

**IMPACTS OF SOIL CALCIUM AVAILABILITY AND NON-NATIVE PLANT
INVASIONS ON AN URBAN FOREST BIRD COMMUNITY**

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment
of the requirements for the degree of Master of Science in Wildlife Ecology

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ABSTRACT

Recent studies suggest that the effects of natural and anthropogenic caused decreases in soil calcium availability result in the decline of migrant bird species and reduced avian reproductive success; however few studies have demonstrated trends in multiple avian species' habitat selection and nest success in relation to natural soil calcium characteristics. Herein I present results on how the availability of soil calcium affected snail abundance, understory non-native plant invasions, and breeding forest bird territory density and nest success in forest fragments. In 2010 and 2011, I sampled 21 forest fragment sites in Newark, Delaware, USA and estimated soil calcium, vegetation composition, snail abundance, and avian territory density. I used linear regressions to determine relationships between exchangeable calcium, snails, and vegetation with species' territory densities. I utilized the unmarked package in R to fit hierarchical models to bird count data to estimate abundance, while accounting for observational and site covariates. I found that snail abundance and non-native shrub density were positively related to exchangeable calcium levels. Northern Cardinals (*Cardinalis cardinalis*) was the only species which had greater territory densities in areas with more non-native shrubs. Soil calcium did not serve as the top model to determine any species abundance, nor did the percentage of non-native stems. I hypothesized that soil calcium may have a weaker influence in the abundance of urban forest bird populations, compared to continuous habitats. Additionally, soil calcium may be an artifact of stand age and vegetation structure, which ultimately influences where avian species establish territories.

Within the same sites in 2009 – 2011, I searched for and documented the outcomes of the nests of four songbird species: American Robin (*Turdus migratorius*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal, and Wood Thrush (*Hylocichla mustelina*). I modeled nest failure against landscape variables, vegetation, and nest characteristics in MCestimate, a Markov chain algorithm program used for estimating daily nest failure probabilities. Soil calcium availability was negatively related to American Robin nest success, and positively related to Northern Cardinal nest success. Northern Cardinals may benefit from an increase of soil calcium within their nest location for supplemental calcium, while American Robins may obtain calcium from other sources. Daily nest failure was positively related to date in the Gray Catbird, while Wood Thrush nest failure rates responded positively to nest height and negatively to vertical vegetation density. Stand structure and nesting habitats seem to drive daily nest failure across all four species, so forests should be maintained and edge area reduced to promote the nest success of a variety of urban forest birds.

Chapter 1

LINKING SOIL CALCIUM, VEGETATION, SNAILS, AND BIRD COMMUNITIES IN URBAN FOREST FRAGMENTS

Introduction

Natural fluctuations within the soil chemistry of forested systems are the drivers of many structural and biotic processes. Since the 1990's, research has highlighted the negative effects of calcium depletion on multiple trophic levels in forested ecosystems (Gärdenfors et al. 1995, Graveland and Drent 1997, Hames et al. 2002, Pabian and Brittingham 2007). Specifically, spatial patterns in vegetation (Huenneke et al. 1990, von Holle and Motzkin 2007), snails (Gärdenfors 1992, Gärdenfors et al. 1995, Graveland and Drent 1997), and avian communities (Hames et al. 2002, Pabian and Brittingham 2007, 2011) have been linked to soil pH and calcium availability.

Stand age and forest succession result in the shift of dominant canopy trees of varying foliar calcium concentrations, such as the shift from calcium-rich pin cherry (*Prunus pensylvanica*) (Hamburg et al. 2003) to calcium-poor beech (*Fagus grandifolia*) (Fahey et al. 1998, Skeldon et al. 2007). Consequently, the age of the forest stand may determine the availability of calcium. Hamburg et al. (2003) demonstrated that the greatest calcium concentrations occurred in stands less than 30 years old, while the lowest calcium concentrations occurred in stands greater than 100 years old. Canopy trees seem to be the driving force of the availability of calcium

within the forested ecosystem (Finzi et al. 1998), however some shrub species may also alter soil chemistry patterns (Kourtev et al. 1999, McGrath and Binkley 2009, Weidenhamer and Callaway 2010).

The interactions between soil chemistry and non-native invasive plant species are relatively unknown, yet may provide insight into the ecological effects of plant invasions and how to potentially control these species. Non-native plants alter the forested ecosystem's hydrology and salinity, resource supply, regeneration and disturbance regimes (D'Antonio and Vitousek 1992, Leicht-Young et al. 2009). In addition, many non-native species alter the soil chemistry and ecosystem biochemistry after they become established (Howard et al. 2004, von Holle and Motzkin 2007, Weidenhamer and Callaway 2010, Kuhman et al. 2011). For example, soil pH and calcium levels under Japanese stilt grass (*Microstegium vimineum*) (Kourtev et al. 1999, McGrath and Binkley 2009), Japanese barberry (*Berberis thunbergii*) (Kourtev et al. 1999), and oriental bittersweet (*Celastrus orbiculatus*) (Leicht-Young et al. 2009) were greater than areas without these species. Due to these chemical changes, some non-native plants may gain a competitive advantage over the native flora (Weidenhamer and Callaway 2010) and easily overtake the habitat, creating monocultures.

Changes within ecosystems caused by the introduction of non-native plants can impact higher trophic levels by decreasing native plant diversity, disrupting ecosystem processes, and altering nitrogen cycling and fire regimes (Vitousek et al. 1996, Higgins et al. 1999). Consequently, other trophic levels may be affected by the change in plant community composition, from a one dominated by native species

compared to another dominated by a non-native invasive species. Bird species rely on the presence of food and nesting resources which can be dramatically altered with the introduction of an invasive species. Native plant species host a greater insect abundance than their non-native counterparts, therefore providing a greater food source for the avian community (Burghardt et al. 2009). In addition, non-native invasive plant species have been found to reduce site fidelity (Ortega et al. 2006), reproductive success (Remeš 2003, Ortega et al. 2006, Rodewald et al. 2010), as well as territory density (Scheiman et al. 2003) in a variety of bird species. Overall, the introduction of a non-native species can negatively alter the ecosystem and many of these changes may be unique to the landscape and invading plant species.

Another taxon which is limited within acidified habitats is land snails. Snails require abundant calcium levels, as calcium carbonate is an essential compound for shell growth and maintenance, reproduction, and digestion. Snails bred experimentally without calcium have resulted in dwarfed individuals and deformed shells (Fournié and Chétail 1984). Snail abundance and diversity are lower in areas with acidic, calcium-poor soils, while areas artificially limed have shown an immediate increase in snail abundance (Gärdenfors 1992, Graveland et al. 1994, Gärdenfors et al. 1995, Pabian and Brittingham 2007, Skeldon et al. 2007).

Calcium is also an essential nutrient for avian reproduction, specifically for egg formation and skeletal development of the embryo. In 1997, the first experimental evidence was published supporting the idea that calcium availability for birds limits reproductive output and success (Graveland and Drent 1997). Calcium must be acquired from environmental sources because skeletal calcium minimally, if

at all, contributes to eggshell formation (Graveland and Van Gijzen 1994, Blum et al. 2001). Females acquire calcium needed for reproduction from local food sources, such as caterpillars and spiders (Graveland et al. 1994, Blum et al. 2001). However, a diet of arthropods can only provide the female a small portion (Taliaferro et al. 2001), specifically 5-10% (Graveland and Van Gijzen 1994), of the calcium needed to reproduce. Only two to three snails (Blum et al. 2001), with a total dry mass of 60 mg (Taliaferro et al. 2001), are needed for sufficient calcium to produce each egg for small songbirds. Birds on poor soils compensated for lack of snail presence by using anthropogenic calcium sources, such as experimentally provided chicken egg shells (Graveland et al. 1994).

Neotropical migratory birds have declined in North American since the 1970's (Robbins et al. 1989, Hagan and Johnston 1992, Peterjohn and Sauer 1994) with eastern forest birds showing more recent continued declines (NABCI 2009). Research on the cause of these declines has primarily focused on habitat and forest fragmentation, climate change, and the impacts of invasive and pest species (Hagan & Johnson 1992, NABCI 2009). In areas of habitat and forest fragmentation, bird populations have decreased due to a reduction in reproductive success and increased Brown-headed Cowbird parasitism (*Molothrus ater*) (Robinson et al. 1995, Burhans and Thompson 2006, Howell et al. 2007); however, recent studies suggest that population declines may also be related to soil acidification caused by acid rain (Hames et al. 2002, Pabian and Brittingham 2007, 2011), which may compound the effects of fragmentation (Hames et al. 2002). In acidic, calcium-poor locations, Hames et al. (2002) determined that Wood Thrush (*Hylocichla mustelina*) would be

less abundant. Ovenbird (*Seiurus aurocapilla*) abundance, clutch size, and nest density were also related to soil calcium availability, after a lime application within the forest (Pabian and Brittingham 2007, 2011)

Although studies have already shown relationships between the availability of calcium and the presence of songbird species such as the Wood Thrush (Hames et al. 2002) and Ovenbird (Pabian and Brittingham 2007, 2011), to this date there have been a lack of studies which address the effect of calcium availability on the community scale and in an urban setting. Herein I present results on how the forest breeding bird community responded to the effects of soil calcium availability, vegetation structure and native status, and snail abundance and weight within a suburban-urban setting.

Methods

Study Area

I conducted my research within 12 urban temperate deciduous forest patches located in Newark, Delaware, USA in 2010 and 2011. Within the 12 larger forest patches, I selected 21 sites (Fig. 1.1) which comprised the entirety or a section of the larger forest patch. Sites ranged in size (2.06 to 16.3 ha) and shape, according to the forest fragment they were located in (Table 1.1). Half of the sites (48%) had a standardized size of 3.5 ha (200 m x 175 m) and were located within larger forest patches. I used sites located within three ecoregions of Delaware: the Northern Piedmont, Southeastern Plains, and the Middle Atlantic Coastal Plain (EPA 2012). The soils of the Northern Piedmont ecoregions ranged from by thin, stony soils on the

ridges and low mountains to limestone rich, clay soils in the valleys (USGS 2011, Wiken et al. 2011), while the Southeastern Plains and Middle Atlantic Coastal Plain had more sandy, poorly drained soils (Wiken et al. 2011).

The canopy trees in these sites were tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), blackgum (*Liquidambar styraciflua*), red oak (*Quercus rubra*), and white oak (*Quercus alba*). The dominant species in the shrub layer were spicebush (*Lindera benzoin*), arrowwood viburnum (*Viburnum dentatum*), and coastal sweetpepperbush (*Clethra alnifolia*).

Study Design

To standardize edge effects, all sites had at least one edge which bordered residential or agricultural land. Within each site, I established a grid with alpha-numerical markers placed in 25 m intervals (Fig. 1.2). The site “Ecology Woods” was the only exception to this pattern. Bray et al. (1965) established a 45.7 x 45.7 m (150 x 150 ft) grid on the property in 1965 for an urban impact research study, which remains today.

I used a systematic random sample to select sampling points, centered at the flag marker. According to the site’s size and shape, I selected 13 – 20 sampling points per site, averaging 15 per site. At each sampling point, I sampled the soil, snails, and vegetation. In addition, I randomly selected five points from these chosen sampling points to sample tree age.

Soil Sampling

At each sampling location, two field technicians extracted five soil core samples from the top 10 cm of the soil, and mixed the samples together to get a testable heterogeneous soil sample. The University of Delaware Soil Laboratory (UDSL; Newark, DE, USA) oven-dried the samples for 72 hours, ground and sieved the soils to 2 mm partials. The UDSL analyzed the soil chemistry for exchangeable calcium via the Mehlich-III method (Mehlich 1984).

Vegetation Sampling

I estimated shrub density, tree basal area, and vertical vegetation density at all sampling points. I sampled shrub cover species within a 2.5 m radius of the sampling point flag. I counted all shrub stems greater than 1 m in height, less than 15 cm in DBH, and identified the shrub to species. I utilized the U.S. Department of Agriculture PLANTS Database to determine if each species was native to the study region (USDA 2006). I determined tree basal area by utilizing Factor-10 prism (Mannel et al. 2006), standing above the sampling point flag. To estimate vertical vegetation density, I used a 2.5 m tall vegetation profile board, “Nudd’s Board”, and measured the percentage of the board obscured by vegetation 15 m from the sampling point flag in each of the four cardinal directions (Nudds 1977).

To determine landscape-scale forest cover, I calculated rasterized landscape values (Fry et al. 2011) by running 100 meter buffers around each site’s perimeter within ArcGIS 9.0 (Environmental Systems Research Institute Inc. (ESRI), Redlands, CA). I selected a buffer of 100 meters because any buffer greater than this resulted in overlapping buffers between neighboring sites. After creating a buffer, I

used Zonal Statistics (ESRI 2009) in the Spatial Analyst extension to ArcGIS to calculate the percent forest cover within the site's buffer. I estimated forest patch size by selecting the appropriate forest patch polygon and calculating the area value within the attribute table in ArcGIS 9.0.

Stand Age

To determine the age of each site, I cored the dominant canopy tree for tree-age analysis at five randomly selected points in each fragment. I utilized a 3-thread, 5.15 mm increment borer (Haglöf Company Group, Långsele, Sweden) for all cores extracted. I dyed all cores with a phloroglucinol solution (1 g phloroglucinol: 100 cc 95% ethyl alcohol), mounted, and visually cross-dated them using standard dendrochronological methods (Stokes and Smiley 1968, Yamaguchi 1991). I utilized the median age of the five cores to serve as the age of each site.

Land Snail Sampling

Two technicians sampled land snails by leaf litter sieving and time constrained searches at all sampling points. The technicians collected a leaf litter sample within a 0.5 m² PVC pipe frame surrounding the location of the soil core sample and stored the sample in a cold room (4°C). The technicians placed the litter in a Berlese funnel (Berlese 1905) which removed all snails and dried the litter. A technician sieved the dried litter for individual snails greater than 3 mm. For the time constrained searches, two technicians conducted a search for 5 minutes total within 2.5 m of the sampling location for any snails. I combined the data on snails collected via the litter sieving and time constrained searches for each sampling point. A technician

preserved all snails in 95% ethanol until the snails were dried, counted, weighed, and identified to genus.

Avian Sampling

I visited each site ten times from 13 May – 20 July in 2010 and 2011, with a mean of 5.1 ± 0.15 (mean \pm standard error; hereafter SE) days between visits. I estimated the territory locations and densities of all observed bird species with the spot mapping method (International Bird Census Committee 1969, Bibby et al. 2000). I spot mapped the sites between the hours of 0630 and 1400, on days without precipitation or high winds (>15 km/h). All observers received training to identify birds by sight and vocalizations, in addition to the spot mapping method. After I spot mapped each site ten times, I created a master map of each site and the locations of all birds seen and heard throughout the season. I defined a territory to be established if a bird was recorded in the same relative location during three site visits, with the sightings at least 10 days apart (Bibby et al. 2000). I calculated the mean avian territory density data for each site across both years, and analyzed this value against habitat variables.

Statistical Analysis

I used linear regressions to determine if vegetation, snail, or territory densities were related to exchangeable calcium. For the linear regressions, I only analyzed bird species which I considered to be common throughout my study area, which I determined to be species which established territories at least within 5 (24%) of my study sites (Table 1.2). I determined if soil calcium predicted the abundance of

non-native shrub vegetation and snail abundance, and if either predicted the territory density of the observed bird species with linear regressions. I ran all linear regressions in SPSS 18.0.0 (SPSS Inc., Chicago, IL) with a significance level of $P < 0.05$.

I estimated avian species richness (s) for each site as the number of species which established territories. I calculated the Shannon Diversity index (H') and community evenness (E) (Shannon and Weaver 1949):

$$H' = - \sum_{i=1}^n p_i \log(p_i) \quad E = \frac{e^{H'}}{s}$$

where n is the number of species observed at each site and p_i is the relative abundance of species i . I determined if the site's avian species richness and evenness could be predicted from the mean exchangeable calcium with a linear regression.

I used “unmarked” (Fiske and Chandler 2011) in Program R (2011) estimate avian abundance, while accounting for observational and site covariates (Table 1.3). I selected 13 species *ad hoc* to analyze in “unmarked” due to their density across all sites and interest in the species (Table 1.2). I first tested for the effects of date, time, percent cloud cover, and temperature on detection probabilities. I ran the observational models for each species, holding abundance constant to determine the observation model to use. For each species, I chose the model which had a ΔAICc value less than two to serve as the observational model in my abundance estimations (Burnham and Anderson 1998). If there were multiple models with a $\Delta\text{AICc} < 2$, I chose the one which had the fewest parameters (K),

I used Pearson's correlation analyses (Pearson 1895; $r \geq 0.45$, $P < 0.05$) to reduce the number of possible covariates in the abundance models. If the covariates were correlated, I selected one which I considered to be the most biological meaningful for each hypothesis. I constructed models *a priori* to test the following hypotheses related to forest breeding bird abundance. To test for the effects of calcium availability and snails on the breeding bird abundance, I used two models which included exchangeable calcium (exchca) and snail weight (snwt). To test for effects of within patch vegetation characteristics and stand age, I used a model which included vertical vegetation density (density), basal area (ba), and stand age (age). I incorporated basal area into this model due to its relation to the successional status of the forest (Seitz and Zegers 1993), which may drive the abundance of specific bird species. To test for the effect of non-native vegetation invasions on bird abundance, I used a model which included the percentage of non-native shrub stems (prctnstem) within each site. To test for landscape scale effects, I developed a model that included forest cover within a 100m radius of each site (forest100) and patch area (patch_ha). I included a constant (.) and global abundance model, for a total of 10 models.

Results

Soils

At the sampling point, the mean (\pm SE) exchangeable calcium concentration was 4.51 ± 0.23 meq/100g (Note: for calcium: 1 meq = 0.5 mmol).

Sites ranged in their mean exchangeable levels from 0.57 ± 0.60 meq/100g at Glasgow II to 11.05 ± 1.40 meq/100g at Iron Hill I (Table 1.4).

Vegetation

For shrub cover vegetation, I detected 62 species (Table 1.5), 15 (24.2%) of which were non-native. The most common native shrub species stems were spicebush (10.3%), roundleaf greenbriar (*Smilax rotundifolia*, 6.9%), and arrowwood viburnum (5.4%). The most common non-native shrub species stems were multiflora rose (23.2%), Japanese honeysuckle (*Lonicera japonica*, 6.1%), and autumn olive (*Elaeagnus umbellata*, 4.5%).

The mean (\pm SE) shrub stem count across all sampling points was 15.4 ± 1.4 shrub stems, 6.7 ± 1.1 of which were from non-native species. At the sampling point, 22.6% (± 1.9 ; mean \pm SE) of the stems were non-native. Exchangeable calcium was positively related to the number of total stems present ($R^2 = 0.033$, $\beta = 0.03$, $P = 0.001$), as well as the percentage of non-native stems present ($R^2 = 0.16$, $\beta = 4.84$, $P < 0.001$). At the site level, stem counts ranged from a mean (\pm SE) 2.67 ± 0.74 stems at Sunset Lake 2 to 47.36 ± 15.43 stems at Christina Creek 2 (Table 1.6). I did not detect any non-native plant species stems at 5 plots (Table 1.6), while the site “White Clay 2” had the most non-native shrub stems (86.6%).

The mean (\pm SE) basal area at the sampling point was $26.9 \text{ m}^2/\text{ha}$ (± 0.5). Sites ranged in mean basal area (\pm SE) of $16.7 \text{ m}^2/\text{ha}$ (± 2.3) at Christina Creek I to $32.5 \text{ m}^2/\text{ha}$ (± 1.6) at Webb Farm (Table 1.6). Exchangeable calcium was negatively related to basal area at the sampling point ($R^2 = 0.02$, $\beta = -0.05$, $P = 0.02$).

The mean (\pm SE) vertical vegetation density at the sampling point was 29.9% (\pm 1.2). Sites ranged in mean vertical vegetation density (\pm SE) of 11.7% (\pm 2.7) at Sunset Lake II to 53% (\pm 7.0) at White Clay II (Table 1.6). Exchangeable calcium was positively related to vertical vegetation density at the sampling point ($R^2 = 0.07$, $\beta = 0.05$, $P < 0.001$).

Stand Age

Stand age ranged from 32 years (Christina Creek II and Dorothy Miller) to 111 years (Sunset Lake II), with a mean (\pm SE) of 65.9 (\pm 5.6) years (Table 1.1). Older stands had less exchangeable calcium ($R^2 = 0.22$, $\beta = -0.05$, $P = 0.030$). Stand age was negatively related to the mean percentage of non-native stems within the site ($R^2 = 0.04$, $\beta = -0.004$, $P = 0.002$). I did not detect a relationship between the site's stand age and mean snail abundance ($R^2 = 0.07$, $\beta = -0.06$, $P = 0.26$) or weight ($R^2 = 0.06$, $\beta = -0.001$, $P = 0.28$).

Snails

Throughout both seasons, I collected 1,599 snails, from 18 genera, via sifting and active searches. I detected a positive relationship between exchangeable calcium and snail abundance ($R^2 = 0.09$, $\beta = 0.11$, $P < 0.001$) and weight ($R^2 = 0.04$, $\beta = 3.15$, $P = 0.001$). I did not detect a relationship between exchangeable calcium and snail genera ($R^2 = 0.01$, $\beta = 0.24$, $P = 0.12$). I detected a positive relationship between the percentage of non-native stems and snail weight ($R^2 = 0.02$, $\beta = 0.09$, $P = 0.012$); however I did not detect a relationship with snail abundance ($R^2 = 0.008$, $\beta = 2.88$, $P = 0.11$) and snail genera ($R^2 = 0.01$, $\beta = 0.42$, $P = 0.08$).

Sites ranged in mean (\pm SE) snail abundance from 0.54 ± 0.42 snails at Motor Pool to 22.5 ± 5.3 snails at Coverdale (Table 1.7). Sites ranged in mean snail weights from $0.00082 \text{ g} \pm 3.99 \text{ E}10^{-4}$ at Sunset Lake II to $0.559 \text{ g} \pm 0.02$ at Coverdale (Table 1.7). Sites ranged in number of snail genera from 0.4 ± 0.19 at Motor Pool to 2.87 ± 0.46 at Iron Hill 1 (Table 1.7). At the site level, I did not detect a relationship between the mean percentage of non-native stems and mean snail weight ($R^2 = 0.05$, $\beta = 0.16$, $P = 0.35$), abundance ($R^2 = 0.06$, $\beta = 8.93$, $P = 0.29$), or genera ($R^2 = 0.2$, $\beta = -0.67$, $P = 0.58$) at the site level.

Birds

Throughout the two field seasons, I detected 31 species which established territories throughout the study sites, 19 of which had territories in more than five sites (Table 1.2). The most common birds across my sites were Northern Cardinal (*Cardinalis cardinalis*), Carolina Chickadee (*Poecile carolinensis*), American Robin (*Turdus migratorius*), and Wood Thrush. The site's mean exchangeable calcium was unrelated to species' territory densities, with the exception of the Hairy Woodpecker (*Picoides villosus*; $R^2 = 0.24$, $\beta = -0.02$, $P = 0.023$). Territory densities of Carolina Wrens (*Thryothorus ludovicianus*, $R^2 = 0.22$, $\beta = 1.33$, $P = 0.030$), Acadian Flycatchers (*Empidonax virescens*; $R^2 = 0.22$, $\beta = 0.30$, $P = 0.034$), and Red-bellied Woodpeckers (*Melanerpes carolinus*, $R^2 = 0.19$, $\beta = 0.95$, $P = 0.047$) were positively related to snail weight, while the territory density of the Eastern Wood-Pewee (*Contopus virens*, $R^2 = 0.19$, $\beta = -0.67$, $P = 0.047$) was negatively related to snail weight. Northern Cardinal was the only species which had territory densities related

to the mean percentage of non-native stems present in the site ($R^2 = 0.23$, $\beta = 2.41$, $P = 0.028$), however Hairy Woodpeckers approached significance ($R^2 = 0.18$, $\beta = -0.33$, $P = 0.056$).

Across the study sites, species richness ranged from 9 to 20 species (Table 1.8), with a mean \pm SE of 13.3 ± 0.63 . Species evenness ranged from a value of 0.14 to 0.25 (Table 1.8), with mean of 0.20 ± 0.007 . Avian species richness and evenness were unrelated to the mean exchangeable calcium (richness, $R^2 = 0.001$, $\beta = 0.02$, $P = 0.92$; evenness $R^2 = 0.03$, $\beta = -0.002$, $P = 0.45$) and percentage of non-native shrubs (richness, $R^2 = 0.06$, $\beta = 0.02$, $P = 0.27$; evenness $R^2 = 0.06$, $\beta = -1.29$, $P = 0.31$).

For the observational covariates, the global model was the top model with the fewest parameters, for 4 of 13 (30.8%) of the species (Table 1.9). Date served as the top model for 5 species: Hairy Woodpecker ($\beta = 0.39$), Carolina Wren ($\beta = 0.25$), Northern Cardinal ($\beta = -0.18$), Eastern Wood-Pewee ($\beta = -0.25$), and Red-bellied Woodpecker ($\beta = -0.27$). The null model served as the top model for the Eastern Towhee (*Pipilo erythrophthalmus*), Red-eyed Vireo (*Vireo olivaceus*), and the Scarlet Tanager (*Piranga olivacea*). Observation start time served as the top model only for the Wood Thrush ($\beta = -0.09$). Within the top observational models, trends across all observational covariates differed by avian species (Table 1.9).

For the abundance models, Eastern Wood-Pewee ($\beta = -0.28$) and Red-bellied Woodpeckers ($\beta = 0.19$) were the only species which had snail weight as their top model. The top model for American Robin abundance was negatively related to forest cover and patch size (forest cover, $\beta = -0.04$; patch size, $\beta = -0.47$). The global model was equally probable for American Robin abundance. Apart from these

species, the global model was the top model for the 10 (77%) remaining species' abundances (Table 1.10). Within these global models, exchangeable calcium was positively related to four species' abundances, while the percentage of non-native stems was positively related to six species' abundances (Table 1.11). From this group of 10 species, with varying model directionalities, I focused my analysis on the following four species' global models due to their strong beta values, abundance across my study sites, and interest in the species: Ovenbird, Wood Thrush, Gray Catbird, and Northern Cardinal.

Ovenbird and Wood Thrush, two interior mature forest bird species (Evans et al. 2011, Porneluzi et al. 2011), exhibited similar trends. I detected both species in greater abundances in older forest patches (stand age: Ovenbird, $\beta = 2.35$; Wood Thrush, $\beta = 1.02$) with more forest cover within the landscape (forest cover at 100 m: Ovenbird, $\beta = 1.32$; Wood Thrush, $\beta = 0.55$). I detected Ovenbird and Wood Thrush in greater abundances within sites with more snail mass (snail weight: Ovenbird, $\beta = 1.43$; Wood Thrush, $\beta = 0.27$) and forest stands with greater stand density (Ovenbird, $\beta = 0.97$; Wood Thrush, $\beta = 0.37$) and vertical vegetation density (Ovenbird, $\beta = 1.60$; Wood Thrush, $\beta = 0.55$). I detected Wood Thrush in greater abundances within sites with more exchangeable calcium and percent non-native stems (exchangeable calcium, $\beta = 0.11$; percent non-native stems, $\beta = 0.37$), while Ovenbirds were less abundant (exchangeable calcium, $\beta = -0.11$; percent non-native stems, $\beta = -0.15$).

Gray Catbirds and Northern Cardinals also exhibited similar directionalities within their abundance covariates. I detected both species in greater

abundances in larger (patch area: Gray Catbird, $\beta = 0.34$; Northern Cardinal, $\beta = 0.04$) and younger (stand age: Gray Catbird, $\beta = -0.51$; Northern Cardinal, $\beta = -0.29$) forest patches, which contained less non-native shrub stems (Gray Catbird, $\beta = -0.84$; Northern Cardinal, $\beta = -0.25$). I detected a weak relationship between Gray Catbird abundance and sites with greater snails weight ($\beta = 0.06$) and less exchangeable calcium ($\beta = -0.21$). Alternatively, I detected Northern Cardinal in greater abundances within sites with greater snail weight and exchangeable calcium (snail weight, $\beta = 0.10$; exchangeable calcium, $\beta = 0.41$).

Discussion

The mean value of exchangeable calcium was lower in my sites compared to studies within continuous forests (6.53 meq/100g, Pabian and Brittingham 2007; 6.2 meq/100g, Pabian and Brittingham 2011). The poor quality of my soil can be attributed to the negative effects of urbanization on soil conditions (reviewed in Pickett et al. 2008). A decrease in soil calcium availability could be a consequence of the potential increases in heavy metal concentrations (Pouyat et al. 1995), soil temperatures, greater C:N ratios, and other human modifications in urban habitats (Pickett et al. 2008).

Invasions by non-native plants were greater within areas of more exchangeable calcium. Changes within soil chemistry are unclear if they resulted from the alterations caused by non-native species, or if non-native species outcompeted their native counterparts for healthier soils. Some studies have determined that non-native species have the ability to change the soil chemistry

(*Microsteigium vimineum*, Kourtev et al. 1999; *Berberis thunbergii*, Kourtev et al. 1999; and *Celastrus orbiculatus*, Leicht-Young et al. 2009); however, there have been a lack of studies which evaluated if multiflora rose, my most common non-native shrub, has the ability to change soil pH or calcium levels. More studies need to be conducted on more non-native plant species to determine the directionality of this relationship and its universality.

Non-native plants were abundant throughout my sites, and may have driven the territory densities and abundances of some bird species. Northern Cardinals were the only species which had their territory density positively associated with the percentage of non-native stems in their sites, which is consistent with their preference for dense habitats for nesting (Baicich and Harrison 2005, Leston and Rodewald 2006). The percentage of non-native stems was positively related to six species' abundance estimates within their top (AICc < 2) global models. Birds may be drawn to areas with more non-native shrubs due to their preference of exotic species' fruits (Lafleur et al. 2007), earlier leafing (Remeš 2003, Rodewald et al. 2010), or abundant nesting habitats (Schmidt and Whelan 1999). For example, American Robin and Wood Thrush were competitors for nesting locations within exotic *Lonicera* shrubs (Schmidt and Whelan 1999). However, these non-native dominant habitats may overall act as an ecological trap (Gates and Gysel 1978) and limit the reproductive success, as seen in a variety bird species (Remeš 2003, Borgmann and Rodewald 2004, Lloyd and Martin 2005, Ortega et al. 2006, Rodewald et al. 2010).

Snail abundance and weight were greater in sites with more calcium available, as demonstrated in numerous studies (Gärdenfors 1992, Graveland et al.

1994, Gärdenfors et al. 1995, Pabian and Brittingham 2007, Skeldon et al. 2007). A number of species territory densities were driven by snail weight, however these trends seem to be the result of habitat structure. For example, Red-bellied Woodpecker abundance was positively related to snails. This can be attributed to the positive association of snails with coarse woody debris (Kappes et al. 2006). Red-bellied Woodpeckers are found in mature woodlands with large-diameter trees (Shackelford et al. 2000), which would have more coarse woody debris than younger stands, and consequently more snails. Other two species which seem to be driven by forces other than snail weight were Eastern Wood Pewee and Acadian Flycatcher. Both are insectivorous species (McCarty 1996, Whitehead and Taylor 2002), and are assumingly not reliant upon snails as a source of calcium, as compared to other small songbirds.

Overall, other additional sources of calcium-rich prey may be necessary for birds to establish territories. Slugs and snails occupying habitats above the ground level were not sampled, which may have an impact on bird populations. I also cannot disregard the importance of some arthropod species for their source of calcium for egg-laying females (Graveland et al. 1994, Blum et al. 2001). Calcium sources, such as arthropods and seeds, can cover an additional 5-10% of the calcium requirement to lay one egg (Graveland and van Gijzen 1994).

Species may cue into a number of landscape, vegetation, and nutritional factors when selecting for habitats to establish territories. Larger and more heterogeneous forest structures generally have more bird species (Freemark and Merriam 1986), allowing for multiple habitat types present within these stands to be

utilized by a variety of species. Even though 10 of my focus species had the global model as their top model, the strengths and directionalities of each covariate varied, implying that species are driven by multiple factors, a few which served more of an importance than others. For example, Northern Cardinal territory selection may be driven primarily by tree height and shrub density (Conner et al. 1986), but the species may also benefit from greater calcium and snail availability, strengthening Northern Cardinal's positive abundance trends.

Across my sites, Ovenbirds' territory densities were negatively related to increases in exchangeable calcium levels, contrary to the findings of Pabian and Brittingham (2007). My observations took place in fragmented, urban forests rather than the continuous forests studied in Pennsylvania (Pabian and Brittingham 2007). Within a continuous forest, Ovenbirds could have potentially been attracted to the experimentally supplemented calcium due to its accessibility (Sauter et al. 2006). Ovenbirds could also be more constrained by landscape traits, rather than calcium availability within urban environments. Patch size and stand age were positively related to Ovenbird abundance within my sites. Ovenbirds were more abundant in older stands with less calcium available; however Ovenbird abundance was positively related to snail weight. When available within older forest stands, Ovenbirds may be attracted more to snail presence, even within calcium-poor sites, than the amount of calcium within the soil.

Wood Thrush, another interior forest bird, exhibited similar trends with habitat variables as seen in Ovenbird abundances. The main differences between the two species were the opposite trends seen in the exchangeable calcium and the percent

non-native stems present within the site. Even though Wood Thrush were found in greater abundances within older stands, which would assumingly have less calcium available, their abundance was positively related to exchangeable calcium. This seemingly opposing trend can be corrected for by the Wood Thrush's positive association with non-native stems. Soils under non-native stems contained more calcium than areas with less non-native stems present (Kourtev et al. 1999, Howard et al. 2004, von Holle and Motzkin 2007, Leicht-Young et al. 2009, McGrath and Binkley 2009). If Wood Thrush were found in sites with more non-native shrubs, the habitat's calcium availability then would reflect the soil changes caused by the vegetation community.

Gray Catbirds and Northern Cardinals also exhibited similar directionalities within their abundance covariates, potentially due to their associations with dense, urban habitats (Halkin and Linville 1999, Smith et al. 2011). Both species' abundances were associated with younger, smaller forest patches, which corresponded to their habitat preferences of shrub-sapling stage and edge habitats (Halkin and Linville 1999, Smith et al. 2011). Gray Catbirds' abundance was driven by habitats with less non-native shrub stems and greater vertical densities. This suggests that Gray Catbirds establish in areas with dense native shrubs, which corresponds to the Gray Catbird's negative association with exchangeable calcium.

Northern Cardinals' abundances were also associated with areas of less non-native shrub stems, but also in less dense areas with more exchangeable calcium. My results were consistent with Conner et al. (1986) with Northern Cardinal's negative association with foliage density. However, the negative association with

Northern Cardinal abundance and percentage of non-native stems was contrary to what I expected, due to the species' nesting preferences in dense habitat (Halkin and Linville 1999). Northern Cardinals are found more often in urban habitats (Leston and Rodewald 2006), which may relax habitat constraints through provisions of shrubby habitats via landscaping and agricultural hedgerows. Northern Cardinals tend to nest in dense shrubs and vine vegetation structures (Halkin and Linville 1999); however their reproductive success was diminished in non-native nest substrates (Rodewald et al. 2010, Shustack and Rodewald 2011). Abundances may be reduced in areas with a greater percentage of non-native shrub stems due to this consequence on their populations within invaded habitats.

Differences between sampling point and site level characteristics on avian territory densities indicated that relationships with soil, vegetation, and snail characteristics may be at a finer scale than what I observed. For example, species' territory densities which were unrelated to calcium on the site-level could be responding to calcium availability on a smaller scale. A finer landscape resolution, as compared to site-level metrics, could be needed to uncover the relationships between species' territory establishment and soil calcium. Sites ranged in calcium richness, vegetation structure, and snail abundance over the landscape, so the measurements of these metrics within each species' territory location should analyzed for habitat preference characteristics. Additionally, a diet analysis should be performed to determine what each species requires for a food source. If snails are not consumed as the primary source of calcium for these urban birds, snail weight should not be used to determine abundance rates within my models.

Overall, birds in fragmented, urban habitats may not be as calcium-limited as birds which occupy continuous, mature forest stands. Natural food sources may be scarce, or limited within the confines of small urban forest patches, which would force birds to seek out anthropogenic nutrient and food sources when it is easily accessible (Sauter et al. 2006, Heiss et al. 2009). Degradation of concrete, anthropogenic food sources, and other sources of calcium, coupled with natural soil calcium resources, may sustain bird populations within suburban and urban habitats. Therefore, urban species may be less constrained by soil calcium richness as compared to species within large forested lands with limited anthropogenic calcium supplements.

The trends that I observed concerning the abundance of bird species across my sites seem to have started at the landscape and vegetation level, rather than soil calcium. Open suburban woodland habitats were generally younger than established forest stands, which had significantly less calcium available. The lack of calcium consequently supported less plant growth (Hepler 2005), which could have limited the density and vertical structure in habitats needed for nesting. Bird diversity was found to follow the vertical physical plant structures found within forests (MacArthur and MacArthur 1961), which could be severely limited due to poor calcium resources. Thus, the trends observed in these species and their associated site's calcium availability could have just been an artifact of stand age and vegetative structure.

Table 1.1. Site size and ages determined by tree cores. Core ages are medians of the 5 cores taken at each site.

Site	Site Area (ha)	Patch Area (ha)	Stand Age
Christina Creek 1	2.56	92.70	38
Christina Creek 2	6.13	188.73	32
Chrysler Woods	3.19	2553.84	46
Coverdale	3.84	4.04	42
Dorothy Miller	2.44	68.13	32
Ecology Woods	16.3	16.33	74
Folk	3.50	855.90	102
Glasgow 1	3.50	188.64	52
Glasgow 2	3.50	188.64	95
Iron Hill 1	3.50	855.90	86
Iron Hill 2	3.50	855.90	96
Laird	2.59	2553.84	46
Motor Pool	3.94	4.99	54
Phillips	2.06	4.50	61
Reservoir	3.50	49.23	88
Rittenhouse	6.97	92.70	74
Sunset Lake 1	3.50	188.64	46
Sunset Lake 2	3.50	188.64	111
Webb Farm	6.00	9.63	59
White Clay 1	3.50	2553.84	105
White Clay 2	3.50	2553.84	45

Table 1.2. List of species which established territories within at least one site. Table present each species' four-letter AOU code, total territory density across all sites, and the percentage of sites which the species had established a territory. Species which established a territory at more than 5 sites (territory density analyses) and my focus species (abundance analyses) are listed.

AOU Code	Species	Established at > 5 Sites	Focus Species
ACFL	Acadian Flycatcher <i>Epidonax virescens</i>	X	
AMGO	American Goldfinch <i>Spinus tristis</i>		
AMRO	American Robin <i>Turdus migratorius</i>	X	X
BHCO	Brown-headed Cowbird <i>Molothrus ater</i>	X	X
BLJA	Blue Jay <i>Cyanocitta cristata</i>	X	
BRTH	Brown Thrasher <i>Toxostoma rufum</i>		
CACH	Carolina Chickadee <i>Poecile carolinensis</i>	X	
CARW	Carolina Wren <i>Thryothorus ludovicianus</i>	X	X
COGR	Common Grackle <i>Quiscalus quiscula</i>		
COYE	Common Yellowthroat <i>Geothlypis trichas</i>		
DOWO	Downy Woodpecker <i>Picoides pubescens</i>		
EAPH	Eastern Phoebe <i>Sayornis phoebe</i>		
EATO	Eastern Towhee <i>Pipilo erythrophthalmus</i>	X	X
EAWP	Eastern Wood-Pewee <i>Contopus virens</i>	X	X
ETTI	Tufted Titmouse <i>Baeolophus bicolor</i>	X	
GRCA	Gray Catbird <i>Dumetella carolinensis</i>	X	X
HAWO	Hairy Woodpecker <i>Picoides villosus</i>	X	X
HOWR	House Wren <i>Troglodytes aedon</i>		
INBU	Indigo Bunting <i>Passerina cyanea</i>	X	
MODO	Mourning Dove <i>Zenaida macroura</i>		
NOCA	Northern Cardinal <i>Cardinalis cardinalis</i>	X	X
NOFL	Northern Flicker <i>Colaptes auratus</i>		
NOMO	Northern Mockingbird <i>Mimus polyglottos</i>		
OVEN	Ovenbird <i>Seiurus aurocapillus</i>	X	X
PIWO	Pileated Woodpecker <i>Dryocopus pileatus</i>		
RBWO	Red-bellied Woodpecker <i>Melanerpes carolinus</i>	X	X
REVI	Red-eyed Vireo <i>Vireo olivaceus</i>	X	X
SCTA	Scarlet Tanager <i>Piranga olivacea</i>	X	X
SOSP	Song Sparrow <i>Melospiza melodia</i>		
WBNU	White-breasted Nuthatch <i>Sitta carolinensis</i>	X	
WOTH	Wood Thrush <i>Hylocichla mustelina</i>	X	X

Table 1.3. Observational and abundance covariates measured at each site and active point for use in “unmarked”.

Covariate	Code	Type	Unit
Date of Observation	date	Observational	julian date
Time of Observation Start	time	Observational	minute
Percent Cloud Cover	cloud	Observational	%
Temperature	temp	Observational	°C
Exchangeable Calcium	exchca	Abundance	meq/100g
Snail Weight	snwt	Abundance	grams
Vertical Vegetation Density	density	Abundance	%
Basal Area	ba	Abundance	m ² /ha
Mean Stand Age	age	Abundance	years
Percentage of Non-Native Shrub Stems	prctnnstem	Abundance	%
Forest Cover Within 100m Radius of the Site	forest100	Abundance	%
Site Area	patch_ha	Abundance	hectare

Table 1.4. Mean \pm SE of exchangeable calcium for all 21 study sites. Sites are organized by their exchangeable calcium value.

Site	Exchangeable Calcium (meq/100g)
Iron Hill 1	11.05 \pm 1.43
White Clay 2	8.884 \pm 0.43
Motor Pool	7.353 \pm 0.87
Coverdale	7.289 \pm 1.15
Dorothy Miller	7.135 \pm 1.75
Chrysler Woods	6.828 \pm 0.99
Christina Creek 2	6.657 \pm 0.6
Laird	6.282 \pm 0.85
Phillips	5.583 \pm 1.31
Christina Creek 1	5.309 \pm 0.47
Rittenhouse	4.318 \pm 1.03
White Clay 1	3.595 \pm 0.76
Reservoir	3.513 \pm 1.04
Folk	3.158 \pm 0.49
Webb Farm	2.901 \pm 1.1
Ecology Woods	2.509 \pm 0.48
Iron Hill 2	2.393 \pm 0.38
Glasgow 1	1.664 \pm 0.31
Sunset Lake 1	1.339 \pm 0.33
Sunset Lake 2	0.837 \pm 0.18
Glasgow 2	0.575 \pm 0.06

Table 1.5. List of shrub species, and total stems, detected during vegetation surveys. Each native status applied to the study region (Delaware), according to the USDA PLANTS Database.

Scientific Name	English Name	Native Status	Number of Stems
<i>Acer negundo</i>	Box Elder	Native	59
<i>Acer platanoides</i>	Norway Maple	Non-Native	3
<i>Acer rubrum</i>	Red Maple	Native	65
<i>Acer saccharum</i>	Sugar Maple	Native	2
<i>Alliaria petiolata</i>	Garlic Mustard	Non-Native	78
<i>Alnus serrulata</i>	Hazel Alder	Native	8
<i>Amelanchier arborea</i>	Common Serviceberry	Native	5
<i>Amelanchier laevis</i>	Allegheny Serviceberry	Native	22
<i>Berberis thunbergii</i>	Japanese Barberry	Non-Native	6
<i>Boehmeria cylindrica</i>	False Nettle	Native	118
<i>Carpinus caroliniana</i>	American Hornbeam	Native	44
<i>Carya cordiformis</i>	Bitternut Hickory	Native	3
<i>Carya glabra</i>	Pignut Hickory	Native	28
<i>Carya ovata</i>	Shagbark Hickory	Native	1
<i>Carya tomentosa</i>	Mockernut Hickory	Native	54
<i>Celastrus orbiculatus</i>	Oriental Bittersweet	Non-Native	98
<i>Clethra alnifolia</i>	Coastal Sweetpepperbush	Native	231
<i>Cornus florida</i>	Flowering Dogwood	Native	5
<i>Diervilla sessilifolia</i>	Southern Bush Honeysuckle	Native	1
<i>Elaeagnus umbellata</i>	Autumn Olive	Non-Native	232
<i>Euonymus alatus</i>	Burning Bush	Non-Native	14
<i>Euonymus americanus</i>	Bursting-Heart	Native	6
<i>Fagus grandifolia</i>	American Beech	Native	89
<i>Fraxinus pennsylvatica</i>	Green Ash	Native	13
<i>Hemerocallis fulva</i>	Orange Daylily	Non-Native	3
<i>Ilex opaca</i>	American Holly	Native	5

continued

Table 1.5. Continued.

Scientific Name	English Name	Native Status	Number of Stems
<i>Impatiens capensis</i>	Jewelweed	Native	167
<i>Kalmia latifolia</i>	Mountain-laurel	Native	19
<i>Leucothoe fontanesiana</i>	Highland Doghobble	Native	16
<i>Ligustrum spp.</i>	Privet sp.	Non-Native	9
<i>Lindera benzoin</i>	Spicebush	Native	531
<i>Liquidambar styraciflua</i>	Sweetgum	Native	13
<i>Liriodendron tulipifera</i>	Tulip Poplar	Native	11
<i>Lonicera japonica</i>	Japanese Honeysuckle	Non-Native	313
<i>Microstegium vimineum</i>	Japanese Stiltgrass	Non-Native	220
<i>Nyssa sylvatica</i>	Blackgum	Native	64
<i>Parthenocissus quinquefolia</i>	Virginia Creeper	Native	6
<i>Phragmites australis</i>	Common Reed	Non-Native	40
<i>Phytolacca americana</i>	American Pokeweed	Native	10
<i>Platanus occidentalis</i>	American Sycamore	Native	1
<i>Prunus serotina</i>	Black Cherry	Native	135
<i>Quercus alba</i>	White Oak	Native	3
<i>Quercus palustris</i>	Pin Oak	Native	3
<i>Quercus phellos</i>	Willow Oak	Native	2
<i>Quercus rubra</i>	Red Oak	Native	16
<i>Rhus glabra</i>	Smooth Sumac	Native	1
<i>Robinia pseudoacacia</i>	Black Locust	Native	2
<i>Rosa multiflora</i>	Multiflora Rose	Non-Native	1191
<i>Rubus occidentalis</i>	Black Raspberry	Native	25
<i>Rubus phoenicolasius</i>	Wine Raspberry	Non-Native	84
<i>Sassafras albidum</i>	Sassafras	Native	14
<i>Smilax rotundifolia</i>	Greenbriar	Native	354

continued

Table 1.5. Continued.

Scientific Name	English Name	Native Status	Number of Stems
<i>Taxus canadensis</i>	Canada Yew	Native	1
<i>Toxicodendron radicans</i>	Poison Ivy	Native	56
<i>Urtica dioica</i>	Stinging Nettle	Non-Native	16
<i>Vaccinium corymbosum</i>	Highbush Blueberry	Native	73
<i>Viburnum acerifolium</i>	Mapleleaf Viburnum	Native	101
<i>Viburnum dentatum</i>	Arrowwood Viburnum	Native	278
<i>Viburnum prunifolium</i>	Blackhaw Viburnum	Native	53
<i>Vitis spp.</i>	Grape sp.	Native	116

Table 1.6. Site means of vegetation characteristics. Values are mean \pm SE.

Site	Density (%)	Basal Area (m²/ha)	All Stems	Non-Native Stems	Percent Non-Native Stems (%)
Christina Creek 1	43.33 \pm 5.85	19.94 \pm 2.83	30.77 \pm 6.61	20.00 \pm 5.06	54.57 \pm 10.59
Christina Creek 2	52.43 \pm 6.18	16.78 \pm 2.30	47.36 \pm 15.43	25.36 \pm 11.60	37.96 \pm 8.50
Chrysler Woods	48.02 \pm 5.65	20.61 \pm 2.97	20.74 \pm 4.09	11.87 \pm 4.40	41.07 \pm 9.84
Coverdale	26.59 \pm 4.13	27.64 \pm 2.61	10.87 \pm 2.27	6.07 \pm 1.45	58.06 \pm 9.59
Dorothy Miller	19.31 \pm 3.17	28.30 \pm 2.77	4.22 \pm 1.91	2.43 \pm 1.15	36.69 \pm 11.78
Ecology Woods	38.17 \pm 4.86	30.06 \pm 2.19	22.50 \pm 4.19	6.60 \pm 4.07	19.5 \pm 7.44
Folk	18.64 \pm 3.13	29.93 \pm 1.64	6.14 \pm 2.12	0 \pm 0	0 \pm 0
Glasgow 1	18.43 \pm 3.09	28.95 \pm 1.92	8.36 \pm 2.31	0.68 \pm 0.61	3.23 \pm 2.40
Glasgow 2	28.59 \pm 3.73	26.11 \pm 1.37	8.96 \pm 2.22	0 \pm 0	0 \pm 0
Iron Hill 1	21.64 \pm 2.93	32.52 \pm 1.63	13.94 \pm 1.97	1.47 \pm 1.03	7.93 \pm 4.79
Iron Hill 2	25.50 \pm 4.65	28.17 \pm 1.85	5.27 \pm 1.99	0 \pm 0	0 \pm 0
Laird	32.89 \pm 6.91	22.90 \pm 3.00	37.16 \pm 18.83	21.39 \pm 15.35	32.21 \pm 10.57
Motor Pool	34.00 \pm 2.41	30.39 \pm 3.43	15.74 \pm 6.58	2.80 \pm 1.86	15.87 \pm 8.06
Phillips	49.84 \pm 4.57	24.28 \pm 1.88	22.47 \pm 4.65	9.34 \pm 3.68	34.29 \pm 9.89
Reservoir	18.74 \pm 5.62	25.27 \pm 1.96	11.60 \pm 5.17	8.80 \pm 4.86	21.87 \pm 10.04
Rittenhouse	18.19 \pm 3.08	30.69 \pm 2.26	7.54 \pm 1.28	0.47 \pm 0.24	6.85 \pm 4.48
Sunset Lake 1	18.57 \pm 3.41	31.30 \pm 2.63	3.34 \pm 1.48	0 \pm 0	0 \pm 0
Sunset Lake 2	11.70 \pm 2.67	29.24 \pm 1.73	2.67 \pm 0.74	0 \pm 0	0 \pm 0
Webb Farm	28.67 \pm 3.15	32.29 \pm 1.96	13.07 \pm 2.59	2.54 \pm 1.46	11.13 \pm 6.08
White Clay 1	21.37 \pm 5.17	23.82 \pm 2.20	5.74 \pm 2.10	3.47 \pm 1.48	32.53 \pm 11.56
White Clay 2	53.00 \pm 6.98	25.35 \pm 2.83	27.07 \pm 5.58	23.87 \pm 5.51	86.57 \pm 4.26

Table 1.7. Site means of snail characteristics, arranged by sites with the most to least abundance. Values are mean \pm SE.

Site	Abundance	Weight (g)	Genera
Coverdale	22.50 \pm 5.30	0.56 \pm 0.18	1.38 \pm 0.20
Dorothy Miller	18.50 \pm 10.30	0.19 \pm 0.08	1.29 \pm 0.32
Iron Hill 1	13.27 \pm 3.04	0.08 \pm 0.02	2.87 \pm 0.46
White Clay 2	10.74 \pm 1.51	0.23 \pm 0.07	3.80 \pm 0.33
White Clay 1	6.74 \pm 1.46	0.09 \pm 0.05	2.27 \pm 0.56
Reservoir	5.14 \pm 1.21	0.10 \pm 0.06	1.87 \pm 0.34
Glasgow 1	4.80 \pm 1.39	0.06 \pm 0.03	2.07 \pm 0.38
Webb Farm	4.14 \pm 1.12	0.04 \pm 0.03	1.80 \pm 0.39
Sunset Lake 1	2.87 \pm 0.99	0.01 \pm 0.003	1.47 \pm 0.48
Folk	2.80 \pm 0.60	0.11 \pm 0.07	1.34 \pm 0.25
Christina Creek 2	2.65 \pm 1.15	0.04 \pm 0.02	1.06 \pm 0.35
Rittenhouse	2.40 \pm 0.62	0.11 \pm 0.04	1.00 \pm 0.26
Laird	1.54 \pm 0.76	0.02 \pm 0.01	1.08 \pm 0.51
Glasgow 2	1.47 \pm 0.55	0.01 \pm 0.002	0.87 \pm 0.27
Iron Hill 2	1.40 \pm 0.42	0.03 \pm 0.02	1.07 \pm 0.33
Chrysler Woods	1.00 \pm 0.44	0.02 \pm 0.007	0.54 \pm 0.19
Christina Creek 1	1.00 \pm 0.45	0.05 \pm 0.02	0.53 \pm 0.21
Sunset Lake 2	0.87 \pm 0.42	0.01 \pm 0.001	0.60 \pm 0.31
Phillips	0.80 \pm 0.49	0.01 \pm 0.005	0.34 \pm 0.16
Ecology Woods	0.70 \pm 0.31	0.05 \pm 0.03	0.50 \pm 0.20
Motor Pool	0.54 \pm 0.29	0.01 \pm 0.001	0.40 \pm 0.19

Table 1.8. The avian community species richness, Shannon Index, and species evenness for all 21 field sites.

Site	Avian Species Richness	Shannon Index	Avian Species Evenness
Christina Creek 1	11	0.956	0.235
Christina Creek 2	18	1.005	0.151
Chrysler Woods	12	0.934	0.211
Coverdale	15	1.038	0.187
Dorothy Miller	9	0.834	0.254
Ecology Woods	20	1.048	0.142
Folk	11	0.903	0.223
Glasgow 1	12	0.963	0.217
Glasgow 2	17	1.089	0.173
Iron Hill 1	14	0.976	0.188
Iron Hill 2	10	0.831	0.228
Laird	14	1.029	0.198
Motor Pool	14	0.982	0.189
Phillips	16	1.055	0.178
Reservoir	12	1.015	0.228
Rittenhouse	15	1.010	0.182
Sunset Lake 1	11	0.974	0.239
Sunset Lake 2	10	0.925	0.251
Webb Farm	15	1.049	0.189
White Clay 1	13	0.981	0.204
White Clay 2	11	0.841	0.210

Table 1.9. Beta estimates for each observational (p) covariate for the top models of the 13 focus forest songbird species. Observational global models (p(global)) included cloud+date+time+temp. Abundance global models (λ (global)) included forest100+patch_ha+snwt+exhca+prctnnstems+ba+density+age.

Species	Top Model	p(cloud)	p(date)	p(temp)	p(time)
AMRO	$\lambda(\text{forest100+patch_ha})p(\text{global})$	-0.04	0.29	0.13	0.19
	$\lambda(\text{global})p(\text{global})$	-0.04	0.30	0.13	0.18
BHCO	$\lambda(\text{global})p(\text{global})$	0.09	-0.59	0.39	-0.40
CARW	$\lambda(\text{global})p(\text{date})$.	0.25	.	.
EATO	$\lambda(\text{global})p(.)$
EAWP	$\lambda(\text{snwt})p(\text{date})$.	-0.25	.	.
GRCA	$\lambda(\text{global})p(\text{global})$	0.09	-0.34	0.09	0.06
HAWO	$\lambda(\text{global})p(\text{date})$.	0.39	.	.
NOCA	$\lambda(\text{global})p(\text{date})$.	-0.18	.	.
OVEN	$\lambda(\text{global})p(\text{global})$	0.09	-0.46	-0.15	-0.12
RBWO	$\lambda(\text{snwt})p(\text{date})$.	-0.27	.	.
REVI	$\lambda(\text{global})p(.)$
SCTA	$\lambda(\text{global})p(.)$
WOTH	$\lambda(\text{global})p(\text{time})$.	.	.	-0.09

Table 1.10. Top ranked models ($\Delta AICc \leq 2$) of variables affecting the abundance of 13 forest songbird species within 21 forested fragments in Newark, Delaware. Table presents the number of parameters in the model (K), Akaike's Information Criterion (AICc), the difference in AIC value compared to the top-ranked model ($\Delta AICc$), the AIC model weight (AICwt), and the cumulative AIC weight (cumltvWt). Lambda (λ) indicates abundance covariates, and p indicates detection covariates. Observational global models (p(global)) included cloud+date+time+temp. The full list of all models can be found in Appendix B.

Species	Model	K	AICc	$\Delta AICc$	AICwt	cumltvWt
AMRO	$\lambda(\text{forest100+patch_ha})p(\text{global})$	8	2340.61	0	0.53	0.53
	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{global})$	14	2340.85	0.24	0.47	1
BHCO	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{global})$	14	492.55	0	1	1
CARW	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{date})$	11	923.29	0	1	1
EATO	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(.)$	10	541.45	0	0.83	0.83
EAWP	$\lambda(\text{snwt})p(\text{date})$	4	894.19	0	0.566	0.57
GRCA	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{global})$	14	846.9	0	1	1
HAWO	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{date})$	11	800.39	0	0.98702	0.99
NOCA	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{date})$	11	1593.76	0	1	1
OVEN	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{global})$	14	565.01	0	1	1
RBWO	$\lambda(\text{snwt})p(\text{date})$	4	1058.88	0	0.7554	0.76
REVI	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(.)$	10	1436.48	0	0.91	0.91
SCTA	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(.)$	10	565.39	0	0.98	0.98
WOTH	$\lambda(\text{forest100+patch_ha+snwt+exchca+prctnnstem+ba+density+age})p(\text{time})$	11	1152.35	0	1	1

Table 1.11. Beta estimates for each abundance (λ) covariate for the top models of the 13 focus forest songbird species. Observational global models (p(global)) included cloud+date+time+temp. Abundance global models (λ (global)) included forest100+patch_ha+snwt+exchca+prctnnstems+ba+density+age.

Species	Top Model	$\lambda(\text{forest100})$	$\lambda(\text{patch_ha})$	$\lambda(\text{snwt})$	$\lambda(\text{exchca})$	$\lambda(\text{prctnnstem})$	$\lambda(\text{ba})$	$\lambda(\text{density})$	$\lambda(\text{age})$
AMRO	$\lambda(\text{forest100+patch_ha})\text{p}(\text{global})$	-0.04	-0.47
	$\lambda(\text{global})\text{p}(\text{global})$	0.01	-0.55	-0.01	0.06	0.11	0.16	0.06	0.07
BHCO	$\lambda(\text{global})\text{p}(\text{global})$	0.72	-0.14	0.74	0.08	-1.82	-0.26	0.61	-0.24
CARW	$\lambda(\text{global})\text{p}(\text{date})$	-0.47	0.01	0.09	0.34	-0.12	-0.43	-0.05	0.15
EATO	$\lambda(\text{global})\text{p}(\cdot)$	0.01	0.38	0.11	-0.67	0.83	-0.50	0.10	-0.05
EAWP	$\lambda(\text{snwt})\text{p}(\text{date})$.	.	-0.28
GRCA	$\lambda(\text{global})\text{p}(\text{global})$	-0.54	0.34	0.06	-0.21	-0.84	0.59	1.46	-0.51
HAWO	$\lambda(\text{global})\text{p}(\text{date})$	0.07	0.44	-0.60	-0.02	0.12	0.41	0.10	-0.14
NOCA	$\lambda(\text{global})\text{p}(\text{date})$	-0.31	0.04	0.10	0.41	-0.25	-0.40	-0.04	-0.29
OVEN	$\lambda(\text{global})\text{p}(\text{global})$	1.32	0.59	1.43	-0.11	-0.15	0.97	1.60	2.35
RBWO	$\lambda(\text{snwt})\text{p}(\text{date})$.	.	0.19
REVI	$\lambda(\text{global})\text{p}(\cdot)$	0.08	0.20	-0.20	0.00	0.11	0.27	-0.19	-0.34
SCTA	$\lambda(\text{global})\text{p}(\cdot)$	0.59	0.53	-0.12	-0.61	-0.05	0.42	0.14	-0.31
WOTH	$\lambda(\text{global})\text{p}(\text{time})$	0.55	-0.05	0.27	0.11	0.37	0.37	0.55	1.02

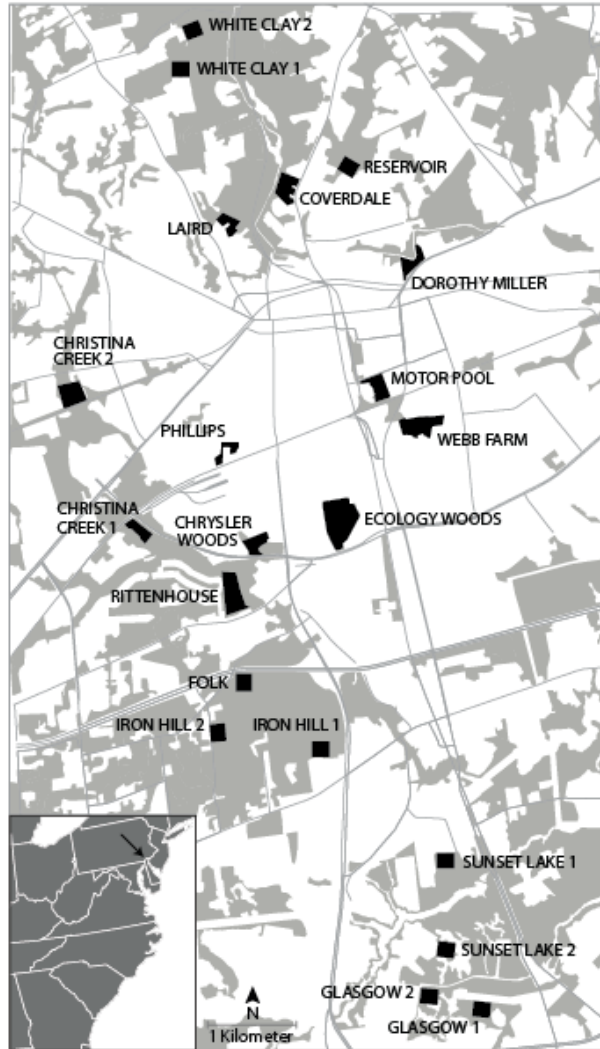


Figure 1.1. Map of the 21 sites, located within Newark, Delaware, USA. Gray polygons represent forested land cover. Black polygons represent the areas within the forested land cover, which served as each of our sites. All sites are labeled with their specific names. The enclosed map is the location of the study region within the eastern United States.

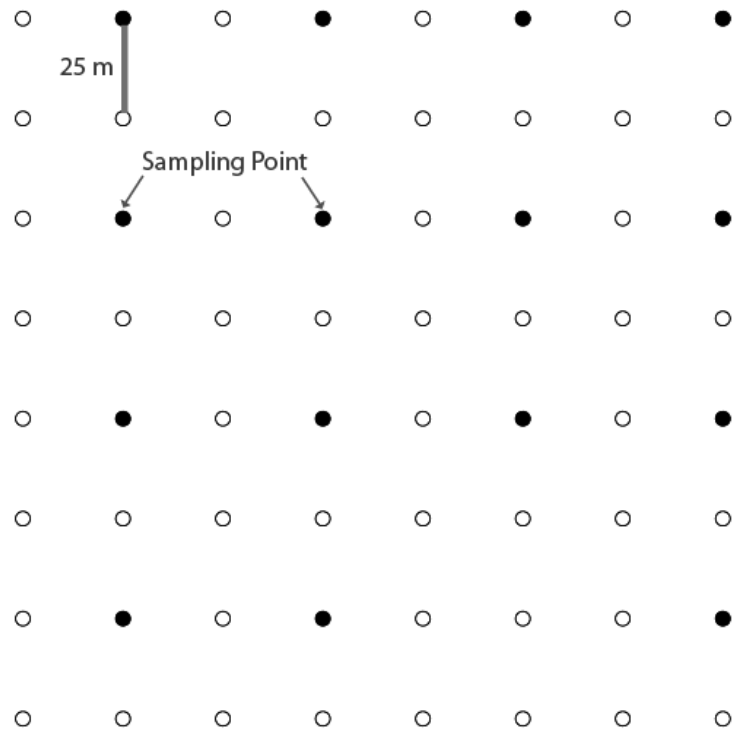


Figure 1.2. Example of grid delineation pattern for the “Folk” site. Flags (open circles) were placed in a 25 m grid. For each site, 13 to 20 randomly chosen flags (filled circles) served as sampling locations.

Chapter 2

ENVIRONMENTAL EFFECTS ON DAILY NEST SUCCESS OF FOUR SONGBIRDS IN URBAN FOREST PATCHES

Introduction

In an increasingly urbanized and fragmented world, habitats have been greatly altered at the detriment of many bird populations. In the northeastern United States, the causes of neotropical migrant bird declines have specifically been attributed to habitat fragmentation (Robinson et al. 1995), which consequently increases nest predation (Wilcove 1985, Robinson and Wilcove 1994) and Brown-headed Cowbird parasitism (*Molothrus ater*; Brittingham and Temple 1983). Nest predation is the leading cause of nest failure for songbirds (Martin 1993), which may be strongly influenced by a number of landscape and vegetation variables within fragmented habitats.

Forest fragmentation causes a reduction in forest cover and patch size, which in turn changes the structure and composition of vegetation and animal communities. Compared to the forest interior, predator species' abundance and predation rates increased along forest edges (Wilcove 1985). Wilcove (1985) also detected greater predation rates within areas near suburban neighborhoods, compared to rural woodlots. Common nest predators within fragmented and urban habitats include raccoons (*Procyon lotor*; Bider 1968, Pedlar et al. 1997, Dijak and Thompson 2000), birds within the Corvidae family (Marini et al. 1995, Chalfoun et al. 2002a), snakes (Durner and Gates 1993, Cox et al. 2012), domestic cats (*Felis catus*; Wilcove

1985, Roth and Johnson 1993, Haskell et al. 2001), and a suite of small mammals (Sekgororaone and Dilworth 1995). Predators can have a significant impact on nesting bird populations by reducing nest success, thus impairing songbird populations within fragmented systems.

Nest predation rates can be influenced by changes within the structural and vegetation characteristics of the fragmented landscape (Martin and Roper 1988, Robinson et al. 1995, reviewed in Chalfoun et al. 2002b). Mammalian and avian nest predators may cue into different physical habitat characteristics, due to habitat preferences and mobility factors. Forest stand density may drive mammalian predator abundances, particularly squirrels and chipmunks (Family Sciuridae), due to their associations with woody debris-rich habitats (DeGraaf and Rudis 1986, King et al. 1998). Increases in forest stand density have been linked to abundances in red squirrels (*Tamiasciurus hudsonicus*) and eastern chipmunks (*Tamias striatus*) (King et al. 1998), two common nest predators. In commercially thinned forested plots, depredation rates on Wood Thrush (*Hylocichla mustelina*) nests also increased within areas with a greater basal area (Thatcher 2007). The height of the nest is also related mammalian predation (Thurber et al. 1994, Schmidt and Whelan 1999). Nests located higher from the ground would generally have less encounters with mammalian predators (Schmidt 1999), reducing the chance of predation. Daily mortality rates of American Robin (*Turdus migratorius*) nests were greater with nests located closer to the forest floor (Schmidt and Whelan 1999). Nests within vegetation with sharp thorns also may deter mammalian predators (Schmidt and Whelan 1999).

With the capability of flight, avian nest predators have the advantage to search for and predate nests aerially. Successional habitats tend to have greater ground cover and shrub densities (Seitz and Zegers 1993), which would benefit the nesting bird by concealing its nest from avian predators. Basal area can be used to assess the successional status of the forest (Seitz and Zegers 1993), with younger successional habitats having less basal area (Auken and Bush 1985). Nest predation rates are also generally reduced in areas with greater forest cover (Robinson et al. 1995) and lateral concealment (Martin and Roper 1988, Hoover and Brittingham 1998). Unlike mammalian predation, avian nest predation is still a threat for nests at greater heights (Thurber et al. 1994), especially in areas with less vegetation density and more perching locations (Schmidt 1999).

Invasions by non-native plants is another alteration of the vegetation structure and composition in fragmented forests, especially along forest edges (Saunders et al. 1991), that can influence nest predation rates directly or indirectly (Schmidt and Whelan 1999, Remeš 2003, Borgmann and Rodewald 2004). Increases in incident light at the edge of fragments promote vegetative growth (Saunders et al. 1991, Murcia 1995), which, combined with disturbances and removal of native vegetation, makes the area prone to invasion (Hobbs and Huenneke 1992). Many non-native invasive shrubs have the potential to form dense understories, such as multiflora rose (*Rosa multiflora*) and Japanese honeysuckle (*Lonicera japonica*) (Morse and Robinson 1999). This abundance of dense vegetation may attract understory birds to build nests (Rodewald et al. 2010), especially for species which prefer a dense habitat structure. Birds could be drawn to these non-native species due to their abundance of

food (Davis 2011), earlier leafing (Remeš 2003, Rodewald et al. 2010), or abundance of nesting habitat. However, these non-native dominant habitats may overall act as an ecological trap (Gates and Gysel 1978) and limit the reproductive success, as seen in a variety habitats and bird species (Table 2.1; Remeš 2003, Borgmann and Rodewald 2004, Lloyd and Martin 2005, Ortega et al. 2006, Nordby et al. 2009, Rodewald et al. 2010).

The causes of reduced avian reproductive success in invaded habitats can be attributed to a variety of factors. Increased nest density due to non-native shrub habitats may lure more nest predators into the area, thus causing greater predation events (Martin and Page 1965, Martin 1996, Remeš 2003, Rodewald et al. 2010). The differing physical characteristics of non-native shrubs, and lower nest placement within these species, may also allow greater predator movement within areas dominated by these species (Schmidt and Whelan 1999, Borgmann and Rodewald 2004).

In addition to nest predation, soil acidification has recently been linked to the decrease in the reproductive success (Graveland et al. 1994) and overall abundance of a variety of bird species (Hames et al. 2002, Pabian and Brittingham 2007, 2011). The availability of soil calcium is limited within acidified habitats throughout the eastern United States (NADP 2007). Calcium is an essential nutrient for avian reproduction, specifically for egg formation and skeletal development of the embryo. In 1997, the first experimental evidence was published supporting the idea that calcium availability for birds limits reproductive output and success (Graveland and Drent 1997). Multiple studies since have shown a strong relationship between avian

reproductive success and the availability of calcium, provided in various forms (Graveland and Drent 1997, Tilgar et al. 2002, Bidwell and Dawson 2005). Even after the egg laying period, nestlings require sufficient calcium over the nesting period for proper bone development (Beintema et al. 1997, Tilgar et al. 2004) and growth (Ormerod et al. 1991, Beintema et al. 1997)

Herein I question what types of environmental factors could drive daily nest failure rates on urban songbirds. I hypothesized that songbird nest success is dependent on the calcium availability and vegetation structure around the nest within the forest fragment, as well as the forest cover within the landscape. In this study, I utilized a novel Markov chain algorithm software, MCestimate (Etterson 2010) to determine daily and overall probabilities of nest success and failure due to predation. I concentrated my efforts on the following species' nests, due to their abundances within my sites: American Robin, Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), and Wood Thrush.

Methods

Study Area

In 2010 and 2011, I established 21 sites within 12 urban temperate deciduous forest fragments located in Newark, Delaware, USA. To standardize edge effects, I selected sites which had at least one edge, boarding residential or agricultural lands. The dominant trees in these sites were tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), blackgum (*Liquidambar styraciflua*), red oak (*Quercus rubra*), and white oak (*Quercus alba*). The dominant species in the shrub layer were

spicebush (*Lindera benzoin*), arrowwood viburnum (*Viburnum dentatum*), and coastal sweetpepperbush (*Clethra alnifolia*). Common mammals observed within the sites included gray squirrels (*Sciurus carolinensis*) and domestic cats.

Soil Sampling

At each sampling location, two field technicians extracted five soil core samples from the top 10 cm of the soil, and mixed the samples together to get a testable heterogeneous soil sample. The University of Delaware Soil Laboratory (UDSL; Newark, DE, USA) oven-dried the samples for 72 hours, ground and sieved the soils to 2 mm partials. The UDSL measured exchangeable calcium via the Mehlich-III method (Mehlich 1984).

In order to determine the soil characteristics for each nest, I calculated a 25 m buffer around each nest using ArcGIS 9.0 (Environmental Systems Research Institute Inc. (ESRI), Redlands, CA). I kriged (Burrough 1986) the values of each soil property via ordinary kriging method with a spherical semivariogram, with an output cell size set at the default 19.7831 value (ESRI 2009). To keep the kriged values restrained to the site's area, I used each site's polygon as a mask. Then I used Zonal Statistics (ESRI 2009) in the Spatial Analyst extension in ArcGIS to calculate averages for these characteristics from within all buffered nest locations.

Vegetation Sampling

I sampled the vegetation which supported each individual nest, while some nests required identification of multiple species. I utilized the U.S. Department of Agriculture PLANTS Database to determine if each species was native to Delaware

(USDA 2006). To measure forest stand density, I determined tree basal area with a Factor-10 prism (Mannel et al. 2006) above the sampling point flag. To estimate vertical vegetation density, I used a 2.5 m tall vegetation profile board, “Nudd’s Board”, and measured the percentage of the board obscured by vegetation 15 m from the sampling point flag in each of the four cardinal directions (Nudds 1977).

I kriged (Burrough 1986) the vegetation properties of basal area and vertical vegetation density across my sites with the same methods as I used for my kriged soil properties. I used Zonal Statistics (ESRI 2009) in the Spatial Analyst extension in ArcGIS to calculate averages for these characteristics from within all buffered nest locations. In order to determine forest cover on the landscape, I calculated rasterized landscape values (Fry et al. 2011) by running 100 meter buffers around the site’s perimeter within ArcGIS 9.0 (Environmental Systems Research Institute Inc., Redlands, CA; ESRI 2009). I selected a buffer of 100 meters because any buffer size greater than this resulted in overlapping buffers between neighboring sites. After I created a buffer around the site, I used Zonal Statistics (ESRI 2009) in the Spatial Analyst extension to ArcGIS to calculate the percent forest cover within the sites’ buffer. I estimated forest patch size by selecting the appropriate forest patch polygon and calculating the area value within the attribute table in ArcGIS 9.0.

Nest Monitoring

I searched for nests and observed their activity during 2010 and 2011, while an independent research team sampled Ecology Woods during 2008 and 2009. I only analyzed nests of American Robin, Gray Catbird, Northern Cardinal, and Wood

Thrush for nest failure rates because only six nests or fewer were found for all other species. I searched for and observed nests five to six times a week, which began in April and ended in August each year. Once a nest was found, I marked the nest with a wire flag, placed at least 1 m from the nest location. I visually estimated the height of the nest from the ground and recorded GPS locations for all nests.

I checked the status of each nest at least every two to three days to observe their progression. I monitored nests until success or failure. I defined a successful nest to be one in which at least one host species nestling fledged. I classified nest failure fates into two categories: predation and abandoned. I defined predation to be one which contents were absent premature to the nestlings expected fledge date, nestlings were found dead within the nest, or if eggs had puncture holes. I defined abandoned to be if the nest had egg contents on a visit, then over time the eggs were continued to be found, usually cold, and without either adult observed in the nest's vicinity. For Wood Thrush nests, I used an additional nest failure for nests which only fledged Brown-headed Cowbirds nestlings.

MCestimate

I used MCestimate (Etterson 2010), a Markov chain algorithm program (Etterson et al. 2007a, Etterson et al. 2007b), to estimate daily nest failure rates due to specific covariates. I analyzed the response variable as a binomial (success/failure) response. The nests considered to be abandoned or ones which only had Brown-headed Cowbirds fledge did not have a sample size large enough to analyze as

independent failure categories. I determined that there needed to be at least 20 nests within each failure category to run independently (Hensler and Nichols 1981).

I constructed ten models *a priori* using eight site, nest, and landscape covariates (Table 2.2) to test the following hypothesis related to nest failure for each of the four species. To test for the effects of soil chemistry, I ran one model to test how exchangeable calcium affected daily nest survival. To test for the effects of surrounding vegetation, I ran two models to test for the effects of vertical vegetation density and basal area on nest survival. To test for the effects of nest characteristics, I ran three models to test for the height of the nest, the native or non-native status of the nest's supporting vegetation, and the date within the year the nest was active. The date covariate was a quantitative covariate which varied within nests with every day of the season, rather than serving as a fixed quantitative variable. To test for landscape-level effects on nest success, I ran two models to test for the effects of the forest patch area and the percentage of forest cover within 100m of the site in which the nest was located. I also included a constant (.) and global model. Models with an Akaike's Information Criterion ($\Delta AICc$) value less than 2 were considered to be equally plausible as a cause for daily nest failure (Burnham and Anderson 1998). To determine the chance of nest success over the nesting period, I utilized mean nest cycle (number of days from incubation to fledging) durations for each species (Baicich and Harrison 2005).

Results

Vegetation

I observed 35 vegetation species used to support the nests, five of which were non-native (Table 2.3). The most common non-native shrub in which the nests were built was multiflora rose, followed by oriental bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle, autumn olive (*Elaeagnus umbellata*), and white mulberry (*Morus alba*).

American Robin

Throughout the 2010 and 2011 field seasons, I found 58 American Robin nests, 24 (41.4%) were successful. I determined 33 (56.9%) nests were predated and one (1.7%) was abandoned. I detected 23.4% of the American Robin nests in American beech (*Fagus grandifolia*) and 13.8% in non-native shrubs (Table 2.3). Multiflora rose was the most common non-native shrub (8.6%) in which I detected an American Robin nest. Exchangeable calcium was the strongest predictor of daily nest failure for the American Robin (Table 2.4), and was positively related (Fig. 2.1; $\beta = 0.30 \pm 0.12$ SE). The daily nest survival rate was 0.969 ± 0.006 (probability \pm standard error), with a 0.408 ± 0.065 rate of fledging within the exchangeable calcium parameter over a 28-day nesting period (Baicich and Harrison 2005).

Gray Catbird

Over the 2008- 2011 field seasons, I found 145 Gray Catbird nests, 66 (45.5%) of which were successful. I determined 73 (50.3%) nests were predated and 6 (4.1%) were abandoned. I detected 44.1% of the Gray Catbird nests in non-native

shrubs and the most common shrub was multiflora rose (38.2% nests; Table 2.3). Julian date was the strongest predictor of daily nest failure for the Gray Catbird (Table 2.4), and was positively related (Fig. 2.2; $\beta = 0.02 \pm 0.005$ SE). For Gray Catbirds, the daily survival rate was 0.971 ± 0.004 (probability \pm standard error), with a 0.413 ± 0.042 chance of fledging within the parameter of Julian date over a 24-day nesting period (Baicich and Harrison 2005).

Northern Cardinal

Throughout the 2010 and 2011 field seasons, I found 52 Northern Cardinal nests, 22 (42.3%) of which were successful. I determined 27 (51.9%) nests were predated and 3 (5.8%) were abandoned. I detected 32.7% Northern Cardinal nests in a non-native shrub and the most common shrub was multiflora rose (20.3% nests; Table 2.3). Exchangeable calcium was the top model of daily nest failure for the Northern Cardinal (Table 2.4), and negatively related (Fig. 2.3a; $\beta = -0.18 \pm 0.083$ SE). The daily nest survival rate was 0.967 ± 0.006 (probability \pm standard error), with a 0.472 ± 0.069 rate of fledging within the exchangeable calcium parameter over a 22-day nesting period (Baicich and Harrison 2005).

Wood Thrush

Over the 2008- 2011 field seasons, I found 119 Wood Thrush nests, 43 (36.1%) of which were successful and 66 (55.5%) were predated. I detected two (1.7%) abandoned nests and 8 (6.7%) nests which fledged only Brown-headed Cowbird nestlings. I detected 29.8% Wood Thrush nests in American Beech and 5.8% nests a non-native plant. The most common non-native shrub in which I

detected Wood Thrush nests was autumn olive (2.5%). I observed 67% Wood Thrush nests that contained at least one Brown-headed Cowbird egg. Nest height was the top model of daily nest failure for the Wood Thrush (Table 2.4), and positively related (Fig. 2.4a; $\beta = 0.081 \pm 0.041$ SE). Nest height ranged from 1 to 13 m, with a mean of 3.54 ± 0.2 m (probability \pm standard error). The daily survival probability for the nest height model was $96.5\% \pm 0.4$. Over a 25-day nest cycle (Baicich and Harrison 2005), there was a $41.2\% \pm 4.5$ chance of fledging due to nest height. Vertical vegetation density (Fig. 2.4b; $\beta = -0.022 \pm 0.014$ SE) and the null model were models which were equally as plausible. Within the vertical vegetation density parameter, the daily survival probability was $96.5\% \pm 0.4$. In a 25-day nest cycle (Baicich and Harrison 2005), there was a $41.0\% \pm 4.6$ chance of fledging due to vertical vegetation density.

Discussion

There was no one universal driver of nest success, however nest failure was influenced by stand structure and nesting habitats for the observed species, with the exception of the Gray Catbird. Areas with greater soil calcium tend to have greater shrub densities (Rega Chapter 1), consequently benefiting nesting birds by concealing nests from predators (Thurber et al. 1994, Hoover and Brittingham 1998, Small et al. 2007) and providing calcium sources for reproductive efforts and nestling nutritional requirements (Ormerod et al. 1991, Beintema et al. 1997, Graveland and Drent 1997, Tilgar et al. 2004). Each observed species responded differently in magnitude and direction to the habitat covariates, potentially caused by habitat nesting preferences.

The fates of American Robin and Northern Cardinal nests were driven by the availability of soil calcium surrounding their nests. American Robin nest success responded negatively to the amount of exchangeable calcium surrounding the nest. The majority (61%) of American Robin nests were found in one calcium-poor site, "Ecology Woods" (Rega Chapter 1). The success or failure of nests located in Ecology Woods could have driven the results obtained, due to differences in predation rates or resource availability within this one site. Regardless, American Robins are considered versatile feeders (Paszkowski 1982) within urban environments (Sallabanks and James 1999), so I assume that they can benefit from anthropogenic calcium sources within suburban and urban environments. Thus, American Robins may not be as constrained by calcium within their nesting sites due to this generality.

Contrary to the American Robin, Northern Cardinal nest success was positively related to the availability of exchangeable calcium within the soil surrounding their nests. Northern Cardinal nests should have a greater chance of success in calcium-rich areas due to the strong link between reproductive success and calcium availability (Graveland and van der Wal 1996, Graveland and Drent 1997, Tilgar et al. 2002). Northern Cardinals with nests located in calcium-rich habitats may benefit from a larger calcium-rich prey source for females laying or tending to their young (Conner et al. 1986, Gärdenfors 1992, Graveland et al. 1994, Gärdenfors et al. 1995, Pabian and Brittingham 2007). Time spent searching for calcium-rich prey should be reduced in calcium-rich areas (Graveland and Berends 1997), allowing more time for nest defense by adults. Thus, nests located in calcium-rich areas would have

sufficient nutrition for nestling development and guarded more frequently from nest predators, allowing for greater nest success.

The driver of Gray Catbird nest failure was the date throughout its nesting period. Trends in seasonal declines of reproductive success have been widely studied (Small et al. 2007, reviewed in Verhulst and Nilsson 2008). Low reproductive success in the late breeding season could be attributed to a reduction in parental effort during molting (Verhulst and Nilsson 2008) and an increase in predation rates (Caccamise 1978, Schaub et al. 1992, Götmark 2002). With the progression of the breeding season, the frequency of nests that contain nestlings, rather than eggs, increases. Predators can cue into the begging calls of nestlings (Young 1963, Schaub et al. 1992) or the increased parental visitation to the nest (Young 1963), which overall increases predator detectability and predation events throughout the season. Midseason peaks in daily predation have been observed in avian, snake, and rodent predators for Indigo Bunting (*Passerina cyanea*) and Acadian Flycatcher (*Epidonax virescens*) nests (Cox et al. 2012), however predator communities and abundances may range widely across different habitat types.

Nest height and vertical vegetation density surrounding Wood Thrush nests were equally probable drivers for daily nest predation. Both characters of the nest and the surrounding vegetation contribute to the nest detectability of predators, particularly avian predators. Nests with greater vegetation concealment tend to be more successful than those in habitats with less (Thurber et al. 1994, Hoover and Brittingham 1998, Small et al. 2007), or patchy (Joern and Jackson 1983) vegetation. My results oppose Newell and Kostalos' (2007) findings with a positive relationship

between nest success and nest height, and a negative relationship with shrub density in an urban Wood Thrush population. This difference in results may be due to the predators present in either location. Nests located higher in the canopy, and with less vegetation to obscure the nest, could be at a greater risk in areas with more avian nest predators. Data on the predator community and predation rates by specific taxa at either study area need to be measured in order to determine these opposing results.

Brown-headed Cowbird parasitism was prominent throughout the Wood Thrush nests in all of the study sites, with 67% of Wood Thrush nests containing at least one Brown-headed Cowbird egg. In particular, the site “Ecology Woods” had the most brood parasitism at a rate of 90.2% of nests. This is in contrast to the lack of Brown-headed Cowbird parasitism that Longcore and Jones (1969) reported in the Ecology Woods in 1965-1966. Even with such high rates of brood parasitism, the majority of nest failures were attributed to predation. Activity at the nest caused by Brown-headed Cowbirds could potentially have influenced predation rates for the Wood Thrush, especially those nesting in less dense habitats. With more activity in these locations, avian predators should have a greater chance of detecting and predating the nest (Joern and Jackson 1983, Martin 1993, Thurber et al. 1994), which results in decreased nest success.

Each of the four species studied failed to have the native status of the nest substrate as their top model for daily nest failure. In previous literature, Northern Cardinals (Borgmann and Rodewald 2004, Rodewald et al. 2010) and American Robins (Schmidt and Whelan 1999) had significantly lower reproductive success in areas with extensive invasive plant cover. However, two species (Gray Catbird and

Northern Cardinal) out of the four studied nested most often in multiflora rose, a highly invasive non-native species, which had limited influence on nest failure rates. I may not have observed a strong suppression of nest success by non-native plants because of the wide range of physical characteristics the non-native plants exhibited throughout my study area. For example, Japanese honeysuckle greatly differs from multiflora rose mainly due to a lack of thorns. In a similar study in Ohio, Northern Cardinals fledged 20% fewer young in nests constructed in exotic honeysuckle species, however there was no difference in fledge rate for individuals nesting in multiflora rose (Rodewald et al. 2010). More studies on the differences of reproductive success should be completed to analyze differences in nest success among native and non-native shrubs of similar physical structures.

Managing for nest sites is important in regards to maintaining bird populations by supporting their breeding efforts. Fragmentation and overall loss of breeding habitats may result in the creation of less preferential habitats, which would force species to nest in locations which give less support for their reproductive efforts (Martin 1993). Each species may respond to different habitat cues, however many habitat variables are universally detrimental to nest success, such as the creation of openings in forested landscapes (Flaspohler et al. 2001). Calcium sources also need to be maintained within these landscapes, via a continual reduction in acid deposition rates, in order to give nesting birds sufficient nutritional resources. Overall, care should be taken to create management plans which benefit a wide range of species, such as maintaining continuous forests, supporting vegetative diversity within the landscape, and continuing to reduce anthropogenic acidification of forests.

Table 2.1. List of bird species which experienced reduced reproductive success within listed non-native shrub(s), as compared to native shrubs.

Bird Species	Non-Native Shrub	Location	Habitat	Authors
Alameda Song Sparrow (<i>Melospiza melodia pusillula</i>)	Atlantic Cordgrass (<i>Spartina alterniflora</i>)	California, USA	Tidal Marsh	Nordby et al. 2009
American Robin (<i>Turdus migratorius</i>)	Amur Honeysuckle (<i>Lonicera maackii</i>)	Illinois, USA	Forest	Schmidt and Whelan 2001
	Common Buckthorn (<i>Rhamnus cathartica</i>)	Illinois, USA	Forest	Schmidt and Whelan 2001
Blackcap (<i>Sylvia atricapilla</i>)	Black Locust (<i>Robina pseudoacacia</i>)	Czech Republic	Floodplain Forest	Remeš 2003
Chestnut-collared Longspur (<i>Calcarius ornatus</i>)	Crested Wheatgrass (<i>Agropyron cristatum</i>)	Montana, USA	Grassland	Lloyd and Martin 2005
Chipping Sparrow (<i>Spizella passerina</i>)	Spotted Knapweed (<i>Centaurea maculosa</i>)	Montana, USA	Savanna	Ortega et al. 2006
Northern Cardinal (<i>Cardinalis cardinalis</i>)	Grouped: Amur Honeysuckle (<i>Lonicera maackii</i>), Tatarian Honeysuckle (<i>Lonicera tatarica</i>), Multiflora Rose (<i>Rosa multiflora</i>)	Ohio, USA	Riparian Forest	Borgmann and Rodewald 2004
	Amur Honeysuckle (<i>Lonicera maackii</i>)	Ohio, USA	Riparian Forest	Rodewald et al. 2010

Table 2.2. Nest covariates measured at each nest for use in developing daily nest success probability for four forest bird species. Codes and measurement units for each covariate are listed, as well as their scope in which they were measured.

Covariate	Code	Scope	Unit
Basal area	ba	50m buffer of the nest	m ² /ha
Exchangeable calcium	exchca	50m buffer of the nest	meq/100g
Forest patch area	patchsize	Landscape	hectare
Height of nest	height	Nest	Meters
Julian date	date	Nest	Julian date
Native or non-native plant	nnplant	Nest	Binomial
Percent forest cover	forestcover	100m buffer of the site	%
Vertical vegetation density	density	50m buffer of the nest	%

Table 2.3. All vegetation species used to support American Robin, Gray Catbird, Northern Cardinal, and Wood Thrush nests. Each species was determined to be native or non-native to the study region (Delaware), according to the USDA PLANTS Database. Quantities of nests found in their respective vegetation are listed by avian species. Nests were supported by one or two vegetation species.

Latin Name	Species Name	Native Status	American Robin	Gray Catbird	Northern Cardinal	Wood Thrush
<i>Acer negundo</i>	Boxelder	Native			1	
<i>Acer rubrum</i>	Red Maple	Native	6	1	5	5
<i>Amelanchier sp.</i>	Serviceberry sp.	Native		1		
<i>Carpinus caroliniana</i>	American Hornbeam	Native	6	1	3	10
<i>Carya glabra</i>	Pignut Hickory	Native		2		
<i>Carya tomentosa</i>	Mockernut Hickory	Native			2	4
<i>Celastrus orbiculatus</i>	Oriental Bittersweet	Non-Native		2	2	2
<i>Clethra alnifolia</i>	Coastal Sweetpepperbush	Native		8		3
<i>Cornus florida</i>	Flowering Dogwood	Native	1	1		
<i>Crataegus sp.</i>	Hawthorn sp.	Native			1	1
<i>Elaeagnus umbellata</i>	Autumn Olive	Non-Native				3
<i>Fagus grandifolia</i>	American Beech	Native	17	2	6	36
<i>Ilex opaca</i>	American Holly	Native		1	1	
<i>Ilex verticillata</i>	Common Winterberry	Native				1
<i>Kalmia latifolia</i>	Mountain Laurel	Native				1

(continued)

Table 2.3. Continued.

Latin Name	Species Name	Native Status	American Robin	Gray Catbird	Northern Cardinal	Wood Thrush
<i>Lindera benzoin</i>	Spicebush	Native	2	15	7	8
<i>Liquidambar styraciflua</i>	Sweetgum	Native			3	
<i>Liriodendron tulipifera</i>	Tulip Poplar	Native		3		1
<i>Lonicera japonica</i>	Japanese Honeysuckle	Non-Native	3		3	
<i>Morus alba</i>	White Mulberry	Non-Native		1		
<i>Nyssa sylvatica</i>	Blackgum	Native	8		5	16
<i>Parthenocissus quinquefolia</i>	Virginia Creeper	Native	2		1	
<i>Prunus americana</i>	American plum	Native	7			
<i>Prunus serotina</i>	Black Cherry	Native	2	2	1	7
<i>Quercus rubra</i>	Red Oak	Native				1
<i>Quercus sp.</i>	Oak sp.	Native		1		3
<i>Rosa multiflora</i>	Multiflora Rose	Non-Native	5	61	12	2
<i>Sassafras albidum</i>	Sassafras	Native	1			1
<i>Smilax rotundifolia</i>	Roundleaf Greenbrier	Native	2	26	5	1
<i>Toxicodendron radicans</i>	Poison Ivy	Native	1			
<i>Tsuga canadensis</i>	Eastern Hemlock	Native		1		
<i>Vaccinium corymbosum</i>	Highbush Blueberry	Native		1		1
<i>Viburnum dentatum</i>	Southern Arrowwood	Native	2	27		9
<i>Viburnum prunifolium</i>	Blackhaw	Native				5
<i>Vitis sp.</i>	Grape sp.	Native			1	

Table 2.4. Top ranked models ($\Delta\text{AICc} \leq 2$) of variables affecting the daily nest survival of four forest songbird species. Table presents Akaike's Information Criterion (AICc), the difference in AIC value compared to the top-ranked model (ΔAICc), the AIC model weight (W), and the number of parameters in the model (K). All models were run binomially against the response variable "fail". Beta estimates (β) and standard errors (SE) are included for each top model. Data on all models ran can be found in Appendix C.

Species	Model	AICc	ΔAICc	W	K	β	SE
AMRO	fail(exchca)	208.97	0	0.59	2	0.2973	0.1151
GRCA	fail(date)	531.56	0	0.99	2	0.0198	0.005
NOCA	fail(exchca)	191.33	0	0.42	2	-0.184	0.0829
WOTH	fail(height)	475.89	0	0.27	2	0.081	0.0411
	fail(density)	476.18	0.30	0.24	2	-0.023	0.0127
	fail(.)	477.25	1.36	0.14	1	.	.

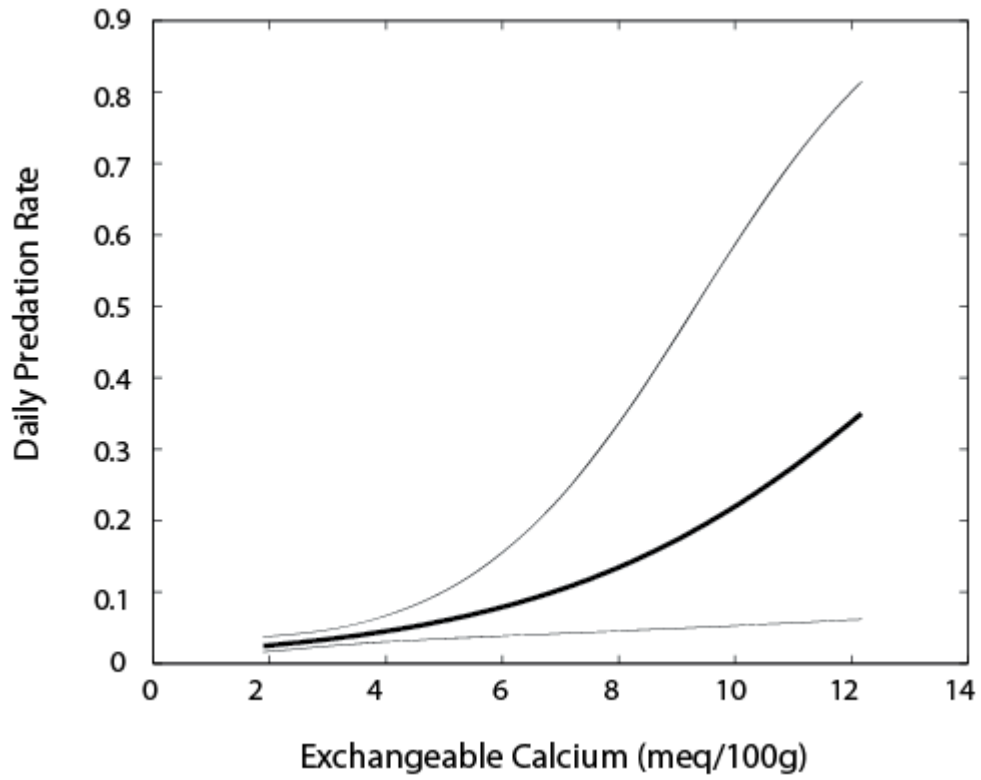


Figure 2.1. The probability of daily nest predation for American Robin nests within the parameter of exchangeable calcium ($\beta = 0.30 \pm 0.12$) found within a 25m buffer. Error lines (light gray) are 95% confidence intervals.

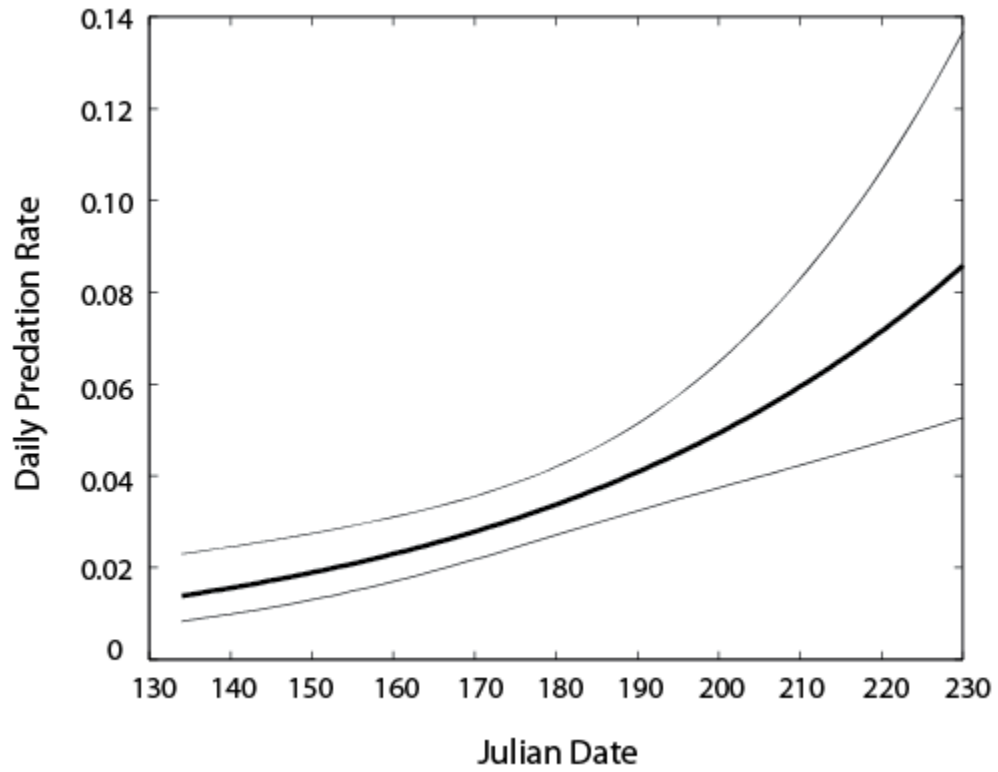


Figure 2.2. The probability of daily nest predation for Gray Catbird nests, within the parameter of julien date ($\beta = 0.02 \pm 0.005$). Error lines (light gray) are 95% confidence intervals.

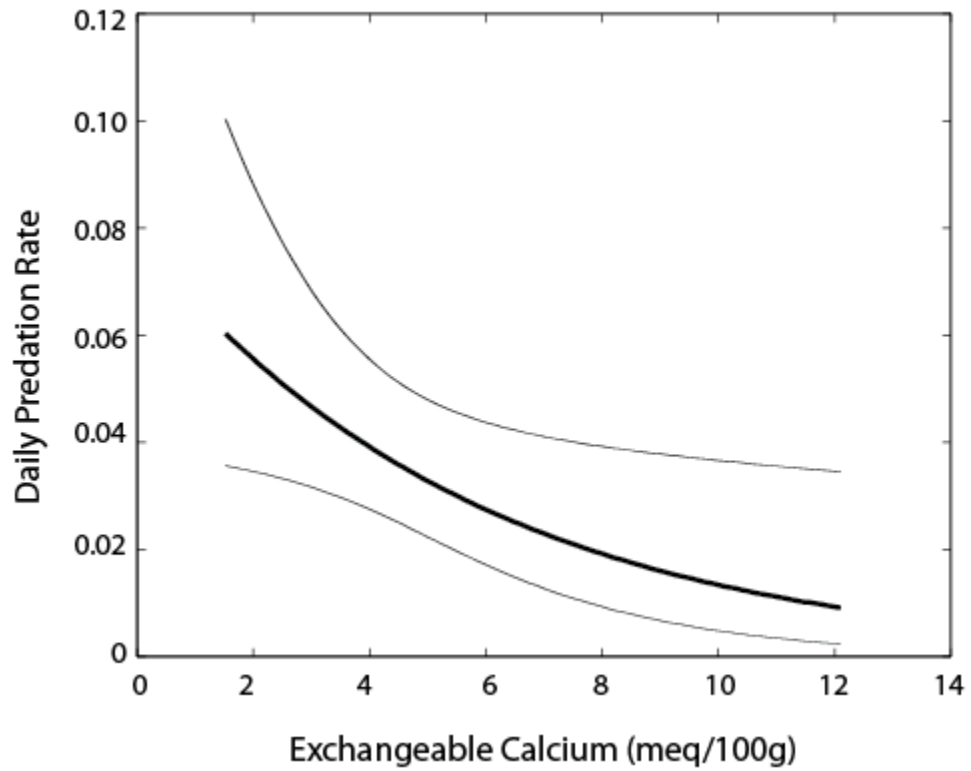


Figure 2.3. The probability of daily nest predation for Northern Cardinal nests, within the parameter of exchangeable calcium ($\beta = -0.18 \pm 0.083$). Error lines (light gray) are 95% confidence intervals.

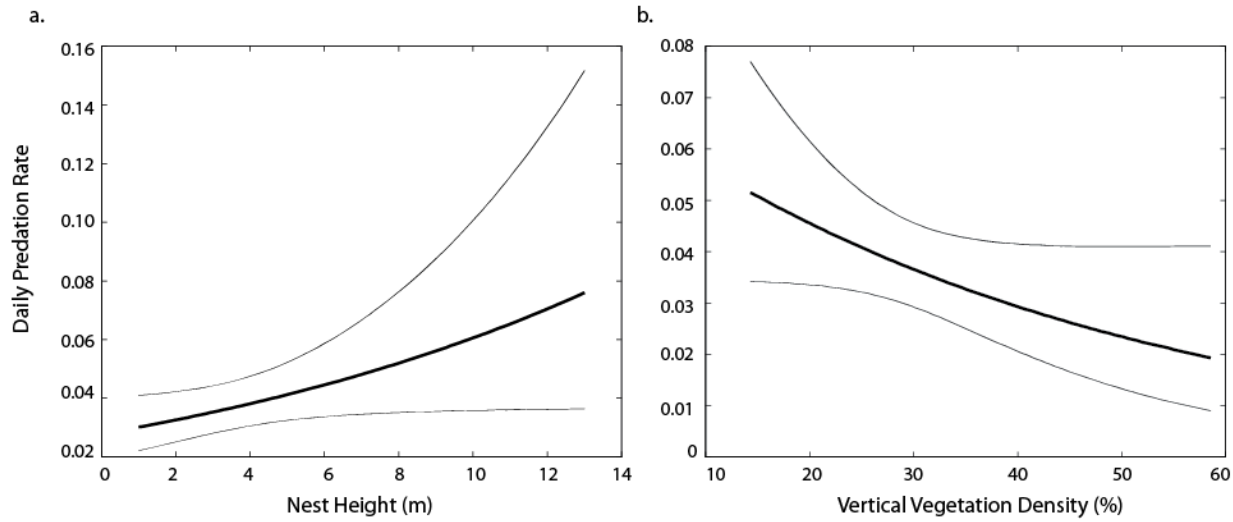


Figure 2.4. The probability of daily nest predation for Wood Thrush nests, within the parameter of nest height ($\beta = 0.081 \pm 0.041$) and vertical vegetation density ($\beta = -0.023 \pm 0.013$). Error lines (light gray) are 95% confidence intervals.

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Appendix A

**MEAN TERRITORY DENSITIES (TERRITORIES/HA) OF ALL SPECIES WHICH ESTABLISHED
TERRITORIES WITHIN THE STUDY SITES**

Appendix A

Site	ACFL	AMGO	AMRO	BHCO	BLJA	BRTH	CACH	CARW	COGR	COYE	DOWO	EAPH
Christina Creek 1	0.00	0.00	1.56	0.00	0.39	0.00	1.17	0.59	0.00	0.00	0.00	0.00
Christina Creek 2	0.08	0.00	0.98	0.00	0.33	0.00	0.90	0.65	0.08	0.00	0.00	0.08
Chrysler Woods	0.00	0.00	1.10	0.00	0.78	0.00	1.41	1.10	0.16	0.00	0.16	0.00
Coverdale	0.13	0.00	0.65	0.00	0.52	0.00	1.30	0.91	0.00	0.00	0.13	0.00
Dorothy Miller	0.20	0.00	1.64	0.00	0.41	0.00	0.61	0.20	0.00	0.00	0.00	0.00
Ecology Woods	0.00	0.00	0.92	0.03	0.06	0.12	0.34	0.09	0.00	0.00	0.03	0.00
Folk	0.00	0.00	1.00	0.14	0.29	0.00	0.43	0.00	0.00	0.00	0.00	0.00
Glasgow 1	0.00	0.00	0.71	0.14	0.00	0.00	0.29	0.00	0.00	0.00	0.14	0.00
Glasgow 2	0.00	0.00	1.29	0.00	0.43	0.00	0.57	0.29	0.00	0.00	0.00	0.00
Iron Hill 1	0.00	0.00	1.43	0.14	0.57	0.00	0.43	0.14	0.00	0.00	0.00	0.00
Iron Hill 2	0.00	0.00	1.14	0.00	0.57	0.00	0.43	0.00	0.00	0.00	0.00	0.00
Laird	0.00	0.19	0.77	0.00	0.19	0.00	1.35	0.58	0.00	0.00	0.00	0.00
Motor Pool	0.25	0.13	1.27	0.00	0.00	0.00	1.02	0.25	0.00	0.00	0.00	0.00
Phillips	0.00	0.00	1.94	0.00	1.46	0.00	1.46	0.97	0.00	0.24	0.00	0.00
Reservoir	0.14	0.00	1.14	0.00	0.43	0.00	0.43	0.43	0.00	0.00	0.00	0.00
Rittenhouse	0.14	0.00	1.65	0.14	0.07	0.00	0.79	0.29	0.00	0.00	0.00	0.00
Sunset Lake 1	0.00	0.00	0.43	0.00	0.29	0.00	0.86	0.00	0.00	0.00	0.00	0.00
Sunset Lake 2	0.00	0.00	0.86	0.14	0.14	0.00	0.57	0.00	0.00	0.00	0.00	0.00
Webb Farm	0.00	0.00	1.75	0.00	0.58	0.00	0.92	0.33	0.00	0.00	0.00	0.00
White Clay 1	0.00	0.00	0.00	0.00	1.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00
White Clay 2	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.14	0.00	0.00

Appendix A

Site	EATO	EAWP	ETTI	GRCA	HAWO	HOWR	INBU	MODO	NOCA	NOFL	NOMO	OVEN
Christina Creek 1	0.39	0.39	0.78	0.00	0.00	0.00	0.00	0.00	1.95	0.00	0.00	0.00
Christina Creek 2	0.08	0.08	0.24	0.24	0.00	0.08	0.08	0.00	1.79	0.00	0.00	0.00
Chrysler Woods	0.00	0.47	0.63	0.16	0.00	0.00	0.00	0.00	2.35	0.00	0.00	0.00
Coverdale	0.26	0.00	0.91	0.13	0.00	1.30	0.00	0.00	1.95	0.00	0.00	0.00
Dorothy Miller	0.00	0.00	0.61	0.00	0.00	0.00	0.00	0.00	1.64	0.00	0.00	0.00
Ecology Woods	0.00	0.18	0.21	1.07	0.03	0.00	0.00	0.03	0.58	0.06	0.00	0.00
Folk	0.00	0.29	0.14	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	1.00
Glasgow 1	0.29	0.43	0.43	0.00	0.14	0.00	0.00	0.00	0.57	0.00	0.00	0.00
Glasgow 2	0.00	0.57	0.29	0.14	0.14	0.00	0.14	0.00	0.14	0.00	0.29	0.57
Iron Hill 1	0.00	0.29	0.29	0.00	0.29	0.00	0.00	0.14	0.43	0.00	0.00	0.57
Iron Hill 2	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00	0.71
Laird	0.39	0.39	0.97	0.00	0.39	0.00	0.39	0.00	2.32	0.00	0.00	0.00
Motor Pool	0.00	0.25	0.38	0.89	0.25	0.00	0.13	0.00	1.65	0.00	0.00	0.00
Phillips	0.49	0.24	0.24	1.94	0.24	0.00	0.73	0.00	2.43	0.00	0.24	0.00
Reservoir	0.29	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.00	0.00	0.00
Rittenhouse	0.00	0.07	1.08	0.00	0.14	0.00	0.00	0.00	1.29	0.07	0.00	0.65
Sunset Lake 1	0.00	0.43	0.29	0.00	0.29	0.00	0.29	0.00	0.14	0.00	0.00	0.00
Sunset Lake 2	0.00	0.29	0.29	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Webb Farm	0.00	0.42	0.58	1.42	0.17	0.08	0.00	0.00	0.83	0.17	0.00	0.00
White Clay 1	0.14	0.57	0.29	0.00	0.29	0.00	0.00	0.00	0.14	0.00	0.00	1.43
White Clay 2	1.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.57	0.00	0.00	1.71

Appendix A

Site	PIWO	RBWO	REVI	SCTA	SOSP	WBNU	WOTH
Christina Creek 1	0.00	0.20	0.78	0.00	0.00	0.00	0.59
Christina Creek 2	0.00	0.16	0.41	0.00	0.00	0.08	0.08
Chrysler Woods	0.16	0.47	0.00	0.00	0.00	0.00	0.00
Coverdale	0.00	0.78	0.78	0.00	0.00	0.13	0.13
Dorothy Miller	0.00	0.00	1.23	0.00	0.00	0.00	0.21
Ecology Woods	0.00	0.21	0.40	0.09	0.03	0.03	0.64
Folk	0.00	0.00	1.14	0.29	0.00	0.00	1.57
Glasgow 1	0.00	0.00	1.43	0.57	0.00	0.00	0.14
Glasgow 2	0.00	0.57	1.71	0.14	0.00	0.14	0.43
Iron Hill 1	0.00	0.14	0.29	0.00	0.00	0.00	2.00
Iron Hill 2	0.00	0.14	0.00	0.14	0.00	0.14	1.86
Laird	0.00	0.00	1.35	0.39	0.00	0.39	0.00
Motor Pool	0.00	0.25	1.65	0.00	0.00	0.00	0.13
Phillips	0.00	0.49	0.00	0.00	0.00	0.24	0.24
Reservoir	0.00	0.57	0.57	0.00	0.00	0.29	1.14
Rittenhouse	0.00	0.36	0.86	0.00	0.00	0.00	1.00
Sunset Lake 1	0.00	0.14	0.57	0.00	0.00	0.00	0.14
Sunset Lake 2	0.00	0.14	0.29	0.00	0.00	0.00	0.43
Webb Farm	0.00	1.00	0.83	0.08	0.00	0.00	0.25
White Clay 1	0.00	0.43	0.43	0.29	0.00	0.43	1.57
White Clay 2	0.00	0.29	1.57	0.29	0.00	0.14	2.43

Appendix B

ALL MODELS OF VARIABLES AFFECTING THE ABUNDANCE OF 13 FOREST SONGBIRD SPECIES WITHIN 21 FORESTED FRAGMENTS IN NEWARK, DELAWARE. TABLE PRESENTS THE NUMBER OF PARAMETERS IN THE MODEL (K), AKAIKE'S INFORMATION CRITERION (AICC), THE DIFFERENCE IN AIC VALUE COMPARED TO THE TOP-RANKED MODEL (Δ AICC), THE AIC MODEL WEIGHT (AICWT), AND THE CUMULATIVE AIC WEIGHT (CUMLTWWT). LAMBDA (λ) INDICATES ABUNDANCE COVARIATES, AND (P) INDICATES DETECTION COVARIATES. OBSERVATIONAL GLOBAL MODELS (P(GLOBAL)) INCLUDED CLOUD+DATE+TIME+TEMP. ABUNDANCE GLOBAL MODELS (λ (GLOBAL)) INCLUDED FOREST100+PATCH_HA+SNWT+EXCHCA+PRCTNNSTEMS+BA+DENSITY+AGE.

Species	Model	K	AICc	Δ AICc	AICwt	cumltvWt
AMRO	λ (forest100+patch_ha)p(global)	8	2340.61	0	0.53	0.53
	λ (global)p(global)	14	2340.85	0.24	0.47	1
	λ (snwt)p(global)	7	2416.04	75.43	2.2E-17	1
	λ (prctnnstem)p(global)	7	2426.09	85.48	1.5E-19	1
	λ (ba+density+age)p(global)	9	2429.74	89.13	2.3E-20	1
	λ (.)p(global)	6	2440.38	99.77	1.1E-22	1
	λ (exchca)p(global)	7	2440.84	100.23	9.1E-23	1
BHCO	λ (global)p(global)	14	492.55	0	1	1
	λ (prctnnstem)p(global)	7	506.73	14.18	8.30E-04	1
	λ (forest100+patch_ha)p(global)	8	508.25	15.70	3.90E-04	1
	λ (ba+density+age)p(global)	9	527.07	34.52	3.20E-08	1
	λ (exchca)p(global)	7	532.17	39.62	2.50E-09	1
	λ (snwt)p(global)	7	540.30	47.75	4.30E-11	1
	λ (.)p(global)	6	540.49	47.94	3.90E-11	1

(continued)

Appendix B

Species	Model	K	AICc	Δ AICc	AICwt	cumltvWt
CARW	$\lambda(\text{global})p(\text{date})$	11	923.29	0	1	1
	$\lambda(\text{forest100+patch_ha})p(\text{date})$	5	936.37	13.09	1.40E-03	1
	$\lambda(\text{ba+density+age})p(\text{date})$	6	941.57	18.28	1.10E-04	1
	$\lambda(\text{exchca})p(\text{date})$	4	947.63	24.35	5.20E-06	1
	$\lambda(\text{prctnnstem})p(\text{date})$	4	951.69	28.4	6.80E-07	1
	$\lambda(.)p(\text{date})$	3	958.27	34.99	2.50E-08	1
	$\lambda(\text{snwt})p(\text{date})$	4	960.27	36.98	9.3E-09	1
EATO	$\lambda(\text{global})p(.)$	10	541.45	0	0.83	0.83
	$\lambda(\text{prctnnstem})p(.)$	3	544.62	3.17	0.17	1
	$\lambda(\text{forest100+patch_ha})p(.)$	4	577.05	35.61	1.50E-08	1
	$\lambda(\text{ba+density+age})p(.)$	5	579.16	37.72	5.4E-09	1
	$\lambda(\text{snwt})p(.)$	3	597.22	55.77	6.4E-13	1
	$\lambda(\text{exchca})p(.)$	3	600.57	59.12	1.2E-13	1
	$\lambda(.)p(.)$	2	611.59	70.14	4.9E-16	1
EAWP	$\lambda(\text{snwt})p(\text{date})$	4	894.19	0	0.566	0.57
	$\lambda(\text{exchca})p(\text{date})$	4	896.54	2.35	0.175	0.74
	$\lambda(\text{prctnnstem})p(\text{date})$	4	897.02	2.83	0.138	0.88
	$\lambda(.)p(\text{date})$	3	898.21	4.02	0.076	0.95
	$\lambda(\text{ba+density+age})p(\text{date})$	6	900.64	6.45	0.022	0.98
	$\lambda(\text{forest100+patch_ha})p(\text{date})$	5	901.78	7.59	0.013	0.99
	$\lambda(\text{global})p(\text{date})$	11	902.08	7.88	0.011	1
GRCA	$\lambda(\text{global})p(\text{global})$	14	846.9	0	1	1
	$\lambda(\text{forest100+patch_ha})p(\text{global})$	8	879.2	32.3	9.70E-08	1
	$\lambda(\text{ba+density+age})p(\text{global})$	9	897.91	51.01	8.4E-12	1
	$\lambda(\text{snwt})p(\text{global})$	7	976.99	130.09	5.6E-29	1
	$\lambda(\text{prctnnstem})p(\text{global})$	7	981.59	134.69	5.7E-30	1
	$\lambda(.)p(\text{global})$	6	982.49	135.59	3.6E-30	1
	$\lambda(\text{exchca})p(\text{global})$	7	982.75	135.85	3.2E-30	1

(continued)

Appendix B

Species	Model	K	AICc	Δ AICc	AICwt	cumltvWt
HAWO	$\lambda(\text{global})p(\text{date})$	11	800.39	0	9.87E-01	0.99
	$\lambda(\text{forest100+patch_ha})p(\text{date})$	5	811.04	10.65	0.0048	0.99
	$\lambda(\text{snwt})p(\text{date})$	4	811.57	11.18	3.69E-03	1
	$\lambda(.)p(\text{date})$	3	812.5	12.11	2.32E-03	1
	$\lambda(\text{prctnnstem})p(\text{date})$	4	814.16	13.76	1.01E-03	1
	$\lambda(\text{exchca})p(\text{date})$	4	814.49	14.1	8.50E-04	1
	$\lambda(\text{ba+density+age})p(\text{date})$	6	816.5	16.11	3.10E-04	1
NOCA	$\lambda(\text{global})p(\text{date})$	11	1593.76	0	1	1
	$\lambda(\text{ba+density+age})p(\text{date})$	6	1649.18	55.43	9.2E-13	1
	$\lambda(\text{exchca})p(\text{date})$	4	1702.53	108.77	2.4E-24	1
	$\lambda(\text{prctnnstem})p(\text{date})$	4	1709.42	115.66	7.7E-26	1
	$\lambda(\text{forest100+patch_ha})p(\text{date})$	5	1717.23	123.48	1.5E-27	1
	$\lambda(\text{snwt})p(\text{date})$	4	1761.47	167.71	3.8E-37	1
	$\lambda(.)p(\text{date})$	3	1766.16	172.41	3.7E-38	1
OVEN	$\lambda(\text{global})p(\text{global})$	14	565.01	0	1	1
	$\lambda(\text{forest100+patch_ha})p(\text{global})$	8	618.08	53.07	3E-12	1
	$\lambda(\text{ba+density+age})p(\text{global})$	9	694.18	129.16	9E-29	1
	$\lambda(\text{snwt})p(\text{global})$	7	715.59	150.57	2E-33	1
	$\lambda(.)p(\text{global})$	6	720.47	155.45	1.8E-34	1
	$\lambda(\text{prctnnstem})p(\text{global})$	7	721.14	156.13	1.2E-34	1
	$\lambda(\text{exchca})p(\text{global})$	7	721.6	156.59	9.9E-35	1
RBWO	$\lambda(\text{snwt})p(\text{date})$	4	1058.88	0	7.55E-01	0.76
	$\lambda(.)p(\text{date})$	3	1063.38	4.5	7.96E-02	0.83
	$\lambda(\text{forest100+patch_ha})p(\text{date})$	5	1063.53	4.65	0.074	0.91
	$\lambda(\text{prctnnstem})p(\text{date})$	4	1064.58	5.7	4.37E-02	0.95
	$\lambda(\text{exchca})p(\text{date})$	4	1065.1	6.22	3.37E-02	0.99
	$\lambda(\text{global})p(\text{date})$	11	1067.81	8.93	8.70E-03	1
	$\lambda(\text{ba+density+age})p(\text{date})$	6	1068.96	10.08	4.90E-03	1

(continued)

Appendix B

Species	Model	K	AICc	Δ AICc	AICwt	cumltvWt
REVI	$\lambda(\text{global})p(\cdot)$	10	1436.48	0	0.91	0.91
	$\lambda(\text{ba}+\text{density}+\text{age})p(\cdot)$	5	1441.17	4.69	0.087	1
	$\lambda(\text{forest}100+\text{patch_ha})p(\cdot)$	4	1454.07	17.59	1.40E-04	1
	$\lambda(\text{snwt})p(\cdot)$	3	1457.69	21.21	2.30E-05	1
	$\lambda(\cdot)p(\cdot)$	2	1459.22	22.75	1.00E-05	1
	$\lambda(\text{exchca})p(\cdot)$	3	1460.71	24.23	5.00E-06	1
	$\lambda(\text{prctnnstem})p(\cdot)$	3	1461.07	24.59	4.20E-06	1
SCTA	$\lambda(\text{global})p(\cdot)$	10	565.39	0	0.98	0.98
	$\lambda(\text{forest}100+\text{patch_ha})p(\cdot)$	4	573.13	7.75	0.02	1
	$\lambda(\text{exchca})p(\cdot)$	3	582.6	17.22	1.80E-04	1
	$\lambda(\text{ba}+\text{density}+\text{age})p(\cdot)$	5	589.31	23.92	6.30E-06	1
	$\lambda(\text{prctnnstem})p(\cdot)$	3	589.51	24.13	5.60E-06	1
	$\lambda(\cdot)p(\cdot)$	2	590.22	24.84	4.00E-06	1
	$\lambda(\text{snwt})p(\cdot)$	3	592.19	26.8	1.50E-06	1
WOTH	$\lambda(\text{global})p(\text{time})$	11	1152.35	0	1	1
	$\lambda(\text{forest}100+\text{patch_ha})p(\text{time})$	5	1215.53	63.18	1.9E-14	1
	$\lambda(\text{ba}+\text{density}+\text{age})p(\text{time})$	6	1247.29	94.94	2.4E-21	1
	$\lambda(\text{exchca})p(\text{time})$	4	1280.8	128.45	1.3E-28	1
	$\lambda(\text{snwt})p(\text{time})$	4	1281.06	128.71	1.1E-28	1
	$\lambda(\cdot)p(\text{time})$	3	1282.28	129.92	6.1E-29	1
	$\lambda(\text{prctnnstem})p(\text{time})$	4	1283.81	131.46	2.9E-29	1

Appendix C

ALL MODELS FOR DAILY NEST SURVIVAL OF FOUR FOREST SONGBIRD SPECIES WITHIN 21 FORESTED FRAGMENTS IN NEWARK, DELAWARE. TABLE PRESENTS AKAIKE'S INFORMATION CRITERION (AICC), THE DIFFERENCE IN AIC VALUE COMPARED TO THE TOP-RANKED MODEL (Δ AICC), THE AIC MODEL WEIGHT (W), AND THE NUMBER OF PARAMETERS IN THE MODEL (K). ALL MODELS WERE RUN AGAINST THE FAILURE PREDATION.

Species	Model	AICc	Δ AICc	W	K
AMRO	fail(exchca)	208.97	0	0.59	2
	fail(density)	211.89	2.92	0.14	2
	fail(.)	213.41	4.44	0.06	1
	fail(date+forestcover+patcharea+ba+density+exchca+height+nnplant)	214.24	5.26	0.04	9
	fail(height)	214.95	5.97	0.03	2
	fail(forestcover)	215.01	6.03	0.03	2
	fail(date)	215.12	6.15	0.03	2
	fail(patcharea)	215.14	6.17	0.03	2
	fail(ba)	215.24	6.26	0.03	2
	fail(nnplant)	215.25	6.27	0.03	2

(continued)

Appendix C

Species	Model	AICc	ΔAICc	W	K
GRCA	fail(date)	531.56	0	0.99	2
	fail(date+forestcover+patcharea+ba+density+exchca+height+nnplant)	543.46	11.9	0	9
	fail(.)	545.42	13.85	0	1
	fail(nnplant)	546.09	14.53	0	2
	fail(ba)	546.55	14.99	0	2
	fail(patcharea)	547.15	15.59	0	2
	fail(forestcover)	547.17	15.61	0	2
	fail(height)	547.38	15.82	0	2
	fail(exchca)	547.39	15.83	0	2
	fail(density)	547.41	15.85	0	2
NOCA	fail(exchca)	191.33	0	0.42	2
	fail(patcharea)	193.77	2.44	0.12	2
	fail(.)	194.02	2.69	0.11	1
	fail(date)	194.55	3.22	0.08	2
	fail(nnplant)	195.42	4.09	0.05	2
	fail(density)	195.43	4.1	0.05	2
	fail(ba)	195.88	4.55	0.04	2
	fail(forestcover)	195.9	4.57	0.04	2
	fail(height)	195.98	4.65	0.04	2
	fail(date+forestcover+patcharea+ba+density+exchca+height+nnplant)	196.94	5.61	0.03	9

(continued)

Appendix C

Species	Model	AICc	ΔAICc	W	K
WOTH	fail(height)	475.89	0	0.27	2
	fail(density)	476.18	0.3	0.24	2
	fail(.)	477.25	1.36	0.14	1
	fail(ba)	478.56	2.67	0.07	2
	fail(forestcover)	478.67	2.79	0.07	2
	fail(date)	479.19	3.3	0.05	2
	fail(patcharea)	479.2	3.31	0.05	2
	fail(exchca)	479.2	3.32	0.05	2
	fail(nnplant)	479.25	3.37	0.05	2
	fail(date+forestcover+patcharea+ba+density+exchca+height+nnplant)	485	9.11	0	9