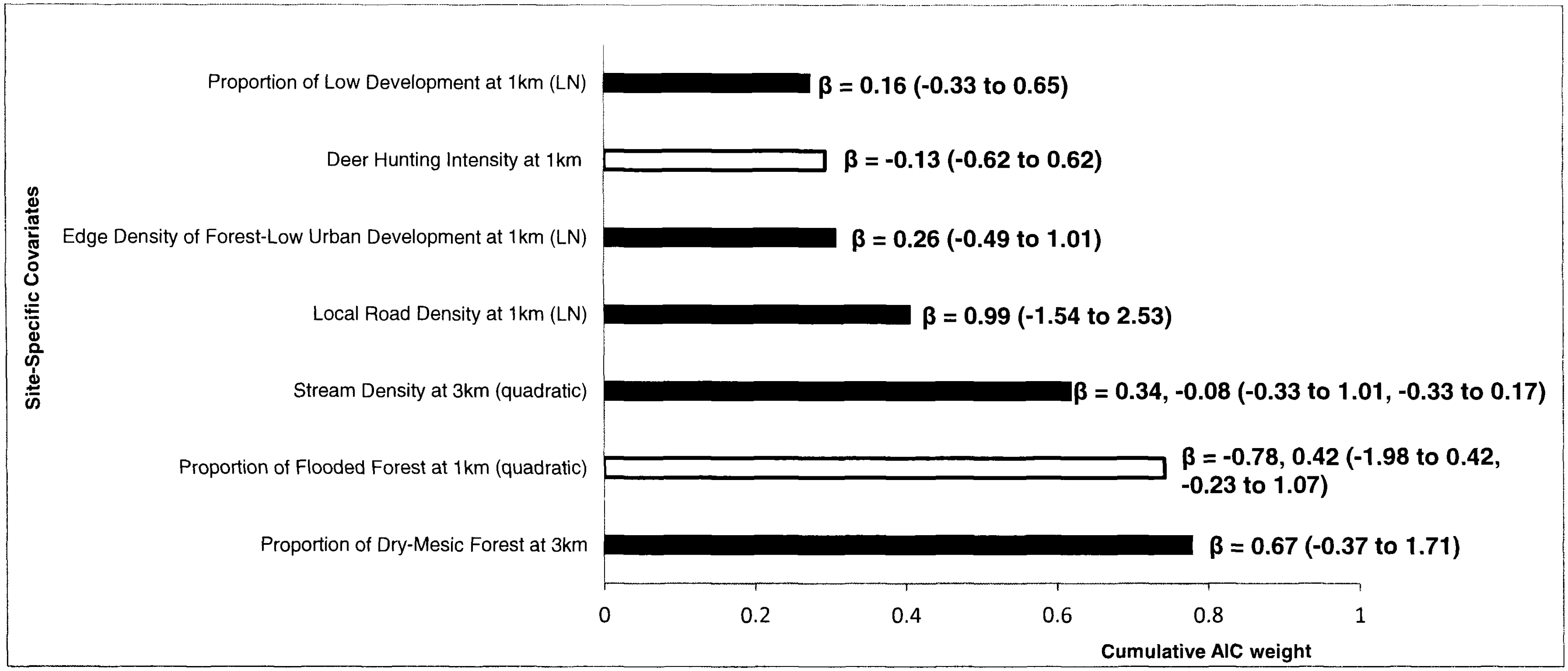

**Figure 2** The relative effects of site-specific covariates on Wood Thrush occupancy. The cumulative AIC weight for each covariate is shown, along with its model-averaged coefficient and 95% Confidence Intervals. The number following each covariate's name is associated with the covariate's scale. LN indicates a pseudothreshold relationship.

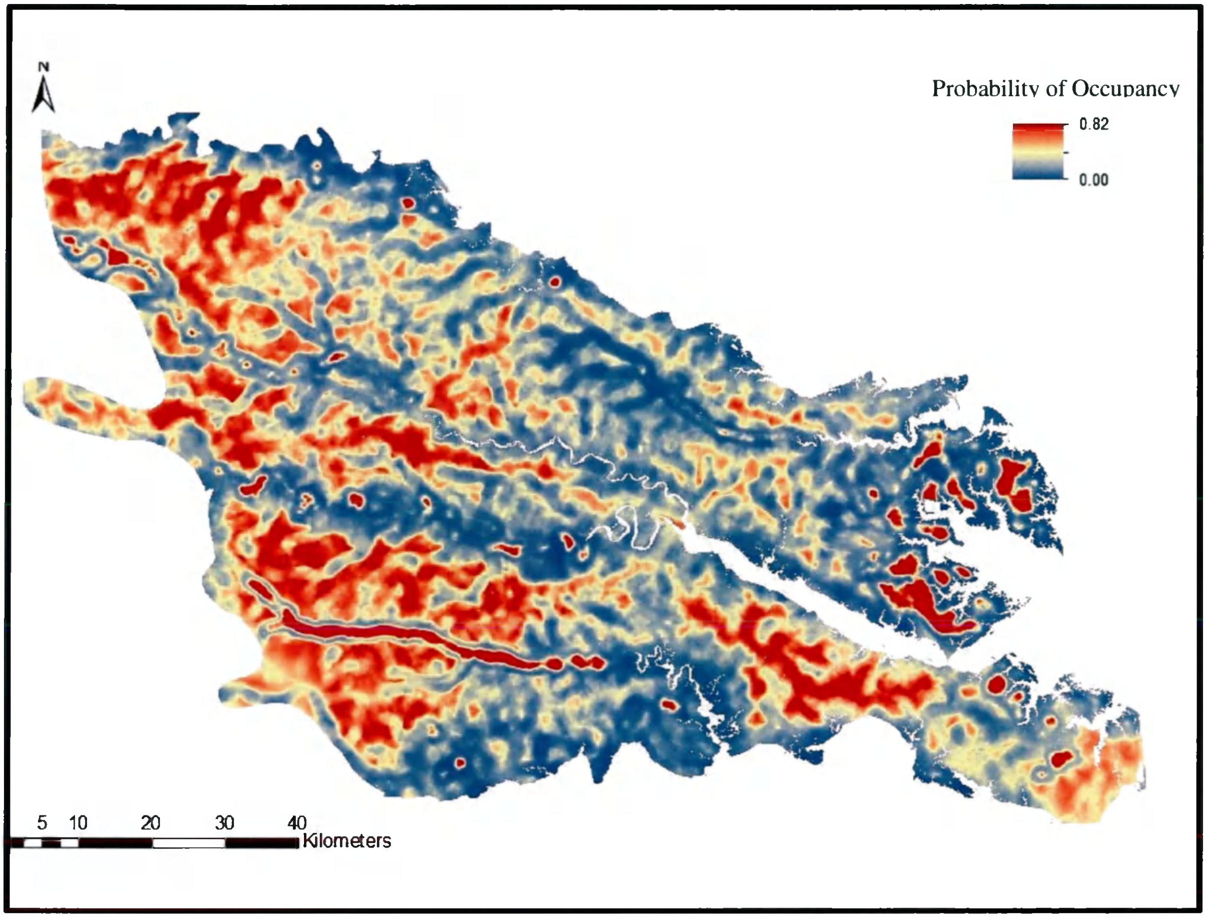

**Figure 3** Spatially applied Wood Thrush occupancy model. Areas in red indicate a high probability of occupancy whereas areas with blue indicate a lower probability of occupancy. Probability of occupancy ranged from 0.00 - 0.82 throughout the study area.

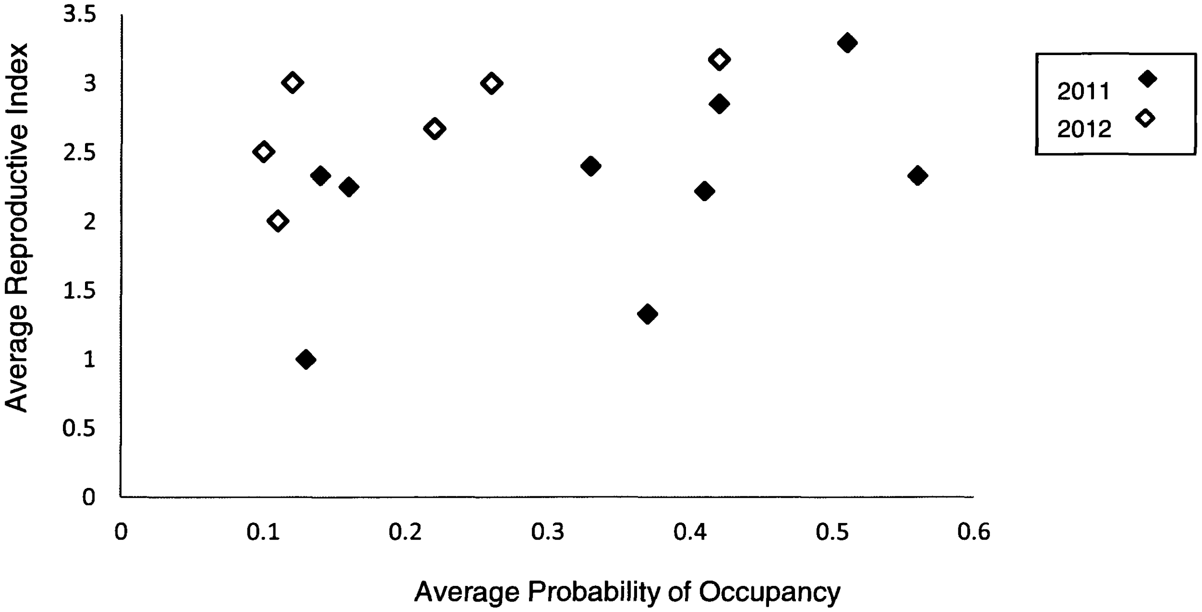

**Figure 4:** Wood Thrush occupancy does not correlate with the reproductive index across 18 study sites ($r_s$= 0.30, p = 0.27). Black data points indicate study sites surveyed in 2011 and white data points indicate study sites surveys in 2012.

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**Appendix 1** Wood Thrush AIC model selection results for the survey-specific multivariate models and the site-specific univariate models. All candidate models, as well as the "null" model without covariates are shown for the survey-specific multivariate models and the site-specific univariate models. $\Psi$ is the occupancy probability and p is the detection probability. Covariate names followed by a numerical value indicate the covariates scale; a LN indicates a pseudo-threshold relationship. Survey-specific covariate names are: Capture Index = **Capture**, Julian Date = **Julian**, Start Time = **Stime**, Windspeed = **Windspeed,** Temperature = **Temp**. Site-specific covariate names are: Proportion of Flooded Forest = **flf**, Proportion of Dry-Mesic Forest = **drymes**, Stream Density = **sden**, Local Road Density = **rd**, Proportion of Low Development = **ldev**, Edge Density of Forest-to-Low Urban Development = **edge**, Deer Hunting Intensity = **deer**, Distance to Open Water = **distw**, Distance to Forest Edge = **distf**.

Appendix 1.a Wood Thrush Survey-Specific Multivariate Models AIC Table

| Model | **AIC** | $\Delta_i$ | $w_i$ | **K** | **-2L** |
|---|---|---|---|---|---|
| $\Psi$(.)p(Capture, Julian) | 360.67 | 0.00 | 0.07 | 4 | 352.67 |
| $\Psi$(.)p(Julian, Stime) | 360.67 | 0.01 | 0.07 | 4 | 352.68 |
| $\Psi$(.)p(Julian) | 360.92 | 0.25 | 0.06 | 3 | 354.92 |
| $\Psi$(.)p(Capture, Julian, stime) | 360.94 | 0.27 | 0.06 | 5 | 350.94 |
| $\Psi$(.)p(Capture, Julian, Windspeed) | 360.94 | 0.27 | 0.06 | 5 | 350.94 |
| $\Psi$(.)p(Capture, Julian, Stime, Windspeed) | 360.98 | 0.30 | 0.06 | 6 | 348.98 |
| $\Psi$(.)p(Julian, Stime, Windspeed) | 361.16 | 0.49 | 0.05 | 5 | 351.16 |
| $\Psi$(.)p(Stime) | 361.35 | 0.67 | 0.04 | 3 | 355.35 |
| $\Psi$(.)p(Capture, Stime) | 361.63 | 0.96 | 0.04 | 4 | 353.63 |
| $\Psi$(.)p(Julian, Windspeed) | 361.69 | 1.01 | 0.04 | 4 | 353.69 |
| $\Psi$(.)p(Capture, Julian, Temp, Windspeed) | 361.76 | 1.08 | 0.04 | 6 | 349.76 |
| $\Psi$(.)p(Capture, Julian, Temp) | 361.89 | 1.21 | 0.04 | 5 | 351.89 |
| $\Psi$(.)p(Julian, Temp) | 362.24 | 1.57 | 0.03 | 4 | 354.24 |
| $\Psi$(.)p(Capture, Julian, Stime, Temp, Windspeed) | 362.58 | 1.91 | 0.03 | 7 | 348.58 |
| $\Psi$(.)p(Julian, Stime, Temp) | 362.58 | 1.93 | 0.03 | 5 | 352.58 |
| $\Psi$(.)p(Julian, Julian$^2$) | 362.60 | 1.91 | 0.03 | 4 | 354.60 |
| $\Psi$(.)p(Capture) | 362.60 | 1.93 | 0.03 | 3 | 356.60 |
| $\Psi$(.)p(Capture, Stime, Windspeed) | 362.71 | 2.04 | 0.02 | 5 | 352.71 |
| $\Psi$(.)p(Julian, Temp, Windspeed) | 362.73 | 2.05 | 0.02 | 5 | 352.73 |
| $\Psi$(.)p(Capture, Julian, Stime, Temp) | 362.74 | 2.07 | 0.02 | 6 | 350.74 |
| $\Psi$(.)p(Stime, Windspeed) | 362.77 | 2.10 | 0.02 | 4 | 354.77 |
| $\Psi$(.)p(Julian, Stime, Temp, Windspeed) | 362.95 | 2.28 | 0.02 | 6 | 350.95 |
| $\Psi$(.)p(Stime, Temp) | 363.20 | 2.53 | 0.02 | 4 | 355.20 |
| $\Psi$(.)p(Stime, Stime$^2$) | 363.33 | 2.66 | 0.02 | 4 | 355.33 |
| $\Psi$(.)p(Capture, Temp) | 363.35 | 2.68 | 0.02 | 4 | 355.35 |
| $\Psi$(.)p(Capture, Stime, Temp) | 363.37 | 2.70 | 0.02 | 5 | 353.37 |
| $\Psi$(.)p(Temp) | 363.79 | 3.11 | 0.01 | 3 | 357.79 |
| $\Psi$(.)p(Capture, Stime, Temp, Windspeed) | 364.26 | 3.59 | 0.01 | 6 | 352.26 |
| $\Psi$(.)p(Capture, Windspeed) | 364.27 | 3.60 | 0.01 | 4 | 356.27 |
| $\Psi$(.)p(Stime, Temp, Windspeed) | 364.51 | 3.84 | 0.01 | 5 | 354.51 |
| $\Psi$(.)p(Capture, Temp, Windspeed) | 364.57 | 3.90 | 0.01 | 5 | 354.76 |
| $\Psi$(.)p(Windspeed) | 364.76 | 4.09 | 0.01 | 3 | 358.76 |
| $\Psi$(.)p(Temp, Windspeed) | 365.41 | 4.73 | 0.01 | 4 | 357.41 |

| | | | | | |
|---|---|---|---|---|---|
| Ψ(.)p(Temp, LNTemp) | 365.76 | 5.09 | 0.01 | 4 | 357.76 |

Appendix 1.b Wood Thrush Proportion of Flooded Forest AIC Table

| Model | **AIC** | $\Delta_i$ | $w_i$ | **K** | **-2L** |
|---|---|---|---|---|---|
| Ψ(flf1km + flf1km$^2$) | 352.64 | 0.00 | 0.76 | 6 | 340.64 |
| Ψ(flf1km) | 356.65 | 4.00 | 0.10 | 5 | 346.65 |
| Ψ(flf2km) | 356.81 | 4.17 | 0.09 | 5 | 346.81 |
| Ψ(flf3km) | 358.89 | 6.25 | 0.03 | 5 | 348.62 |
| Ψ(.) | 360.67 | 8.03 | 0.01 | 4 | 352.67 |
| Ψ(flf300m) | 361.62 | 8.97 | 0.01 | 5 | 351.62 |
| Ψ(flf120m) | 362.67 | 10.03 | 0.01 | 5 | 352.67 |

Appendix 1.c Wood Thrush Proportion of Dry-Mesic Forest AIC Table

| Model | **AIC** | $\Delta_i$ | $w_i$ | **K** | **-2L** |
|---|---|---|---|---|---|
| Ψ(drymes3km) | 350.64 | 0.00 | 0.59 | 5 | 340.64 |
| Ψ(drymes2km) | 351.66 | 1.02 | 0.33 | 5 | 341.66 |
| Ψ(drymes1km) | 354.15 | 3.51 | 0.10 | 5 | 344.15 |
| Ψ(drymes300m) | 358.79 | 8.15 | 0.01 | 5 | 348.79 |
| Ψ(.) | 360.67 | 10.03 | 0.01 | 4 | 352.67 |
| Ψ(drymes120m) | 362.31 | 11.67 | 0.00 | 5 | 352.31 |

Appendix 1.d Wood Thrush Stream Density AIC Table

| Model | **AIC** | $\Delta_i$ | $w_i$ | **K** | **-2L** |
|---|---|---|---|---|---|
| Ψ(sden3km + sden3km2) | 353.38 | 0.00 | 0.44 | 6 | 341.38 |
| Ψ(sden3km) | 353.60 | 0.22 | 0.39 | 5 | 343.60 |
| Ψ(sden2km) | 357.08 | 3.71 | 0.07 | 5 | 347.08 |
| Ψ(sden1km) | 357.67 | 4.29 | 0.05 | 5 | 347.67 |
| Ψ(sden300m) | 358.20 | 4.83 | 0.04 | 5 | 348.20 |
| Ψ(sden120m) | 360.59 | 7.22 | 0.01 | 5 | 350.60 |
| Ψ(.) | 360.67 | 7.29 | 0.01 | 4 | 352.67 |

Appendix 1.e Wood Thrush Local Road Density AIC Table

| Model | **AIC** | $\Delta_i$ | $w_i$ | **K** | **-2L** |
|---|---|---|---|---|---|
| Ψ(LNrd1km) | 351.00 | 0.00 | 0.78 | 5 | 341.00 |
| Ψ(rd1km) | 354.96 | 3.86 | 0.11 | 5 | 344.86 |
| Ψ(rd3km) | 355.97 | 4.97 | 0.06 | 5 | 345.97 |
| Ψ(rd2km) | 356.70 | 5.70 | 0.05 | 5 | 346.70 |
| Ψ(.) | 360.67 | 9.67 | 0.01 | 4 | 352.67 |

Appendix 1.f Wood Thrush Proportion of Low Urban Development AIC Table

| Model | AIC | Δ$_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(LNldev1km) | 353.69 | 0.00 | 0.76 | 5 | 343.69 |
| Ψ(ldev1km) | 356.68 | 2.99 | 0.17 | 5 | 346.68 |
| Ψ(ldev2km) | 359.29 | 5.60 | 0.05 | 5 | 349.29 |
| Ψ(ldev3km) | 360.39 | 6.70 | 0.03 | 5 | 350.39 |
| Ψ(.) | 360.67 | 6.98 | 0.03 | 4 | 352.67 |

Appendix 1.g Wood Thrush Edge Density of Forest-Low Urban Development AIC Table

| Model | AIC | Δ$_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(LNedge1km) | 352.59 | 0.00 | 0.47 | 5 | 342.59 |
| Ψ(edge1km) | 353.39 | 0.78 | 0.32 | 5 | 343.39 |
| Ψ(edge3km) | 355.35 | 2.76 | 0.12 | 5 | 345.35 |
| Ψ(edge2m) | 355.96 | 3.37 | 0.09 | 5 | 345.96 |
| Ψ(.) | 360.67 | 8.08 | 0.01 | 4 | 352.67 |

Appendix 1.h Wood Thrush Deer Hunting Intensity AIC Table

| Model | AIC | Δ$_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(deer1km) | 357.68 | 0.00 | 0.39 | 5 | 347.68 |
| Ψ(deer120m) | 357.74 | 0.06 | 0.38 | 5 | 347.74 |
| Ψ(deer300m) | 359.51 | 1.83 | 0.16 | 5 | 349.51 |
| Ψ(deer2km) | 361.85 | 4.17 | 0.05 | 5 | 351.85 |
| Ψ(deer3km) | 362.85 | 4.81 | 0.03 | 5 | 352.49 |
| Ψ(.) | 360.67 | 7.29 | 0.01 | 4 | 352.67 |

Appendix 1.i Wood Thrush Distance to Open Water AIC Table

| Model | AIC | Δ$_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(.) | 360.67 | 0.00 | 0.47 | 4 | 352.67 |
| Ψ(distw300m) | 362.63 | 1.96 | 0.18 | 5 | 352.63 |
| Ψ(distw180m) | 362.63 | 1.96 | 0.18 | 5 | 352.63 |
| Ψ(distw90m) | 362.64 | 1.96 | 0.18 | 5 | 353.64 |

Appendix 1.j Wood Thrush Distance to Forest Edge AIC Table

| Model | AIC | Δ$_i$ | $w_i$ | K | -2L |
|---|---|---|---|---|---|
| Ψ(.) | 360.67 | 0.00 | 0.46 | 5 | 352.67 |
| Ψ(distf90m) | 362.55 | 1.87 | 0.18 | 5 | 352.55 |
| Ψ(distf180m) | 362.57 | 1.89 | 0.18 | 5 | 352.57 |
| Ψ(distf300m) | 362.63 | 1.95 | 0.17 | 5 | 351.63 |