

© 2014

Jean Elizabeth Deo

ALL RIGHTS RESERVED

MIXED SPECIES NESTING ASSOCIATIONS IN A NORTHEASTERN DECIDUOUS
FOREST

By

JEAN ELIZABETH DEO

A dissertation submitted to the
Graduate School-New Brunswick
Rutgers, The State University of New Jersey
In partial fulfillment of the requirements

For the degree of
Doctor of Philosophy
Graduate Program in Ecology and Evolution

Written under the direction of
Peter J. Morin and Richard S. Ostfeld

And approved by

New Brunswick, New Jersey

October, 2014

ABSTRACT OF THE DISSERTATION

Mixed Species Nesting Associations in a Northeastern Deciduous Forest

By JEAN ELIZABETH DEO

Dissertation Directors:

Peter Morin

Richard Ostfeld

Mixed species nesting associations (MSNA) occur when two or more species aggregate nests in space and time. In this study I describe nesting associations among songbirds breeding in forested habitat at Powdermill Nature Reserve in Western Pennsylvania, test if the distribution of nests correlates with habitat characteristics, and determine if MSNA impacts daily nest survival rates (DSR). I examined nesting associations involving Wood Thrushes (*Hylocichla mustelina*) and modeled DSR of thrushes. I also conducted artificial nest experiments in which I looked at the effects of density and nesting strata on nest survivorship. 65% of Wood Thrushes nested within 50 m of one to four other birds, and the nests were spatially aggregated. In contrast, only 15% of sites that lacked a Wood Thrush nest had 2 or more nests. Habitat characteristics including stem density and diversity were not correlated with the number of nests in an area. The best supported model of Wood Thrush DSR includes the interaction of time and number of nesting neighbors. DSR slightly decreased with increasing neighbor density. In three of the four artificial nest experiments, nest success decreased with higher nest density. In 2011, DSR decreased when nests were placed at different heights, but increased when nests were placed at the same height. MSNA are prevalent at Powdermill Nature Reserve, and birds

do not aggregate nests around specific habitat features. However, daily nest survival is, in general, negatively affected by these associations, although these negative effects are marginal at low nest densities, such as those observed on the reserve. The question remains, then as to why these birds form these associations. One possibility is that adult survival is higher among birds in MSNA than among solitary nesters, or that other species in the association benefit from nesting near Wood Thrushes.

DEDICATION

I dedicate this dissertation to Anthony Deo, who provided unwavering support and encouragement throughout this entire process.

ACKNOWLEDGEMENTS

I thank Peter Morin, Richard Ostfeld, Andrew Mack, and Julie Lockwood for their support and guidance during my Ph.D. I thank Olaf Jensen and Philipp Neubauer for help with the spatial analysis in Chapter one. I am grateful to Marsha Morin for administrative and moral support. I thank Anthony Deo, John Rothe, Sara Bednarik, Clifton McKee, Matt Natali, Joseph Moore, Liz Boeckmann, Nick Giacobbi, Amantha Michalopoulos, Conor Higgins, Chris Hensley, Jonathan Mandell, Emily Shelly, Heather Ludwig, Katie Abele, and Chris Tully for providing field help. This research was funded by a Rea Grant through Powdermill Nature Reserve and through an Academic Excellence Award through the Ecology and Evolution Graduate Program at Rutgers University.

TABLE OF CONTENTS

Title Page	i
Abstract	ii
Dedication.....	iv
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vi
List of Illustrations.....	vii
Introduction.....	1
Chapter One.....	7
Chapter Two.....	27
Chapter Three.....	40
Chapter Four/Conclusions.....	61
Bibliography.....	64

LIST OF TABLES

Chapter 1:

Table 1: Distribution patterns of nests at Wood Thrush plots.....	26
---	----

Chapter 2:

Table 1: Mean Values of habitat variables at Wood Thrush and Control sites.....	35
---	----

Table 2: ANOVA scores of habitat covariates.....	38
--	----

Table 3: Percentage of variance explained by first seven principal components.....	39
--	----

Table 4: PCA loadings for first two principle components of habitat variables.....	39
--	----

Chapter 3:

Table 1: Experimental treatments in Artificial Nest Study.....	52
--	----

Table 2: Proportion of Successful and Attacked Nests:.....	53
--	----

Table 3: Comparison of MARK models for Wood Thrush nest study, 2009-2011.....	54
---	----

Table 4: Predator composition at artificial nests:.....	55
---	----

Table 5: Significance of nest height and number of neighbors on nest outcome.....	56
---	----

Table 6: Comparison of MARK models for 2011 artificial nest study	59
---	----

Table 7: Influence of nest height and density on artificial nest survival.....	59
--	----

Table 8: Estimates of Daily Nest Survival for 2011 Artificial Nest Experiments	60
--	----

LIST OF ILLUSTRATIONS

Chapter 1:

Figure 1: Survey design for nearest neighbor searches.....	21
Figure 2: The number of interspecific nests at Wood Thrush plots and plots without Wood Thrush nests (control plots).....	22
Figure 3: Proportion of sites with zero to four interspecific (non-Wood Thrush) neighbors.....	23
Figure 4: Number of neighboring species at Wood Thrush nests and control plots.....	24
Figure 5: Species composition across Wood Thrush and control plots	25

Chapter 2:

Figure 1: Box plots showing how each measured habitat variable varies at sites with zero to four nests.....	36
Figure 2: Ordination of number of nests versus habitat factors.....	37

Chapter 3:

Figure 1: Experimental design for Artificial Nest Study.....	52
Figure 2: Number of Nests vs. Nest Fate (Same nest heights).	57
Figure 3: Number of Nests vs. Nest Fate (Different nest heights).	57
Figure 4: Nest Survival vs. Nest Height in 2010 and 2011.....	58

INTRODUCTION

Predation is the top source of nest failure in a multitude of avian species (Martin 1993, Richardson et al. 2009), and is therefore a major evolutionary force driving reproductive behaviors (Martin 1993, Schmidt et al. 2006, Quinn and Ueta 2008). Nest predators are prevalent in the environment and include species from multiple taxa including reptiles, birds, and mammals (Richardson et al. 2009). In response to predation pressure, birds evolved several nest defense strategies which include nest site selection (Forstmeier and Weiss 2004) and direct behavioral responses such as mobbing (Lima 2009). Recent work by (Kleindorfer et al. 2009) highlighted another potential anti-predator strategy that crosses the boundary between nest site selection and direct behavioral responses: mixed species nesting associations in which three or more birds nest in close proximity to one another. Mixed species nesting associations can be a successful anti-predator defense strategy if heterospecifics contribute anti-predatory behaviors to the group and if these benefits outweigh potential costs such as increased cues for predators, increased risk of disease transmission and competition among neighbors. The goal of my dissertation is to examine mixed species nesting associations in northeastern deciduous forests and to study the implications of nest density on nest success of the Wood Thrush, a Neotropical migratory songbird that breeds in northeastern deciduous forests.

Mixed species nesting associations occur when multiple species of birds cluster their nests in both space and time (Slagsvold 1980, Kleindorfer et al. 2009). The majority of described associations are protective nesting associations in which one or more species place nests nearby a more aggressive species (Quinn and Ueta 2008). In these

associations, the more aggressive species indirectly protects the other species through early warning of predators and aggressive response to predators. (Clark and Robertson 1979) showed that Yellow Warblers (*Dendroica petechia*) preferentially nested by Gray Catbirds (*Dumetella carolinensis*) or Red-Winged Blackbirds (*Agelaius phoeniceus*), which were both more aggressive than Yellow Warblers. Slagsvold (1980) described an association in which several passerine species nested nearby a more aggressive species, *Turdus pilaris*. Recently, Kleindorfer et al (2009) showed that Darwin's Small Tree Finches (*Camarhynchus parvulus*) nesting in heterospecific associations had lower nest predation as compared to solitary nesters. Although Kleindorfer et al. did not specify a protector species, they did find that these associations typically involved at least one larger species. The possibility exists that the larger species in the association served as the protector species if it was able to defend nests more effectively against larger predators than the smaller passerines in the group. Finally, although not covered in these examples, mixed nesting associations may involve multiple aggressive species that will participate in mobbing predators. Group mobbing of predators is a widely documented occurrence (Lima 2009).

Aside from nesting near a protector species, birds participating in mixed species nesting associations may lower their predation rates through the density of nests. By nesting near other birds, an individual lowers the probability that its nest will be discovered and /or selected by a predator. This phenomenon was described by Hamilton and coined the selfish herd hypothesis (Hamilton 1971).

Additionally, nesting with neighbors that use different nest sites can dampen the efficiency with which predators locate nests in a cluster. Predation rates are often lower

in clustered nests that are in different nest substrates than in clusters where the nests are in the same vegetation strata (Martin 1993, 1996). Although the total number of nests in a cluster remains constant, the density of nests in each stratum is reduced. Therefore, predators will have to search every stratum to find all nests and will receive less reward as they encounter unoccupied nest sites in each stratum. If birds choose to nest near heterospecific neighbors, then to get the most benefit, birds should choose to nest by neighbors that occupy different nest strata and should choose areas with structurally complex vegetation that provide a high number of potential nest sites that predators will need to search. (Chalfoun and Martin 2009) showed that birds do preferentially nest in structurally complex vegetation that contains many possible nest sites (Chalfoun and Martin 2009).

Given that mixed nesting associations are proving to be common and often result in higher reproductive success than solitary nesters, it is easy to overlook the potential negative consequences of these associations. The possibility of increased predation among associated nesting species exists as nest clusters invoke more cues for predators to use while searching for prey (Varela et al. 2007). Additionally, when a predator finds a cluster of nests, the reward is greater than for a solitary nest, which could drive predators to forage more extensively for nest clusters than for solitary nests (Martin 1993). Additionally, recent evidence shows that transmission of mobile parasites is greater in nest clusters than in solitary nests (Kleindorfer and Dudaniec 2009). Finally, competition for resources can be greater for species nesting in associations than for solitary nesters, if they overlap in resource use (Slagsvold 1980).

Nest site selection is an adaptive strategy that has evolutionary consequences due to its direct correlation with reproductive fitness. As an adaptive strategy, nest site selection necessitates that 1) birds are capable of gathering information about the habitat, 2) birds select habitat based on this information, and 3) these decisions have consequences related to reproductive fitness. Researchers have shown that reproductive success is affected when birds select nest sites based on the abundance of predators (Forstmeier and Weiss 2004, Schmidt et al. 2006), the structure of vegetation (Chalfoun and Martin 2009), the reproductive success of birds in the prior year (Betts et al. 2008), and the presence of conspecifics (Ahlering et al. 2010). Mixed nest associations represent another type of nest site selection in which birds use the presence of other species' nests as information when choosing nest sites. Previous work shows that birds that choose to nest near heterospecific nests lower their risk of nest predation (Kleindorfer et al. 2009), but these results are highly dependent on the species in the association, the density of nests, and the locations of those nests.

Through my dissertation research, I aim to contribute a better understanding of the occurrence and costs and benefits of multi species nesting associations. To meet this goal, I plan to quantify the costs and benefits incurred to Wood Thrushes (*Hylocichla mustelina*) which engage in mixed species nesting associations and to examine predation rates on different patterns and densities of nests.

To examine multi species nest associations, I answered the following central questions:

1. Are heterospecific nests more aggregated around focal Wood Thrush nests than around control sites? Do more species and individuals nest around Wood Thrush nests than around control sites?
2. Does the reproductive success of Wood Thrush correlate with the density and diversity of neighboring nests?
3. Does the aggregation of songbird nests correlate with specific habitat features?
4. A. Does daily nest survival change with increasing density of nests?
B. Are predation rates lower when nests are aggregated in 3-dimensional space (different nest heights) than when they are aggregated in 2-dimensional space (same nest height)?

Research Site:

Powdermill Avian Research Center, located in Rector, PA (Western PA, 75 km from southeast of Pittsburgh) is a 900-hectare reserve, surrounded by Forbes State Forest (24,000 ha) and Linn Run State Park (250 ha) and small, mostly non-commercial agricultural plots of land interspersed with homes. The majority of the reserve is comprised of mixed deciduous forest, and the remainder of the reserve contains man-made ponds and fields, a bird banding station with multiple net lanes, and some buildings. My study was conducted entirely in the forested areas of the reserve. Many of the forested areas in my study sites have dense shrub layers dominated by Common Spicebush (*Lindera benzoin*). There is a small trail system and four roads through the forested parts of the reserve. The entire reserve is delineated by a staked grid system, which was put in place three years ago to map vegetation distributions on the reserve. The stakes are 120 meters apart from one another, are GPS marked, and represent the center points of vegetation plots.

Study Species:

Wood Thrushes are medium-sized Neotropical migratory passerines that breed throughout much of the eastern United States and over-winter in Southeastern Mexico and in Central America (Evans et al. 2011). Wood Thrushes are ground foragers but nest in mid-shrub layer vegetation, typically in small shrubs such as Common Spicebush or small trees, such as Sugar Maples (*Acer saccharum*) (Evans et al. 2011). At Powdermill Nature Reserve, Wood Thrushes typically place nests between 1-2 meters above ground, but occasionally place nests 10 meters or higher. Wood Thrush nests are predated upon by a multitude of animals including Black Bears (*Ursus americanus*), American Crows (*Corvus brachyrhynchos*), Red Squirrels (*Tamiasciurus hudsonicus*), owls, and Eastern Chipmunks (*Tamias striatus*) (Richardson et al. 2009).

I chose to study the Wood Thrush because they are one of the most abundant breeding avian species at Powdermill Reserve, their nests are easy to locate, and I observed multi-species nesting associations involving Wood Thrush during my first field season. Additionally, nest predation is the most commonly observed cause of nest failure for this species at the reserve (Newell and Kostalos 2007). Finally, Wood Thrush biology has been extensively studied in relation to a multitude of factors including nest predation (Schmidt et al. 2006), trophic interactions (Schmidt et al. 2008), and habitat use (Newell and Kostalos 2007).

CHAPTER ONE

Spatial point pattern analysis reveals nesting associations among Wood Thrushes (*Hylocichla mustelina*) and other nesting passerines

ABSTRACT

Mixed species nesting associations (MSNA) occur when species nest in close proximity to one another. These associations result from species selecting the same habitat patches or from heterospecific attraction in which species use the presence of other species to locate good quality habitat or to reduce individual predation risk. MSNA involving Wood Thrushes (*Hylocichla mustelina*) were described in a northeastern deciduous forest by surveying neighboring nests at sites with and without thrushes and by conducting spatial point pattern analyses of nest locations. These associations consisted of two to five birds, and Red Eyed Vireos (*Vireo olivaceus*) and Scarlet Tanagers (*Piranga olivacea*) were the most common associates of Wood Thrushes. Associated species did not typically share nest or foraging site preferences, and nests were highly aggregated at local scales, suggesting that protection from predators might be the driving force behind these associations. MSNA, especially those occurring in northeastern deciduous forests, warrant further study as populations of many of these species are declining, and a decline in one species can cause concomitant declines in associated species.

Key Terms: Mixed Species Nesting Association, nest site selection, Wood Thrush, nearest neighbor analysis, heterospecific attraction

INTRODUCTION

Mixed species nesting associations (MSNA) occur when multiple species nest near one another (Slagsvold 1980, Kleindorfer et al. 2009). Nesting associations occur among many organisms, including birds (Quinn and Ueta 2008, Kleindorfer and Dudaniec 2009, Reiter and Andersen 2013), insects (Windsor 1972), and between birds and insects (Young et al. 1990). These associations can occur incidentally when organisms choose to nest within the same patchily distributed habitat (Morales et al. 2012), or deliberately when species use the presence of other species when making settling decisions, an occurrence termed heterospecific attraction (Mönkkönen et al. 1997, Forsman et al. 2002, Lima 2009).

Species may exhibit heterospecific attraction if they use other species as sources of information on habitat quality or if they gain protective benefits from nesting near other species (Goodale et al. 2010). Migratory birds have limited time to select breeding sites, and using the presence of heterospecifics as an indicator of high quality habitat can allow them to initiate egg laying earlier (Forsman et al. 2002). Additionally, nesting in groups reduces the per capita predation risk on each individual in the group, allows for earlier detection of predators, and provides opportunities for group defense against approaching predators (Hamilton 1971, Martin 1993).

The majority of described nesting associations involve a special case of predation risk abatement in which one or more species nest near a more aggressive protector species (Slagsvold 1980, Quinn and Ueta 2008). In these associations, the more aggressive species indirectly protects the other species by warning of the presence of predators and by attacking predators. For example, Yellow Warblers (*Dendroica*

petechia) were shown to preferentially nest by Gray Catbirds (*Dumetella carolinensis*) or Red-Winged Blackbirds (*Agelaius phoeniceus*), which were both more aggressive against shared predators than Yellow Warblers (Clark and Robertson 1979).

Participation in MSNA should lead birds to aggregate their nests regardless of whether they are reacting to similar habitat requirements or to each other (Reiter and Andersen 2013). Evaluating the spatial distribution of nests and the composition of participants in nesting assemblages can lend insight into the reasons for a particular nesting association (Bayard and Elphick 2010, Sebastian-Gonzalez et al. 2010, Morales et al. 2012). This information can then serve as a baseline to inform future research, whether it is evaluating habitat requirements for species assemblages or testing for heterospecific attraction and reduction in predation risk directly.

For example, birds that are utilizing the same patchy habitat resource would likely nest near that resource but would maximize the space between themselves and their neighbors, creating a pattern of over dispersion within a small area (Forsman et al. 2002). In this situation, birds would be more likely to have similar resource requirements as they are either selecting the habitat directly or using other similar species as a proxy for habitat selection (Seppanen 2007).

Alternatively, birds that are exhibiting heterospecific attraction to reduce predation risk may aggregate their nests at the local scale as information on predation risk is most accurate at small distances (Seppanen 2007). In addition, birds would likely nest at different heights and in different substrates to reduce competition for nest sites and to decrease predator foraging efficiency (Martin 1993, 1996).

Regardless of whether habitat or protection is the driving force, interspecific associations are important factors in shaping local communities (Fletcher 2007b, Goodale et al. 2010, Sebastian-Gonzalez et al. 2010, Morales et al. 2012). In addition, these associations have conservation implications as they warrant conservation at the community level rather than at the species level. Specifically, the fates of associated species are connected as a decline in one species can cause parallel declines in associated species.

In this study, the spatial point patterns and composition of mixed species nesting associations were studied in an eastern deciduous forest located at Powdermill Nature Reserve in western Pennsylvania. I tested the hypothesis that multiple species of songbirds aggregate their nests on the reserve. I expected migratory birds that experience high rates of nest depredation and short breeding periods to form MSNA. These species would benefit the most from aggregated breeding as they could potentially use the social information available from earlier arriving species to more quickly establish their territories and commence nesting. These species could also potentially reduce their individual risk of nest attack by breeding near others. Specifically, I predicted that Wood Thrushes would be aggregated with other species. The major pulse of migrating thrushes through the reserve occurs later than many other migratory species, and thrushes are vulnerable to a wide variety of predators, both conditions which have been shown to foster participating in MSNA in other species (Mönkkönen et al. 1997).

METHODS

Study Site:

Research was conducted at Powdermill Nature Reserve (PNR), located in Rector, PA (latitude +40.16019891, longitude -79.27180242). The 890 hectare reserve is comprised of mostly maple and oak dominated deciduous forest and is surrounded by Lynn Run State Park, Forbes State Forest, and privately owned farms. The reserve contains a square grid system, with stakes located every 100 m on north-south, east-west gridlines. All stake geolocations are mapped and tagged. This grid system was set up by scientists to map the vegetation on the reserve, and vegetation surveys were centered at the locations marked with the stakes. In this study, a subset of these staked locations were used as starting points for nest searches. Using ArcView software, fifty stake points were selected throughout the reserve at random with the selection criteria that points were greater than 100 meters from a road or building to avoid most edge effects of nesting songbirds. With this method, the entire reserve was represented in the study and search locations were not biased to locations close to trails.

Locating and Monitoring Wood Thrush Nests:

Nest searching took place during 0600-1000 hours from May 10 through July 31 2009-2011 and May 10-31 in 2012. Stake points were visited a minimum of two times per year. I searched visually and aurally for Wood Thrushes at each point for up to 10 minutes or until a Wood Thrush was detected. Once a Wood Thrush was detected, I searched for its nest by following singing and calling individuals to the nest or by visual searching of vegetation in appropriate habitat within a male's territory. I visited all 50 stake points in 2009, 40 sites in both 2010 and 2011, and 15 points in 2012. I included

incidental nests found while hiking to the survey points. Nest positions were recorded using a Garmin GPS 72 handheld unit and sometimes discretely marked in dense vegetation to facilitate relocation.

Locating nearest neighbors

Searches for non-Wood Thrush nests took place from July through October each season. In an effort to minimize disturbance to nesting thrushes, I conducted these surveys after each Wood Thrush finished its nesting attempt. I searched for nests within 50 meters of each Wood Thrush nest (circular plot, search area per site = 7854 m^2). I selected this plot size to reflect the typical territory width of nesting Wood Thrushes (100 m), as the diameter of the plot was 100 m. Within each plot, I looked for nests along four 50-meter long transects, one in each cardinal direction starting from the focal Wood Thrush nest (Fig 1). I walked along each transect and scanned for nests along both the transect and the area surrounding the transect to maximize coverage of each site. Every ten meters, I stopped and did a thorough scan of the plot area that was visible. With this method I was able to standardize search efforts across sites and find well concealed nests such as those positioned on the ground and in high canopy vegetation. It is possible that extremely small and cryptic nests, such as those of Black and White Warblers, were missed, resulting in an underestimation of the number of neighboring nests in an area. Nest searching was completed by J. Deo. I recorded the location of each nest with a handheld Garmin GPS 72 unit. I identified the species that built each nest by either observing the parents at the nest or by using specific characteristic nest traits including size, appearance, and location (Harrison et al. 1975).

Control sites

Control sites were used to compare the density of nests in areas without Wood Thrush nests. Control points were located in a random direction 200 meters away from known Wood Thrush nests. Using the same techniques outlined above, neighboring nests were located on four transects (Fig 1). Nest searches at control sites were conducted within one week of the neighbor surveys for Wood Thrush nests.

Statistical Analysis

All statistical analyses were performed using R studio and R 2.15.2 (R Development Core Team). In 13 out of 40 control sites, Wood Thrush nests were found during nest searches along at least one of the four transects. T-tests were used to compare the number of nests and nesting species between control sites with off center Wood Thrush nests and sites with central Wood Thrush nests. No significant difference was found between these sites, so these sites were combined in all analyses and referred to as Wood Thrush sites. With this reclassification, 61 Wood Thrush sites were compared to 27 control sites.

T-tests were then used to compare the mean number of neighboring nests and the mean number of nesting species (excluding Wood Thrushes) on Wood Thrush and control sites. Chi square tests were used to compare the abundance of each species nesting at plots with and without Wood Thrushes.

Nearest neighbor analysis was done at sites that had at least two nests. Within a site (Wood Thrush or Control), the distance from every nest to its closest neighbor was calculated. Using the method outlined in Clark and Evans (1954), a ratio score was calculated by comparing the observed nearest neighbor distance (r_A) to the nearest

neighbor distance expected under the null hypothesis of complete spatial randomness (r_E). r_A and r_E were calculated using formulas 1.1 and 1.2, where N = the number of nests at a site, r = the distance from a nest to the nearest neighboring nest, and p = the number of nests/the area of the site. Formula 1.1 calculates the mean nearest neighbor distance between nests at a site.

$$1.1 \quad \hat{r}_A = \frac{\sum r}{N}$$

Formula 1.2 calculates the expected mean nearest neighbor distance between nests at a site if those nests were placed in a pattern of complete spatial randomness. This formula is based on the probability of finding N points at a site of a specified area (Clark and Evans 1954). p is the density of nests at a site.

$$1.2 \quad \hat{r}_E = \frac{1}{2\sqrt{p}}$$

The ratio R was then calculated as stated in formula 1.3 by dividing the observed mean nearest neighbor distance by the mean nearest neighbor distance expected in complete spatial randomness. An R score of 1 indicates spatial randomness, $R < 1$ signifies aggregation, and $R > 1$ denotes over dispersion.

$$1.3 \quad R = \frac{r_A}{r_E}$$

Additionally, significance tests (Clark and Evans 1954) were conducted to compare the expected (in complete spatial randomness) and observed mean nearest neighbor distances at each site (Formula 1.4). These tests are based on the normal probability distribution. C represents the standard normal variate, calculated here by subtracting the expected mean nearest neighbor distance from the observed mean nearest neighbor distance and dividing by the standard error of the expected nearest neighbor distance. $\sigma_{\hat{r}_E}$ is the standard error of the expected mean distance to the nearest neighbors in complete spatial randomness.

A C value of 1.96 or higher indicates a significant departure from spatial randomness ($p \leq 0.05$).

$$1.4 \quad C = \frac{r_A - r_E}{\sigma_{rE}} \text{ where } \sigma_{rE} = \frac{0.26136}{\sqrt{Np}}$$

RESULTS

Number of Interspecific Nests

There were significantly more nests at sites with Wood Thrushes than sites without (1.4 vs 0.7 nests, Figure 2). Additionally, 90% of control sites contained either zero nests or one nest. Only 34% of Wood Thrushes were solitary nesters, and the remainder nested near at least one neighbor (Figure 3).

Number of Neighboring Species

Species richness of nesting birds around focal nests (0-3 species) was significantly higher (t-test, $P < 0.05$) than that of nests in control sites (0-2 species, Figure 4). Twelve species nested near Wood Thrush nests, and eight species were found nesting at sites without Wood Thrushes (Figure 5). There were significantly more Acadian Flycatchers (*Empidonax virens*), Scarlet Tanagers (*Piranga olivacea*), and Red-Eyed Vireos (*Vireo olivaceus*) nesting at sites with Wood Thrushes than at control sites (Chi-square $P < 0.05$). More Eastern Towhees (*Pipilo erythrophthalmus*) nested at sites lacking Wood Thrushes than at sites with them (Chi-square, $P < 0.05$).

Nearest Neighbor Analysis:

Nearest neighbor analysis requires exact distances between at least two points. In this analysis, sites had to have at least two nests within the 50-m radius search area to be included. Therefore, I completed nearest neighbor analysis on sites where Wood Thrushes nested within 50 meters of at least one other nest (40 sites out of 61). For the

control sites, I ran nearest neighbor statistics on only four out of the 27 plots. The remainder of sites had either zero nests (13 sites) or one nest (10 sites), so nearest neighbor statistics could not be calculated for these sites

R scores were calculated for 40 Wood Thrush plots to determine if the distribution of nests at sites departed from complete spatial randomness. Ten sites (25%) were significantly aggregated ($P < 0.05$) and nine sites (22.5%) were nearly significant ($0.09 > P > 0.05$). Nests at one site (2.5%) were significantly over-dispersed ($P < 0.05$). The remaining 20 sites (50%) had nests placed in a spatially random pattern ($P > 0.09$). One of the control plots had aggregated nests ($P = 0.055$), two plots had over-dispersed nests ($P < 0.05$), and nests at the last plot were spatially random.

DISCUSSION

The goal of this study was to examine whether breeding songbirds in eastern deciduous forests aggregate their nests and to see if other species are aggregated around breeding Wood Thrushes. These questions were answered by using spatial point pattern analyses to quantify the degree of aggregation of nests and by comparing nest density and species composition at plots with and without Wood Thrush nests. Both of these methods demonstrate that forest songbirds do form nesting associations, Wood Thrushes are key players in these groups, and songbirds are aggregating their nests.

MSNA in Eastern Deciduous Forests

Mixed species nesting associations involving Wood Thrushes were a common occurrence on the reserve, with 65% of surveyed thrushes having other species associated with them. The number of participants in these mixed species groups was small, with most associations having two to four nesting pairs. These small groupings are consistent

with what Kleindorfer et al (2009) found in MSNA involving Darwin's small Tree Finch in which finches typically nested near one to three heterospecific nests and did not exceed five nesting neighbors.

In theory, as the number of participants increases, the costs of these associations (increased detectability by predators and competition) could increase and eventually outweigh any potential benefits such as group mobbing of predators and early detection of predators (Forsman et al. 2002). That threshold of costs/benefits may occur at low numbers for nesting songbirds, possibly due to high numbers of nest predators. At Powdermill, I observed that nest predation caused the majority of nest failures in Wood Thrush nests, an occurrence which is typical of nesting songbirds (Newell and Kostalos 2007, Lima 2009). Therefore, it is possible that nesting near a few species might provide some anti-predator benefits such as earlier warning and group mobbing without incurring as much cost of extra cues for predators provided by having multiple active nests in an area.

Formation of MSNA

As the order of arrival of these birds was not studied, the question of who is choosing to nest near whom remains unclear. Two possible scenarios are that Wood Thrushes choose to nest near other species or that other birds seek out thrushes. Both of these scenarios would result in the observed patterns of nest aggregation involving thrushes and other species. Studying the order of arrival and conducting directed heterospecific attraction experiments (Mönkkönen et al. 1997, Forsman et al. 2002) would help identify which scenario is most likely.

Species Composition of Associations

Red-Eyed Vireos, Acadian Flycatchers and Scarlet Tanagers appear to be important nesting associates of thrushes. These three species built more nests in sites that had thrushes compared with sites that lacked a nesting thrush. In addition, half of the nests found at sites with nesting thrushes belonged to these three species. Vireos, flycatchers and tanagers nest in different strata and forage in locations different from thrushes (Mowbray 1999, Cimprich et al. 2000, Whitehead and Taylor 2002). These differences potentially allow these birds to cluster their nests without experiencing negative competitive effects from these associations (Seppanen 2007). Additionally, birds with different nesting strata which associate could potentially maximize anti predator benefits because they can detect approaching predators in different strata (Goodale et al. 2010). Finally, Monkkonen et al (1997) found that Red-Eyed Vireos selected nest sites that had an artificially inflated number of resident birds, suggesting a strong heterospecific attraction by vireos toward other species and that forming nest associations might be a common occurrence for this species.

In contrast, Eastern Towhees (*Pipilo erythrophthalmus*) did not typically co-occur with nesting thrushes. The presence of strong competitive effects could keep these species apart, since the strength of competition is a factor in whether species form associations (Fletcher 2007b). Towhees nest at similar heights as thrushes and forage on the ground like thrushes (Greenlaw 1996, Evans et al. 2011). Unlike Pied flycatchers which gained benefits from nesting near resident titmice (*Parus* spp.) despite their similarities in resource use (Forsman et al. 2002), thrushes might be avoiding areas where Hooded Warblers and towhees occur if they are competing for similar resources.

Implications of MSNA

What benefits, if any, are birds at Powdermill gaining from participating in nesting associations? One potential benefit of being in a group is reduced risk of predation (Seppanen 2007, Kleindorfer et al. 2009, Goodale et al. 2010). Wood Thrushes aggressively defend their nests via bouts of loud calling and mobbing behaviors (Evans et al. 2011). As sympatric insectivorous songbirds and thrushes have common predators, these species could benefit from the anti-predator behaviors of thrushes. In this case, Wood Thrushes would act as the protector species for the other birds (Clark and Robertson 1979, Quinn and Ueta 2008). Additionally, the common participants in these associations (Thrushes, Tanagers and Vireos) nest in different strata, which enable birds to scan for different types of predators (Goodale et al. 2010). By nesting together but at different heights, birds can minimize the risk of density dependent predation as overall density within a stratum is lowered and predators have to use different search tactics to find all nests (Martin 1993, Schmidt and Whelan 1999).

Nesting associations can also form when birds use the presence of other birds as an indicator of habitat quality (Forsman et al. 2002, Fletcher 2007b). This strategy allows birds to quickly assess habitat resources upon arrival to potential territories, as birds are more successful when they start nesting earlier (Forsman et al. 2002). Since MSNA on the reserve typically involve species with different nesting and foraging strategies, birds are less likely to benefit from the habitat selection criteria of their nesting associates, at least at local spatial scales.

Conclusions

This study presents evidence for heterospecific associations among songbirds breeding in eastern deciduous forests. Sites with breeding Wood Thrushes have higher

incidences of nesting associations than sites without thrushes, suggesting that thrushes are choosing areas with higher nest densities or that other species are selecting sites based on the location of breeding thrushes. Thrushes could possibly act as protector species for nearby nesting birds and/or gain anti-predator benefits by nesting in association with other songbirds.

Many of the songbirds that form these associations have declining populations and experience high rates of nest predation, further constraining population numbers (Robinson and Wilcove 1994, Lima 2009). Understanding the prevalence and formation of interspecific associations is important as the fate of the species involved could be intertwined - a decline in one species could lead to concurrent declines in other species involved in the nesting associations.

Figure 1: Survey design for nearest neighbor searches. Non-Wood Thrush nests were located by walking along four 50-m transects that each started at either a focal Wood Thrush nest (left picture) or a control site (right picture).

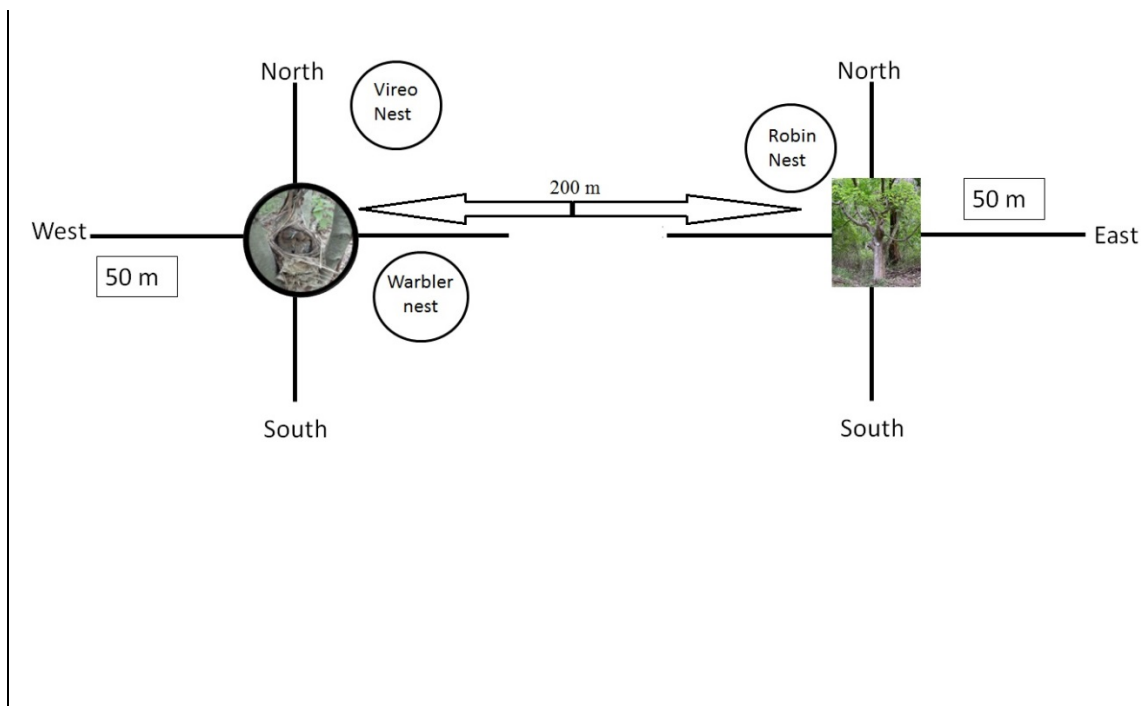


Figure 2: The number of interspecific nests at Wood Thrush plots and plots without Wood Thrush nests (control plots). Diamonds indicate means, dark horizontal bars are medians.

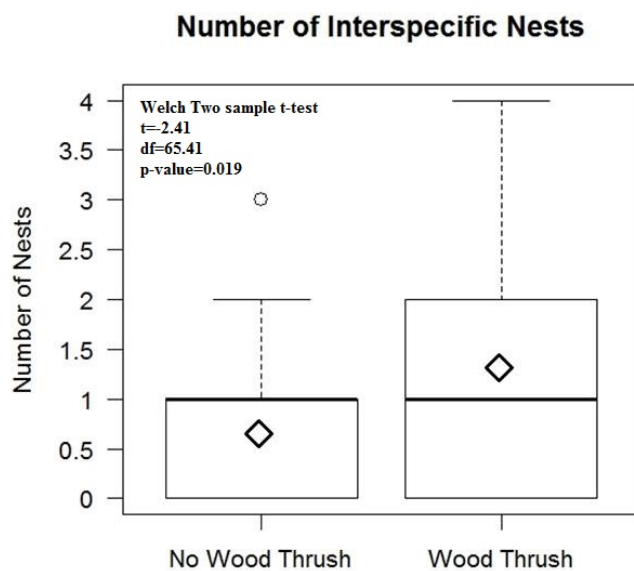


Figure 3: Proportion of sites with zero to four interspecific (non-Wood Thrush) neighbors. Each bar represents the proportion of Wood Thrush or control sites that had zero to four nesting pairs of sympatric species within 50 meters. Purple bars represent sites that had a nesting Wood Thrush and green bars are the sites that lacked a nesting Wood Thrush (control sites).

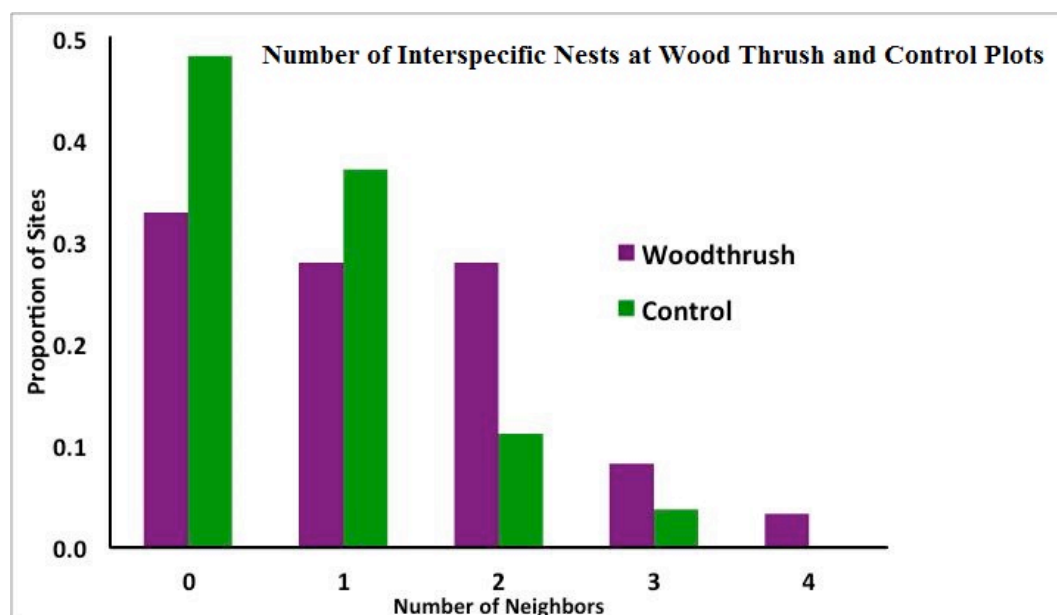


Figure 4: Number of neighboring species at Wood Thrush (focal) nests and control plots. The mean number of neighboring species around focal nests is 1.26 and around a control point is 0.63. Diamonds indicate the mean, and central bolded line is the median.

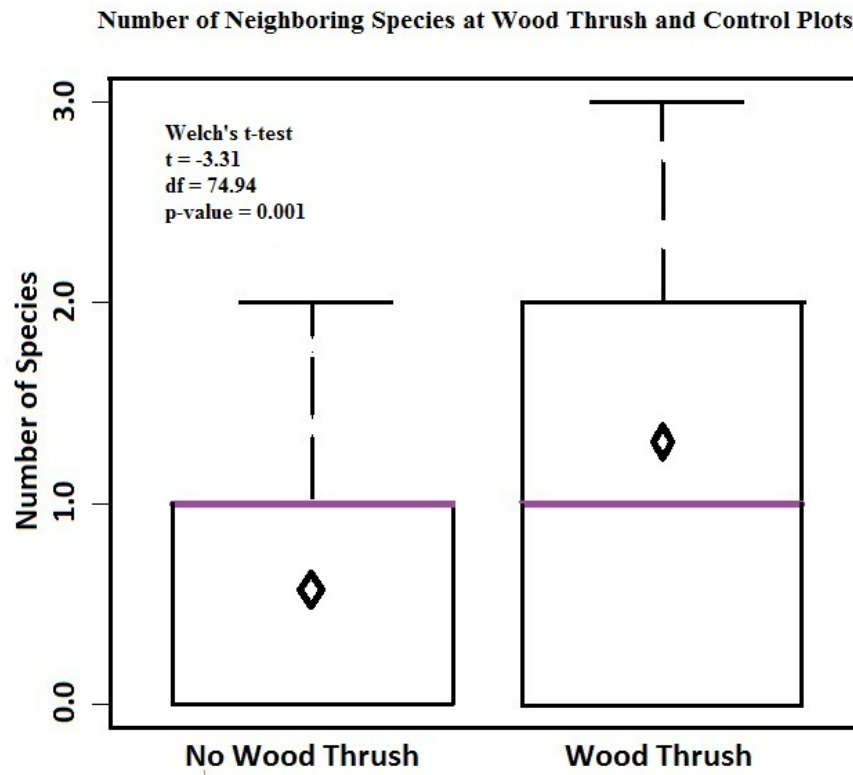


Figure 5: Species composition across Wood Thrush and control plots. This figure shows the proportion of sites that had each species nesting within it. Species found at survey sites include Acadian Flycatcher (*Empidonax virescens*), American Crow (*Corvus brachyrhynchos*), American Redstart (*Setophaga ruticilla*), American Robin (*Turdus migratorius*), Black Throated Blue Warbler (*Dendroica cerulean*), Downy Woodpecker (*Picoides pubescens*), Eastern Towhee (*Pipilo erythrophthalmus*), Gray Catbird (*Dumetella carolinensis*), Hooded Warbler (*Wilsonia citrine*), Northern Cardinal (*Cardinalis cardinalis*), Ovenbird (*Seiurus aurocapillus*), Rose breasted Grosbeak (*Pheucticus ludovicianus*), Red-eyed Vireo (*Vireo olivaceus*), Red-bellied Woodpecker (*Melanerpes carolinus*), and Scarlet Tanager (*Piranga olivacea*). Significance values are based on chi-square tests of abundances of each nesting species at sites with and without Wood Thrushes (*= $0.05 < P < 0.09$, **= $P \leq 0.05$, ***= $P \leq 0.01$).

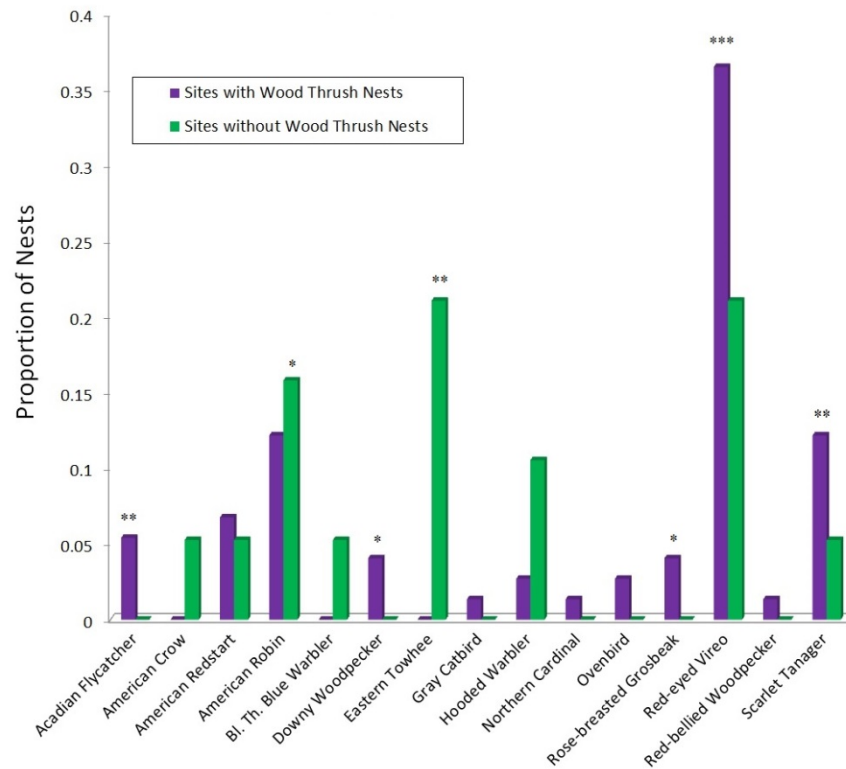


Table 1. Distribution patterns of nests at Wood Thrush plots. Table 1 shows the number of plots that had aggregated, random, or over-dispersed nests, based on the R value (observed nearest neighbor distance/expected nearest neighbor distance in spatial random pattern). All plots had a central Wood Thrush nest and one or more songbird species nesting within 50 m of that Wood Thrush. Plots with nests that were significantly closer or farther from one another than expected in a spatially random pattern are denoted as follows: **= $P \leq 0.05$, *= $0.05 < P < 0.09$

Spatial Pattern	Number of Sites with Pattern
Aggregated	19 (10**, 9*)
Random	20
Over-dispersed	1 *
Total	40

CHAPTER 2

Heterospecific attraction as a possible cause of aggregated nests in a songbird community

ABSTRACT:

Mixed species nesting associations (MSNA) occur when multiple species aggregate nests in areas with patchily distributed resources or when birds select sites based on the presence of other species (heterospecific attraction). Nesting associations were observed among songbirds at Powdermill Nature Reserve in western Pennsylvania, but the causal factor behind these associations remains unknown. The goal of this study was to test the hypothesis that birds form MSNA by selecting the same habitat features. To test this hypothesis, I compared habitat variables in plots that had zero to four nests. Specifically, I measured average leaf litter depth, percent cover of leaf litter, ground vegetation, canopy cover, water cover, and rock cover within 5 meter radii plots. In addition, I determined the number and species composition of shrubby stems and trees within five and 10 meter plots respectively. None of the habitat variables were significantly associated with the number of nests in an area, providing preliminary evidence that nest associations do not form because birds select sites with the same habitat features. Instead, these results suggest that a different mechanism, such as heterospecific attraction, or founder effects might be causing multiple species to aggregate nests on the reserve.

INTRODUCTION:

Mixed species nesting associations occur when different species aggregate their nests in time and space (Kleindorfer et al. 2009). These associations can form when 1) individuals select the same patchily distributed resources (Morales et al. 2012) and 2) when individuals use the presence and behaviors of other organisms as cues when making settlement decisions (Seppanen 2007, Nocera et al. 2009, Fletcher and Sieving 2010). These two mechanisms are not mutually exclusive, as organisms can select an area based on resources, and then be further constrained within that area by choosing locations near other individuals (Morales et al. 2012).

Birds that co-occur are predicted to be generalist species that select similar habitats and therefore can benefit from the information provided by the location and behavioral cues of other birds nesting nearby (Mönkkönen et al. 1997, Morales et al. 2012). In addition, nest associates are usually not direct competitors, especially for food resources, and nest and forage at different heights, a strategy that can reduce density dependent predation within each strata (Martin 1993, Schmidt and Whelan 1999, Fletcher 2007a, Goodale et al. 2010). Therefore, species that participate in MSNA are predicted to nest and forage in different sites yet select similar habitat features, such as abundant canopy cover or a high diversity of plants.

An additional consideration in nest selection studies is the extent to which organisms use social information when choosing habitats. Several studies have documented cases where the presence (real or simulated) of other organisms has influenced settlement decisions, even causing individuals to settle in poorer quality habitat (Fletcher 2007a, Betts et al. 2008, Morales et al. 2012, Miller et al. 2013).

Conspecific and heterospecific attraction are more common in migratory species that use the presence of their own and other species as indicators of habitat quality to expedite the habitat selection process (Mönkkönen et al. 1997, Forsman et al. 2002).

The goal of this study was to determine if forest breeding passerines select the same habitat factors. I hypothesized that there was a positive correlation between the number of nests and local scale habitat features, if birds are using habitat cues in nest site selection. If these correlations are not found, then that result will lend support to alternate hypotheses, including that MSNA are forming because birds are selecting areas based on social information independent of habitat cues.

METHODS:

Study Sites:

Habitat surveys were conducted at a subset of the Wood Thrush and control plots established in the spatial analysis study (Chapter 1) from August through October 2010-2012 at Powdermill Nature Reserve (GPS coordinates +40.16019891, -79.27180242). In total, habitat surveys were conducted at 51 sites. These sites consisted of locations without nesting Wood Thrushes (n=18) and places with nesting Wood Thrushes (n=33).

I followed a modified protocol based on the Breeding Bird Survey methods for measuring habitat characteristics (Martin et al. 1997). I established two circular plots that had radii of 5 and 10 meters at each site and divided them into quarters with the center either below the Wood Thrush nest or at a tree in the center of the control site.

Five Meter Radius Plot

I estimated the percent cover of ground vegetation (vegetation less than 50cm tall), rocks, fallen snags, water, and leaf litter. To estimate these values, I visually

estimated the percent ground cover in each quadrant and then took the mean of all quadrants. Using a densitometer, I measured the percent canopy cover in each quadrat of the circle and then took the average of the four measurements. I also measured litter depth in each quadrant at locations that best represented litter coverage of each quadrant and took the mean of the four values.

Additionally, I identified all herbaceous plant species taller than 50 cm (Petrides 1973) and counted the number of stems of each species. Most plants were identified to species, but certain groups of plants, including *Smilax* and *Rubus*, were identified only to genus. I typically counted stems at the base of each plant. For large entanglements of *Smilax* spp., where the base of the plants could not be seen, I counted the number of stems coming off of the center of the plant.

Ten Meter Radius Plots

I measured the diameter at breast height (DBH) of each tree >8 cm DBH within the ten meter radius and identified the species (Petrides 1973, Tekiela 2004).

Statistical Analysis

Statistical analyses were conducted in R Studio (RStudio 2012, R Core 2014). Habitat variables at Wood Thrush and Control sites were compared using MANOVA and PCA. No significant differences were found for any habitat variable between thrush and control sites (see results). Therefore, these sites were combined, and MANOVA and PCA were conducted again, using the full survey sample of 51 sites. These analyses were run to identify differences in habitat factors among sites with zero to four nests.

RESULTS:

Wood Thrush and Control Sites:

There were no differences in habitat between sites with and without Wood Thrush nests (MANOVA: $F = 1.1313$, $p = 0.3647$, $df=1$). Individual habitat variables including tree and shrub species abundance and richness, leaf litter depth, percent cover of ground vegetation and percent canopy cover did not differ between Wood Thrush and control sites (ANOVA: $P > 0.05$, Table 1).

Number of Nests:

Because there were no differences between Wood Thrush and control sites, I combined all sites and looked for differences in habitat variables among sites that had zero to four nests. Sites with zero to four nests did not differ in vegetation composition, leaf litter cover, and percent cover of water and downed logs (MANOVA: $F=0.81227$, $p=0.7872$, $df=4$). The mean values of all habitat factors, including stem density and richness, tree density and richness, and canopy cover, were not significantly different across sites with zero to four nests (ANOVA: $p > 0.05$, Figure 1, Table 2).

I ran a principle component analysis to determine which habitat factors explained the variation in the dataset and to determine if sites with different nest densities clustered in ordination space based on any habitat factors. The first and second principle components combined explained only 39.4% of the total variation in the dataset (Table 3). Percent cover of ground vegetation and litter were significantly correlated with the first principle component. The number of trees and the species richness of trees were significantly correlated with the second principle component (Table 4). Sites with the same nest density were not clustered along these components.

DISCUSSION:

The habitat factors measured in this study did not explain the occurrence of nest associations at Powdermill Nature Reserve. Of the eleven habitat traits measured, tree density and richness, percent cover of ground vegetation, and leaf litter cover explained most of the overall variation in the dataset. However, none of these traits were significantly associated with the number of nests at a site. These results suggest that an alternate causative mechanism, such as heterospecific attraction, may be behind the nest aggregations seen at Powdermill.

The lack of correlation between habitat factors and nest density is a surprising result, given the large number of studies that show links between measured habitat factors and nest placement and daily nest survival rates (Martin 1991, Frank R. Thompson 2007). The number of potential nest sites, for example, is a factor that is positively associated with nest site selection in songbirds, as predator foraging efficiency decreases in areas with more potential prey sites to search (Chalfoun and Martin 2009). In addition, nest placement has been correlated with high vegetation cover as this feature can impede predators and help conceal nests (Martin 1993, Driscoll et al. 2005). Several of the aggregated species in this study (Red-Eyed Vireos, Wood Thrushes) tend to select nest sites in areas with moderate to dense understory vegetation (Cimprich et al. 2000, Evans et al. 2011), yet no pattern existed between the number of nests and vegetation density. One possibility for this lack of correlation is that birds are selecting habitats with more potential nest sites rather than total vegetation cover. My survey techniques did not test for the number of nest sites directly, so perhaps areas with more birds had more potential nest sites, despite not having more vegetation cover.

Another possible cause of aggregated nests is that birds select sites based on common food resources. The birds involved in MSNA are all insectivores, so availability of food could be a contributing factor in the occurrence of MSNA. Birds are able to assess the abundance of food at different sites, and select areas with more food (Burke and Nol 1998). The typical foraging locations of the most commonly aggregated species, Wood Thrushes (leaf litter), Red-Eyed Vireos (lower canopy), and Scarlet Tanagers (upper canopy), do not overlap (Mowbray 1999, Cimprich et al. 2000, Evans et al. 2011), making the presence of food resources is an unlikely contributor to MSNA.

In addition to selecting sites based on similar habitat traits, birds may also form MSNA by using social cues in settlement decisions. Social cues are common and powerful drivers in site selection in many avian species, including some of the species studied at Powdermill (Mönkkönen et al. 1997, Monkkonen and Forsman 2002, Seppanen et al. 2007, Betts et al. 2008). Social cues can be strong enough to override an individual's assessment of habitat. Researchers manipulated Black-Throated Blue Warblers (*Setophaga caerulescens*) into selecting poorer quality sites in year two of their study by simulating conspecific cues in poor quality patches in year one. Hemipteran insects (*Narnia femorata*) selected resource rich nest sites in the absence of social cues, but would select resource poor sites in the presence of heterospecific insects that were placed in poor quality sites (Miller et al. 2013).

Species involved in nesting associations at Powdermill would likely benefit from using social cues to select habitat. Nest survival is higher in birds that initiate egg laying earlier, so for these migratory species, quickly assessing potential nesting habitat is crucial to their reproductive success (Forsman et al. 2002). Migratory songbirds breeding

in forests can be short-lived and many species produce only one to two broods per year, so their opportunities to select appropriate breeding habitats is limited (Nocera and Betts 2010). Finally, given the high degree of nest predation generally seen in songbirds breeding in forests (Lima 2009), individuals in MSNA can potentially reduce the risk of predation by earlier detection of predators, detection of different types of predators by birds nesting at different heights, and by lower individual predation risk (Hamilton 1971, Goodale et al. 2010).

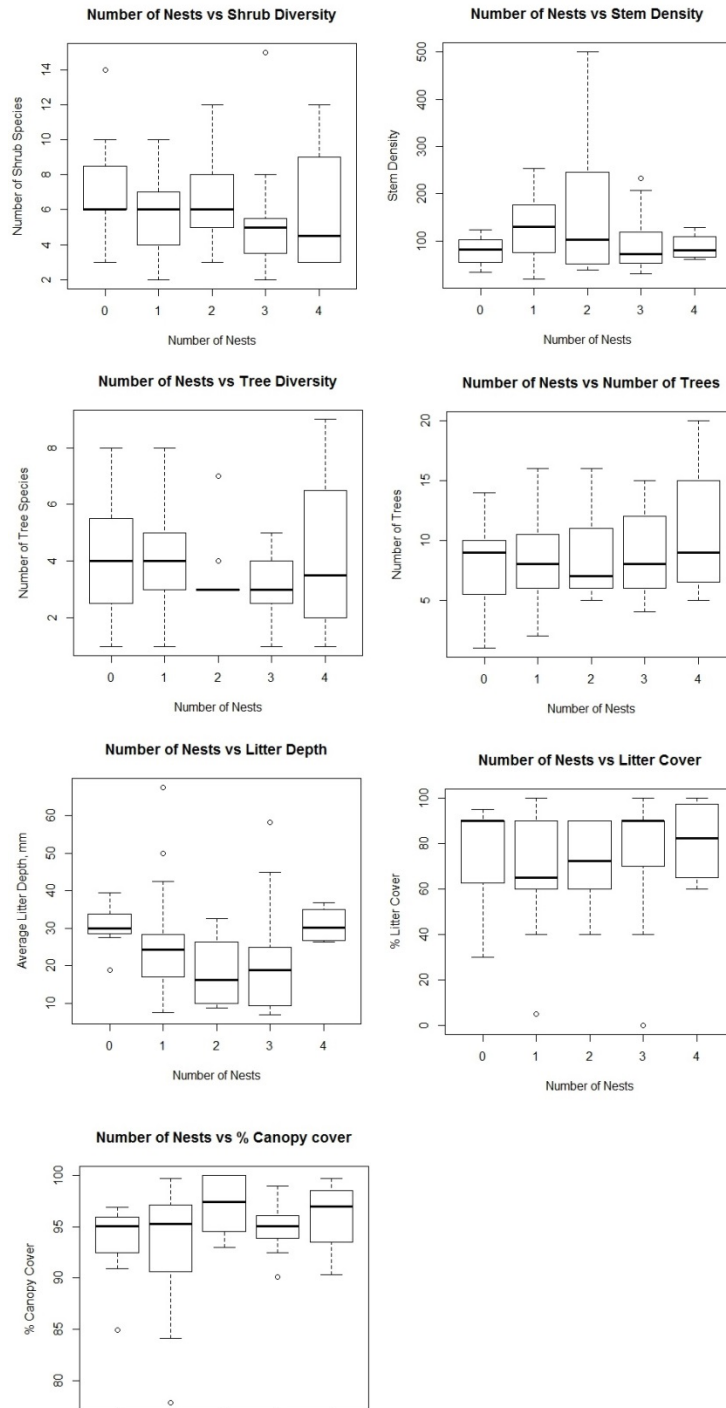
Conclusions

The number of breeding songbirds at Powdermill Nature Reserve is not correlated with local habitat features. This result suggests that another mechanism is driving the formation of mixed species nesting associations on the reserve. Participating birds typically do not overlap in foraging sites, so the likelihood that shared food resources cause birds to aggregate their nests is low. Birds could choose the same areas because these sites have a greater number of potential nest sites, a strategy that could reduce predation risk. Alternatively, MSNA could form due to the use of social information, specifically heterospecific attraction, in which individuals use the presence of other species to select sites. Migratory songbirds on the reserve are good candidate for heterospecific attraction because they have limited time in which to select habitat and lose the majority of their nests to predation, so could benefit from the information on habitat quality and the anti-predator behaviors of other species. Future studies that test for heterospecific attraction, are needed to confirm that the presence of other species alter settlement decisions of forest breeding songbirds at Powdermill.

Table 1: Mean Values of habitat variables at Wood Thrush and Control sites. This table lists the mean value and standard deviation of each habitat factor at sites with and without Wood Thrushes. P-values are based on ANOVA.

Variable	Wood Thrush Sites Mean \pm St. Dev.	Control Sites Mean \pm St. Dev.	P-value
Litter Depth	24.3 \pm 14.0	26.1 \pm 11.7	0.64
% Rock Cover	9.8 \pm 13.4	13.3 \pm 24.5	0.51
% Water Cover	2.1 \pm 8.6	0.6 \pm 2.4	0.45
Number of Trees	8.2 \pm 3.7	9.4 \pm 4.1	0.28
Number of Stems	131.4 \pm 100.9	94.2 \pm 49.4	0.15
% Canopy cover	95.1 \pm 3.8	93.4 \pm 5.6	0.21
% Litter Cover	74.5 \pm 19.7	66.1 \pm 29.5	0.23
% Ground Vegetation Cover	37.3 \pm 23.3	39.7 \pm 27.9	0.74
# of Shrub Species	6.0 \pm 3.0	6.3 \pm 2.7	0.75
# of tree species	3.6 \pm 1.6	3.9 \pm 2.0	0.52
% log cover	11.9 \pm 8.7	9.8 \pm 5.7	0.36

Figure 1: Box plots showing how each measured habitat variable varies at sites with zero to four nests. Shrub and tree diversity represent the number of shrub and tree species found within a 5 or 10 meter radii vegetation sampling plot (see methods). Litter cover is the percent cover of leaf litter within a 5 meter radius vegetation sampling plot.



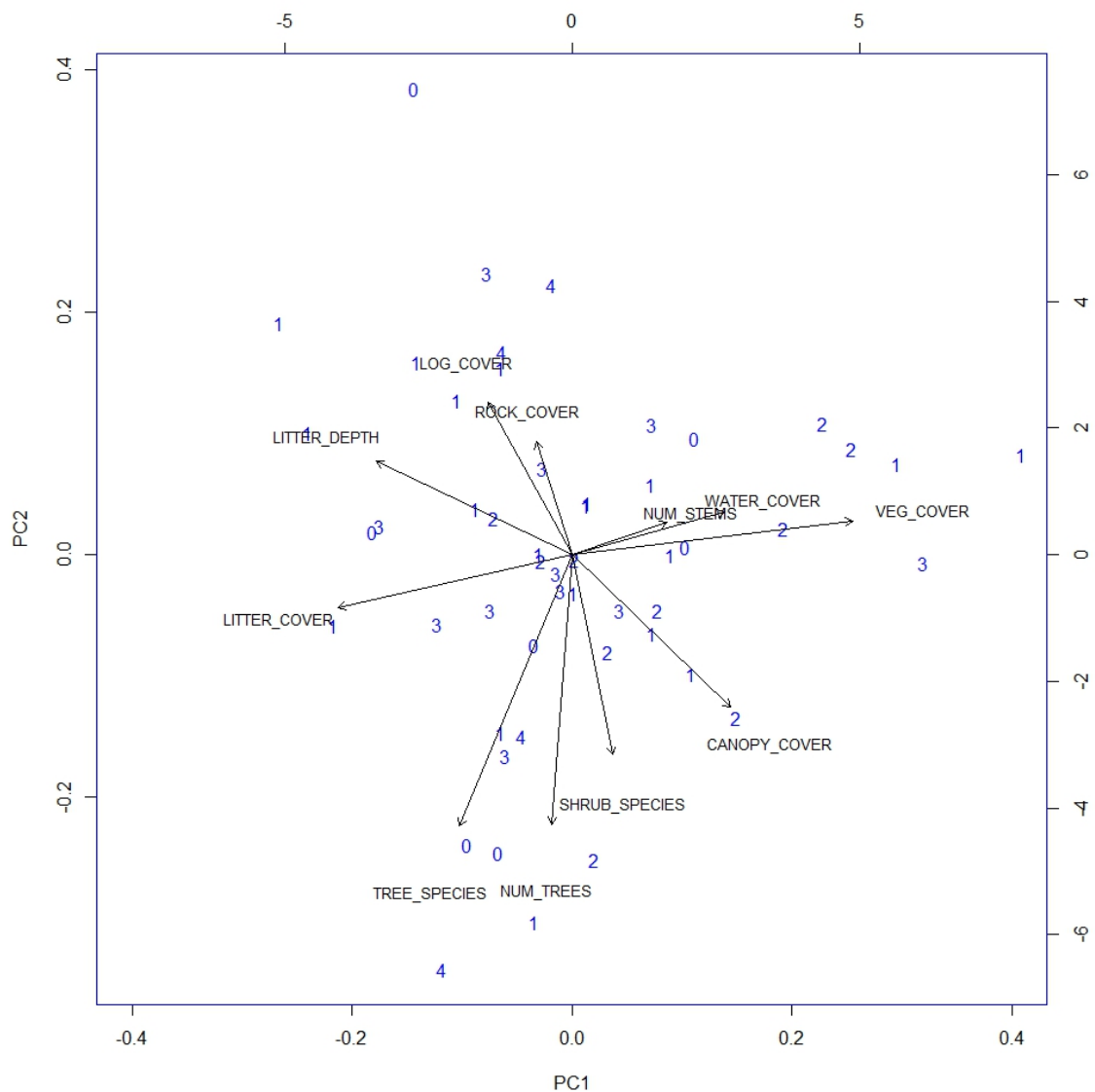


Table 2: ANOVA scores of habitat covariates. This table shows no significant difference for each habitat variable across sites having zero to four nests.

VARIABLE	Sum Sq	Mean Sq	F value	Pr(>F)
Average Litter Depth	825.2	206.3	1.214	0.3178
Percent Cover of Rock	246.8	61.71	0.1794	0.9479
Percent Cover of Water	63.01	15.752	0.3005	0.8761
Number of Trees	25.01	6.2521	0.3991	0.8083
Number of Stems	38531	9632.7	1.2839	0.2901
Percent Canopy Cover	133.31	33.328	1.7373	0.158
Percent Cover of Litter	870.7	217.67	0.3694	0.8292
Percent Cover of Ground Vegetation	2013.4	503.35	0.8111	0.5246
Percent Cover of Downed Logs	237.26	59.314	0.9876	0.4238
Shrub Species Richness	20.41	5.1026	0.5986	0.6655
Tree Species Richness	6.624	1.656	0.5094	0.729

Table 3: Percentage of variance explained by first seven principal components. The first two components explain 39% of the variation in the dataset.

PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.5298	1.4122	1.1023	1.03603	1.01025	0.94475
Proportion of Variance	0.2127	0.1813	0.1105	0.0975	0.09278	0.08114
Cumulative Proportion	0.2127	0.3941	0.5045	0.60210	0.69488	0.77602

Table 4: PCA loadings for first two principle components of habitat variables.

	PC1	PC2
Percent canopy cover	0.31552288	-0.29834267
Average litter depth	-0.38990174	0.18231068
Percent cover of litter	-0.46554748	-0.10286149
Percent cover of rock	-0.07101081	0.22240008
Percent cover of ground vegetation	0.55874443	0.06701524
Percent cover of water	0.30279240	0.08344186
Percent cover of downed logs	-0.16799604	0.29908075
Shrub species richness	0.08114778	-0.39130982
Number of trees	-0.04023186	-0.52745372
Tree species richness	-0.22467687	-0.53053594
Number of stems	0.18936855	0.06332544

CHAPTER 3

Nest predation varies with number of neighbors and nest height

ABSTRACT

The goal of this study was to examine the effects of nest density and vertical distribution on daily egg survival rates. This study consisted of two parts – a field study of nesting Wood Thrushes and an artificial nest study where nest density and vertical distribution were manipulated. For the field study, I examined how daily survival rates (DSR) of Wood Thrush nests varied when birds nested near different numbers of nesting neighbors. I also examined DSR for artificial nests placed at different heights and densities. DSR of thrushes showed no correlation with the number of neighboring nests and a positive correlation with distance from the nearest neighbor. In three of the four artificial nest studies, DSR decreased as the number of nests at a site increased, and was lower when nest height varied at those sites. These results suggest that density dependent predation is occurring on the reserve, and that nesting in different strata does not diffuse the impacts of this type of predation. Questions remain about why thrushes aggregate their nests with other species, given that neighboring nests negatively affects DSR.

INTRODUCTION

Given the decline of many songbird populations, understanding factors that affect breeding success is an important goal (Robinson and Wilcove 1994). The majority of losses during the nesting season in forest breeding songbirds is due to nest attacks,

indicating that predation is an important factor potentially limiting songbird populations (Robinson and Wilcove 1994, Lima 2009). One factor that can affect rates of nest survival is the arrangement and density of nests in an area. Birds that aggregate their nests can lower the risk of nest attacks through group defensive strategies and reduced individual risk (Martin 1993). However, songbirds nesting in areas with density dependent predators potentially increase predation risk by aggregating nests (Schmidt and Whelan 1999). The goal of this chapter is to explore how the number and arrangement of nests affects daily nest survival rates.

Songbirds that nest near other birds can reduce their individual risk of predation in several ways. First, nest aggregations lowers the risk to each individual in the group because predators could become satiated after consuming the contents of other nests, could focus foraging efforts on the outermost nests of a group, or could miss a nest within a larger group (Hamilton 1971, Mönkkönen et al. 1997). In addition, birds often show group mobbing behaviors, where several adults will attack a predator (Seppanen 2007, Lima 2009). This communal response again lowers the individual risk of harm to the adult participants and creates a stronger response to drive away the predator.

The configuration of nests can also impact nest survivorship. Group nesting can lower predation risk, and this risk can be further abated if birds nest at different heights (Martin 1993, 1996). Nesting in different strata reduces the density of nests in each stratum, which can lower the risk of density dependent nest predation (Martin 1993). Predator efficiency could also decrease if predators have to search multiple strata and sites to find nests (Chalfoun and Martin 2009). Another potential benefit is that birds

breeding at different heights can detect different types of predators (Kleindorfer et al. 2009, Goodale et al. 2010).

Aggregated nesting also poses potential risks to breeding birds. Clustered nests can be easier for predators to detect because olfactory, auditory, and visual cues increase with each additional nest (Varela et al. 2007). Multiple nests provide a larger reward for foraging predators, causing them to seek out nest clusters (Martin 1993). Finally, density-dependent predation can result in several nests being attacked over a small area (Schmidt and Whelan 1999).

Songbirds at Powdermill Nature Reserve form small nest aggregations of two to four nests, and these associations do not seem to correlate with measured habitat characteristics. In this study, I test the hypothesis that Wood Thrushes increase their daily nest survival rates by breeding within 50 meters of other songbird nests. Additionally, I conducted two artificial nest experiments to examine the effects of nest density and height on nest survival. I tested the hypotheses that nest survival varies with the number of nests in area, peaking at moderate densities and decreasing at high densities. I then examined if nest survival increases when nests are placed at different heights. Comparing the results of the study on Wood Thrushes to the artificial nest study can bridge the gap between theory and reality regarding the optimal configuration of nests in an area.

METHODS

Locating and Monitoring Wood Thrush Nests:

Nest searching took place during 0600-1000 hours from May 10 through July 31 2009-2011 in the forested areas of Powdermill Nature Reserve in Western Pennsylvania. The reserve contains a square grid system, with stakes located every 100 m on north-

south, east-west gridlines. All stake geolocations are mapped and tagged. This grid system was set up by scientists to map the vegetation on the reserve, and vegetation surveys were centered at the locations marked with the stakes. In this study, a subset of these staked locations were used as starting points for nest searches. Using ArcView software, fifty stake points were selected throughout the reserve at random with the selection criteria that points were greater than 100 meters from a road or building to avoid most edge effects of nesting songbirds.

Stake points were visited a minimum of two times per year. I searched visually and aurally for Wood Thrushes at each point for up to 10 minutes or until a Wood Thrush was detected. Once a Wood Thrush was detected, I searched for its nest by following singing and calling individuals to the nest or by visual searching of vegetation in appropriate habitat within a male's territory. I visited all 50 stake points in 2009 and 40 sites in both 2010 and 2011. I included incidental nests found while hiking to the survey points. Nest positions were recorded using a Garmin GPS 72 handheld unit and sometimes discretely marked in dense vegetation to facilitate relocation.

I revisited active nests every three to five days until the nestlings had fledged or the nest had failed. At each visit, I recorded the number of eggs and the number and approximate age of nestlings. If the nest was empty, I observed the nest contents and the nest site for signs of predation or fledging. I considered a nest successful if at least one nestling fledged. I assumed a brood had fledged if the nest was empty 12 days after the last nestling hatched (Evans et al. 2011) and the nest did not show signs of predation (broken branches around nest, nest on ground, claw marks on trunk, etc.). Additionally, I looked for signs of fledgling activity including droppings in and around the nest, a

molded down nest cup, high levels of Wood Thrush activity in the area, and sighting of fledglings near the nest.

Locating nearest neighbors

Searches for non-Wood Thrush nests took place from July through October each season. In an effort to minimize disturbance to nesting thrushes, I conducted these surveys after each Wood Thrush finished its nesting attempt. I searched for nests within a 50-meter radius circle around each Wood Thrush nest (total search area per site = 7854 m²). To standardize search efforts across sites, I looked for nests every ten meters along four 50-meter long transects, one in each cardinal direction starting from the focal Wood Thrush nest (see Fig 1 in Chapter 1). I scanned for nests along each transect and the surrounding area to maximize coverage of each site. With this method I was able to systematically search the site and find well camouflaged nests such as those positioned on the ground and in high canopy vegetation. It is possible that extremely small and cryptic nests, such as those of Black and White Warblers, were missed, resulting in an underestimation of the number of neighboring nests in an area. Nest searching was completed by J. Deo with the assistance of several trained field assistants. J. Deo confirmed the identity of all nests. I recorded the location of each nest with a handheld Garmin GPS 72 unit. We identified the species that built each nest by either observing the parents at the nest or by using specific characteristic nest traits including size, appearance, and location (Harrison et al. 1975).

Daily nest survival

I used the program MARK to model daily nest survival rates (White and Burnham 1999, Dinsmore et al. 2002). I compared multiple models and selected the model with

the lowest AIC value. The candidate model set included models which incorporated nest age, number of neighboring nests, distance to the nearest nest and year (see Table 2 for list of models). I used the likelihood ratio test in MARK to determine if covariates in the top ranked model had a significant effect on nest survival.

Artificial nest study

In 2010 and 2011, I conducted two experiments at Powdermill Nature Reserve to look at the effects of nest density and nest strata on nest predation. I used artificial canary nests baited with two quail eggs and one plasticine egg that was the same size and shape of the quail eggs. To minimize human scent cues, I used gloves when handling the nests and eggs. I attached nests to plants with wire, and covered the wires with leaf litter. For ground nests, I pushed the wire into the ground and then covered the wires with leaf litter. Nests were exposed to potential predators for 10-14 days. In 2010, I collected nests after 10 days and recorded their binary outcome (successful or attacked). In 2011, I collected nests after 11-14 days and monitored nests every three to four days to estimate DSR.

Experimental set-up

Ten sites (2010) and eight sites (2011) across Powdermill Nature Reserve were selected. The center point of each site was 175 m away from a trail and in mixed deciduous forest habitat. Each site consisted of four treatments consisting of one, three, six, and nine nests. Treatments were arranged in the shape of a plus, with each treatment being located one point of the plus (Figure 1). For the multi-nest treatments, one nest was the designated focal nest, and the other nests were the neighboring nests. The neighboring nests were placed at equal angles from one another around the focal nests. For example, the treatment with nine nests consisted of the focal nest and eight

neighbors. In that treatment, each neighboring nest was placed 45 degrees from its neighbor. To equalize bias caused by being the treatment closest to the trail, treatments were rotated in each replicate so that each different density treatment was closest to the trail in at least one replicate.

Density Experiment:

In this experiment, I examined the effects of nest density on predation. I set up 89 nests in 2010 and 76 nests in 2011. Nests were placed in sites typical of Wood Thrush use (low shrub). All nests were placed in shrubs or small trees, and nests were placed between 0.9-1.5 meters above the ground on a branch. The only variation among treatments was the number of nests (Table 1). In 2011, I monitored nest predators with four thermo-sensing camera traps. I placed one camera at a random nest in each density treatment within the same replicate.

Height Experiment:

This experiment examined the effects of varied nest height on predation. I set up 83 nests in 2010 and 76 nests in 2011. The focal nest was placed in a site typical of Wood Thrush use (low shrub), and neighboring nests were placed on the ground (0 meters off ground), in low shrubs (0.9-1.5 m off ground) and high shrubs (> 1.8 meters off ground) strata (Table 1). In 2011, I monitored nest predators with four thermo-sensing camera traps. I placed one camera at a nest in each density treatment within the same replicate. I put two cameras at ground nests, one camera at a high shrub nest, and one camera at a low shrub nest.

Nest Survival Analyses

I used logistic regression to model the effects of nest density and nest height on nest survival. I used R studio to do the logistic regressions. I ran four separate analyses, one for each experiment in each year. In 2011, I also analyzed daily nest survival using the program MARK. I ran several candidate models to test whether different factors, including nest height and the number of neighbors, best explained daily nest survival (see Table 6). For all models, I assumed DSR was constant over time. I used model averaging to determine the weighted average estimate of daily nest survival when candidate models had similar weights.

RESULTS

Overall Nest Success:

Nest success was recorded for Wood Thrush nests in 2009-2011 and artificial nests in 2010 and 2011 (Table 2). Overall survival of Wood Thrush nests was high, with 79% of observed nests having at least one nestling fledge. In the experiments where the number of artificial nests at a site varied, 66% (2010) and 46% (2011) of nests survived during the course of the experiment. 69% (2010) and 9% (2011) of nests survived the duration of the artificial nest experiment where both nest density and nest height varied.

Daily Nest Survival Analysis of Wood Thrushes:

Daily nest survival (DSR) data was analyzed for 29 Wood Thrush nests. The model in which DSR varied with time, the number of neighbors, and the interaction of time and neighbor number received the most support out of all tested models (AIC Weight=0.992). This model showed a significant interaction effect between time and the number of neighbors (likelihood ratio test $P < 0.01$). The remaining models received nominal to zero support (Table 3).

Artificial Nest Study: Predator Species Composition

Images were retrieved from six of the eight camera traps set up at artificial nests. Two of the cameras malfunctioned. Nine mammalian species were photographed approaching nests (Table 4). Black Bears (*Ursus americanus*) and White-Tailed Deer (*Odocoileus virginianus*) were the most common visitors to the nests and were photographed eating quail eggs.

Artificial Nest Study-Effects of Nest Density and Nest Height on Nest Outcome

Logistic regression was used to model the effects of nest density and nest height on the survival outcome of artificial nests (Table 5). High nest density significantly increased nest predation of nests placed at similar heights in 2010 ($P < 0.05$) and had a nearly significant effect in 2010 ($P = 0.08$) on nests placed at different heights (Figures 2a and 3a). Lower nests were attacked more frequently than higher nests in both the density and height experiments in 2010 ($P < 0.01$, Figure 4a). Neither nest density (Figures 2b, 3b) nor nest height (Figure 4b) predicted nest outcome in 2011 ($P > 0.05$).

Artificial Nest Study-Modeling Daily Nest Survival in 2011

Nest survival models were run using MARK for the density and height experiments in 2011 (Table 6). In the density experiment, the four candidate models which included models for nest density and height effects on nest survival, received roughly equal support (AIC weights 0.233-0.293). The number of nests was not significantly correlated with survival (Table 7, Chi-square: $P > 0.05$). For the height experiment, the models that included the number of nests (survival and number of nests) and the null model (survival) best predicted daily nest survival (AIC weights of 0.384 and

0.338, respectively). However, neither nest density nor nest height was significantly correlated with daily nest survival (Table 7, Chi-square >0.05).

In both experiments, the daily nest survival rates were averaged across models as multiple candidate models received equal support (Table 8). Average daily survival rates did not differ between the two experiments (t test: $t = 1.36$, $df = 6$, $p = 0.89$)

DISCUSSION

Number of neighbors

The best fitting nest survival models in the natural thrush study included the interaction between the number of nests and time as a significant covariate. The time dependent model with nest density but no interaction effect received no support. This result indicates that the number of neighbors by itself does not affect Wood Thrush nest success. Nest survival depending on the interaction between time and nest density is reasonable, given the phenology of the nesting season and the potential effects of multiple breeding pairs within one location. Nest survival has been shown to change over time, as the cues given by birds increase during the nesting season due to nestling calls and increase parental activity at the nest (Lima 2009). In addition, nest survival could potentially change to a greater extent over time when neighbors are factored in, because sympatric nesters also give off cues that predators can detect, but also share in detecting predators (Martin 1993, Varela et al. 2007).

For the artificial nest experiments in 2010, nest survival decreased as the number of neighboring nests increased. The results suggest the presence of density-dependent predation. One of the predictions in density-dependent predation is that the predator will consume a larger proportion of prey as prey density increases (Schmidt and Whelan

1999). Density dependent predation could also explain the high levels of predation seen in 2011 when many nests were attacked by bears (evident from camera trap images and patterns of nest destruction).

In 2010, the proportion of successful nests was high (0.8-1) for solitary nests and nests in groups of three. At these low densities, the probability of detection by predators is potentially lower, especially because of lower olfactory cues than at sites with higher nest density (Varela et al. 2007). Interestingly, Wood Thrushes nested near up to four neighbors. Theoretically, there may be an “ideal” number of neighbors where the benefits of nesting in aggregation are not outweighed by the ability of predators to detect larger clusters of nests (Forsman et al. 2002). At Powdermill, this balance seems to be reached at relatively low nest densities.

Nest Height and Stratum:

In 2010, artificial nest survival was positively correlated with nest height for both the density and height experiments. Studies show conflicting results on whether nests on the ground or in shrubs have higher predation risk (Schmidt and Whelan 1999). Nesting at different heights can potentially increase nesting success because the density of nests per stratum is reduced, and predators have to search more potential nest sites to find occupied ones. However, in 2011, the average daily survival estimates for artificial nests were not different between nests placed at similar heights (density experiment) and nests placed at different heights (height experiment). This result contrasts that found in a study of nests in Arizona, where nest success increased when nests were placed at multiple strata (Martin 1993). One possibility is that predation rates vary among strata, in which

case, analyzing survival within a stratum instead of across strata could provide clearer results (Schmidt and Whelan 1999).

Limitations of Artificial Nests

While useful in studies such as this one, artificial nests have limitations (Faaborg 2004). These nests lack parents and nestlings, so cues given off by birds are absent, a factor which can influence how nests are detected by predators (Villard and Part 2004). In this study, these experiments were conducted after most birds finished breeding for the season (late July and August), so the composition of predators searching for nests might be different from earlier in the season. Regardless of these limitations, the artificial nests used in this study provided a way to vary nest density and nest height in a standardized manner.

Conclusions

This study showed that nest success generally decreases as the number of nests within an area increases. In addition, nest success was higher when nests were spaced farther apart and in the same stratum. However, Wood Thrushes aggregate their nests with other species that often nest in different strata than the thrushes. The question, then remains - what benefit, if any thrushes gain from breeding near other birds? One possibility is that parental survival is higher when thrushes form nesting associations with other species. Additionally, thrushes may use other species to make rapid habitat assessments upon arrival of the breeding grounds. Alternatively, other species may gain benefits from nesting near thrushes, and thrushes may not incur significant costs or benefits from participating in mixed species associations.

Figure 1: Experimental design for Artificial Nest Study. *DIST from trail to nest: 100 m; DIST from center to nest: 75 m. The treatment placed closest to the trail was rotated so that each treatment was closest to the trail in at least one replicate.

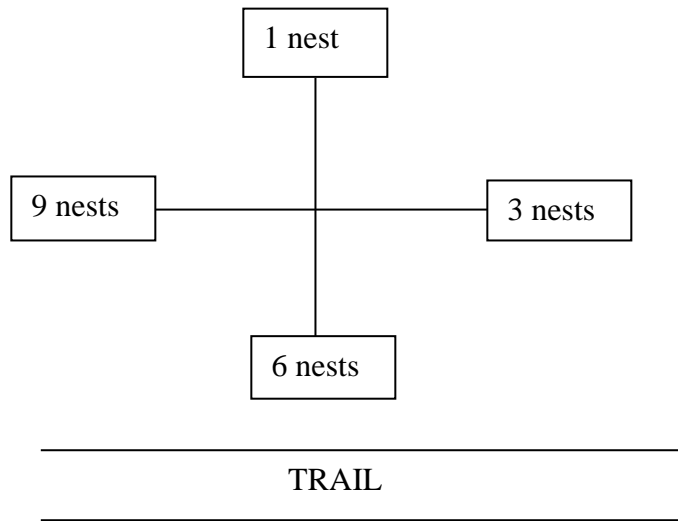


Table 1: Experimental treatments in Artificial Nest Study. In the density experiment, I examined predation rates among different densities of nests placed in the same strata (2-dimensional space). For the height experiment, I examined predation rates among nests placed in different strata (3-dimensional space).

Number of Nests	Density Experiment	Height Experiment
1 NEST	Low Shrub	Low Shrub
3 NESTS	Low Shrub	1 Low Shrub, 1 Ground, 1 High Shrub
6 NESTS	Low Shrub	2 Low Shrub, 2 Ground, 2 High Shrub
9 NESTS	Low Shrub	3 Low Shrub, 3 Ground, 3 High Shrub

Table 2: Proportion of Successful and Attacked Nests: Table 2a displays the number (n) and proportion of successful and depredated nests for each experiment in each year. Table 2b shows the number (n) and proportion of Wood Thrush nests that survived and were depredated from 2009-2011.

Table 2a: Artificial Nest Success

	Same Height		Different Height	
Artificial Nests 2010	n	proportion	n	proportion
Survived	59	0.66	57	0.69
Depredated	30	0.34	26	0.31
Total	89		83	
Artificial Nests 2011	n	proportion	n	proportion
Survived	35	0.46	7	0.09
Depredated	41	0.54	69	0.91
Total	76		76	

Table 2b: Wood Thrush Nest Success

2009-2011 Wood Thrush	n	proportion
Survived	21	0.72
Depredated	8	0.26
Total	29	

Table 3: Comparison of MARK models for Wood Thrush nest study, 2009-2011.

Table 3 lists the candidate model set for daily survival rates for Wood Thrush nests.

Models listed under time dependent survival included a time effect on daily nest survival.

Nest survival was held constant over time for models listed under constant daily survival.

Wgt = AICc model weight, relative to other models, Par=the number of parameters,

Dev= deviance. *** indicates that the interaction of time and number of neighbors was

significant in explaining nest survival (Likelihood ratio test: chi-sq:11.684, df: 1; P=0.0006,

compared to time dependent survival model).

Model	AICc	Δ AICc	Wgt	Likelihood	Par	Dev	-2logL
Time-Dependent Daily Survival	44.3	9.6	0.01	0.008	6	32.05	32.05
*** + number of neighbors + time/number of neighbor interaction	34.7	0.0	0.99	1.000	7	20.37	20.37
+age of nest on day one of season	55.0	20.3	0.00	0.000	12	30.10	30.10
+ the number of neighbors	56.9	22.2	0.00	0.000	12	32.01	32.01
+ study year	57.1	22.4	0.00	0.000	13	30.06	30.06
+ distance to the nearest neighbor + time/distance interaction	60.3	25.6	0.00	0.000	18	22.33	22.33
+ distance to the nearest neighbor	61.1	26.4	0.00	0.000	14	31.89	31.89
+ number of neighbors + distance to the nearest neighbor	62.6	27.9	0.00	0.000	15	31.25	31.25
Constant Daily Survival	57.1	22.5	0.00	0.000	1	55.12	55.12
+ distance to the nearest neighbor	58.8	24.1	0.00	0.000	2	54.77	54.77
+ the number of neighbors	58.9	24.2	0.00	0.000	2	54.89	54.89
+ study year	60.6	25.9	0.00	0.000	3	54.50	54.50
+ number of neighbors + distance to the nearest neighbor	60.8	26.2	0.00	0.000	3	54.77	54.77

Table 4: Predator composition at artificial nests. This table shows the species composition of mammals that approached artificial nests baited with quail and plasticine eggs at 6 camera traps in 2011. Numbers indicate the number of times an individual of that species approached a nest.

Predator Species	# of sightings
Black Bear (<i>Ursus americanus</i>)	8
Raccoon (<i>Procyon lotor</i>)	2
White-Tailed Deer (<i>Odocoileus virginianus</i>)	5
White-Footed Mouse (<i>Peromyscus leucopus</i>)	1
Gray Squirrel (<i>Sciurus carolinensis</i>)	1
Canine spp.	1
Weasel sp. (<i>Mustela spp.</i>)	1
Chipmunk (<i>Tamias striatus</i>)	1
Porcupine (<i>Erethizon dorsatum</i>)	1

Table 5: Significance of nest height and number of neighbors on nest outcome. This table shows how nest height and number of neighbors affect nest predation. Results are from logistic regressions of each experiment in 2010 and 2011. Significance codes: *** $P < 0.01$; ** $P < 0.05$; * $P < 0.1$

2010 Density Experiment				
Variable	Estimate	Std. Error	z value	Pr(> z)
Intercept	3.2406	2.3147	1.400	0.16511
Number of Nests at Site	0.2884	0.1145	2.518	0.01365 **
Nest Height	-3.7533	1.4057	-2.670	0.00907 ***
2010 Height Experiment				
Variable	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.2242	0.9085	-1.347	0.18162
Number of Nests at Site	0.2144	0.1193	1.796	0.07620*
Nest Height	-0.9283	0.2955	-3.142	0.00235 ***
2011 Density Experiment				
Variable	Estimate	Std. Error	z value	Pr(> z)
Intercept	3.34726	1.90699	1.755	0.0834*
Number of Nests at Site	-0.13808	0.09748	-1.416	0.1609
Nest Height	-1.84868	1.46099	-1.265	0.2098
2011 Height Experiment				
Variable	Estimate	Std. Error	z value	Pr(> z)
Intercept	1.93735	1.64454	1.178	0.239
Number of Nests at Site	-0.02307	0.22666	-0.102	0.919
Nest Height	-1.80224	1.44031	-1.251	0.211
Interaction of nest number and nest height	0.54178	0.33266	1.629	0.103

Figure 2: Number of Nests vs. Nest Fate (Same nest heights). Figure 2 depicts the outcome of quail eggs in solitary and grouped artificial nests in 2010 (2a) and 2011(2b), all of which were placed at similar heights (low-shrub height). The number of nests at a site varied from 1-9. Light gray indicates the proportion of depredated nests and dark gray indicates the proportion of successful nests.

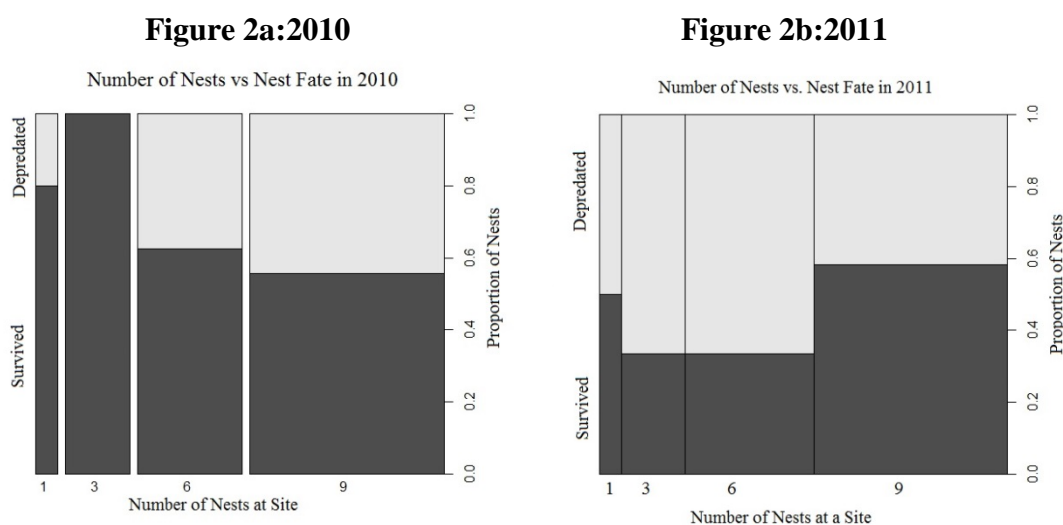


Figure 3: Number of Nests vs. Nest Fate (Different nest heights). Figure 5 depicts the outcome of quail eggs in solitary and grouped artificial nests in 2010 (3a) and 2011(3b) that were placed at three different height classes (ground, low-shrub, high-shrub). The number of nests at a site varied from 1-9. Light gray indicates the proportion of depredated nests and dark gray indicates the proportion of successful nests.

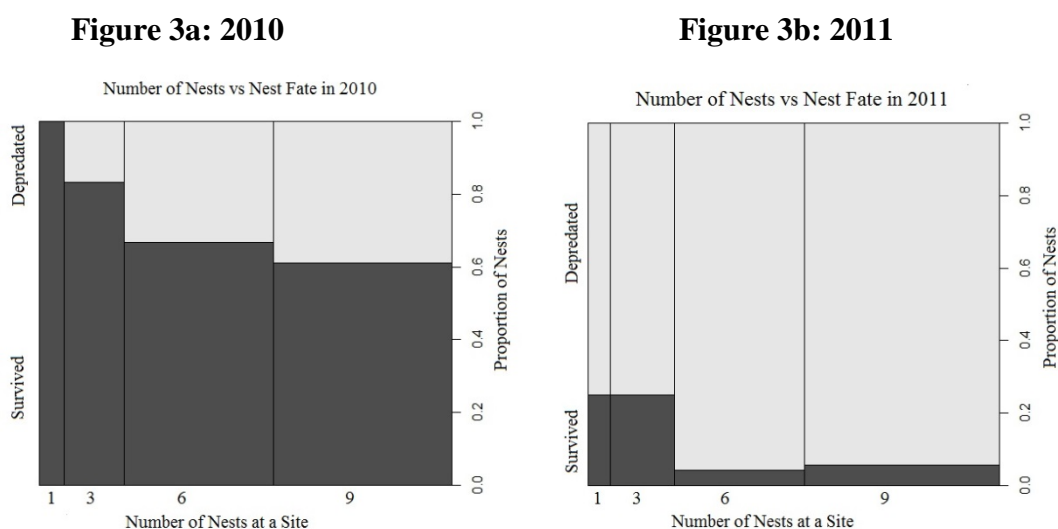


Figure 4: Nest Survival vs. Nest Height in 2010 and 2011. These figures show the outcome of quail eggs in artificial nests that were placed at three different height categories (ground, low shrub, high shrub). The dark horizontal lines indicate the medians, and the green circles represent the means. Nest number at a site varied from zero to nine nests. Figure 4a shows data from 2010 and 4b from 2011.

Figure 4a: 2010

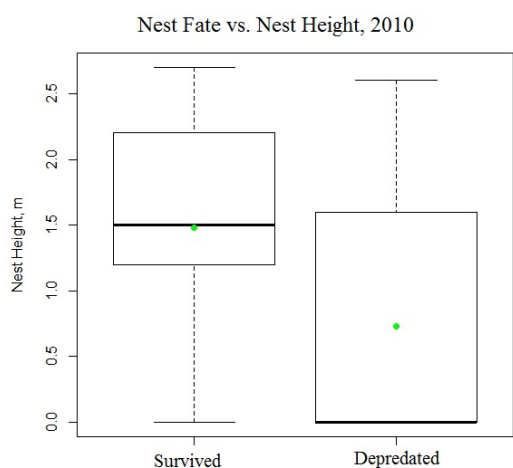


Figure 4b: 2011

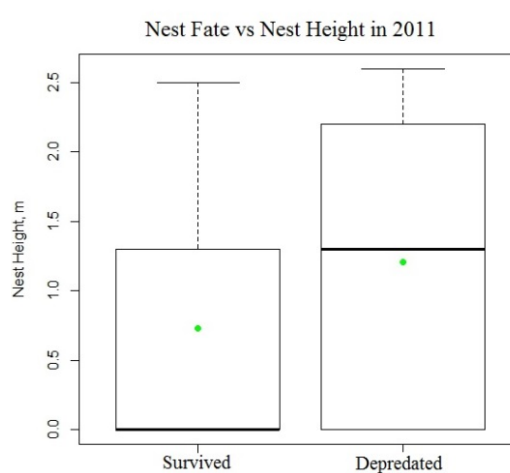


Table 6: Comparison of MARK models for 2011 artificial nest study. Table E lists the candidate model set for daily survival rates for nests in the same strata and different strata experiments.

SAME STRATA							
Model	AICc	Δ AICc	AICc Wgt	Likelihood	Par	Deviance	-2logL
phi. + nest height	187.162	0.000	0.293	1.000	2	183.135	183.135
phi. + number of nests	187.554	0.392	0.240	0.822	2	183.528	183.528
phi.	187.608	0.446	0.234	0.800	1	185.599	185.599
phi. + number of nests + nest height	187.618	0.456	0.233	0.796	3	181.565	181.565
DIFFERENT STRATA							
Model	AICc	Δ AICc	AICc Wgt	Likelihood	Par	Deviance	-2logL
phi. + number of nests	192.095	0.000	0.384	1.000	2	188.059	188.059
phi.	192.346	0.252	0.338	0.882	1	190.335	190.335
phi. + number of nests + nest height	193.966	1.872	0.151	0.392	3	187.896	187.896
phi. + nest height	194.301	2.206	0.127	0.332	2	190.265	190.265

Table 7: Influence of nest height and density on artificial nest survival. This table shows the chi-square results comparing models of artificial nest survival that included the number of nests and nest height.

DENSITY EXPERIMENT				
Reduced Model	General Model	Chi-sq.	df	Prob.
Survival	Survival + number of nests	2.071	1	0.1501
HEIGHT EXPERIMENT				
Reduced Model	General Model	Chi-sq.	df	Prob.
Survival	Survival + number of nests	2.275	1	0.1315
Survival	Survival + nest height	0.069	1	0.7924

Table 8: Estimates of Daily Nest Survival for 2011 Artificial Nest Experiments.

Table 8 lists the model averaged estimates of daily survival rates, standard errors and confidence intervals for nests in the artificial nest experiments where nest density was altered (density experiment) and where both nest density and nest height were altered (height experiment). The variation is the percent of variation in the values attributable to the variation in the models.

Experiment	DSR Estimate	Standard Error	Lower CI	Upper CI	Variation
Density	0.886	0.038	0.790	0.942	43.81%
Height	0.863	0.032	0.789	0.914	44.10%

CHAPTER 4

Study Conclusions

The goal of this project was to examine mixed species nesting associations (MSNA) among songbirds breeding in eastern deciduous forests. This study addressed three primary questions. 1) Do songbirds breeding in deciduous forests form MSNA? 2) Do birds form MSNA because they use or respond to the same habitat features? 3) Do birds that breed near other species display increased daily survival rates of eggs in the nests?

The results presented in Chapter 1 showed that birds do form spatially nonrandom nesting associations. These groups involved two to five nesting birds that aggregated their nests. Red-Eyed Vireos, Scarlet Tanagers, and Wood Thrushes were the most common members of these groups. Sites with breeding Wood Thrushes had higher incidences of nesting associations than sites without thrushes, suggesting that thrushes are choosing areas with higher nest densities or that other species are selecting sites based on the location of breeding thrushes.

In the habitat study detailed in Chapter 2, I found that birds do not appear to be forming MSNA in response to the same vegetation features. None of the surveyed habitat features, including stem density and diversity, percent canopy cover, and percent leaf litter cover, were correlated with the number of nests in an area. The lack of correlation of nest density with vegetation features suggests that another factor is driving MSNA. One possibility is that birds are selecting another common habitat feature that I did not survey, such as prey or predator density.

Another possibility, however, is that birds are exhibiting heterospecific attraction and selecting sites based on the presence of other nesting birds. Other studies have shown that birds gain improved breeding success by nesting near other species. If this is the case, then nest success should increase as the number of nests increases. However, the study presented in Chapter 3 showed that Wood Thrush nest success nominally decreased and artificial nest success drastically decreased as the number of nests within an area increased. The only exception was the 2011 artificial nest study in which nests placed at the same height had a positive relationship between survival and nest density. Daily nest survival also increased with increasing distance from Wood Thrush nests to their nearest neighbor.

Despite seemingly negative reproductive consequences of nesting near others, Wood Thrushes aggregate their nests with other species. The question, then remains - what benefit, if any do thrushes gain from breeding near other birds? One possibility is that thrushes gain other benefits from MSNA, such as an increase in adult survival. Also, thrushes are typically double brooders, and their overall breeding success might be higher by initiating breeding earlier. They could potentially use the presence of other birds as proxies for good habitat rather than spending time prospecting. Alternatively, other species may gain benefits from nesting near thrushes.

Thrushes incur minor reductions in DSR from nesting near one to four neighbors. The artificial nest study mirrors these results in that nest survival remained relatively high in associations involving only three nests. While the benefits of these associations to Wood Thrushes remains unknown, it is possible that birds gain another benefit from

participating in MSNA that outweighs the minor reproductive cost from nesting near a few neighbors.

BIBLIOGRAPHY

- Ahlering, M. A., D. Arlt, M. G. Betts, J. Robert J. Fletcher, J. J. Nocera, and M. P. Ward. 2010. Research needs and recommendations for the use of conspecific-attraction methods in the conservation of migratory songbirds. *The Condor* **112**:252-264.
- Bayard, T. S. and C. S. Elphick. 2010. Using Spatial Point-Pattern Assessment to Understand the Social and Environmental Mechanisms That Drive Avian Habitat Selection. *The Auk* **127**:485-494.
- Betts, M. G., A. S. Hadley, N. Rodenhouse, and J. J. Nocera. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society of Biological Sciences* **275**.
- Burke, D. M. and E. Nol. 1998. influence of food abundance, nest site habitat and forest fragmentation on breeding Ovenbirds. *The Auk* **115**:96-104.
- Chalfoun, A. D. and T. E. Martin. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *Journal of Animal Ecology* **78**.
- Cimprich, D., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*).in A. Poole, editor. *The Birds of North America Online* Cornell Lab of Ornithology, Ithaca.
- Clark, K. L. and R. J. Robertson. 1979. Spatial and Temporal Multi-Species Nesting Aggregations in Birds as Anti-Parasite and Anti-Predator Defenses. *Behavioral Ecology and Sociobiology* **5**:359-371.
- Clark, P. J. and F. C. Evans. 1954. Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. *Ecology* **35**:445-453.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced Techniques for Modeling Avian Nest Survival. *Ecology* **83**:3476-3488.
- Driscoll, M. J., T. Donovan, R. Mickey, A. Howard, and K. K. Fleming. 2005. Determinants of Wood Thrush Nest Success: A Multi-Scale, Model Selection Approach. *Journal of Wildlife Management* **69**:699-709.
- Evans, M., E. Gow, R. R. Roth, M. S. Johnson, and T. J. Underwood. 2011. Wood Thrush (*Hylocichla mustelina*) in A. Poole, editor. *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca.
- Faaborg, J. 2004. Truly Artificial Nest Studies. *Conservation Biology* **18**:369-370.
- Fletcher, R. J. 2007a. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* **76**:598-606.
- Fletcher, R. J., Jr. 2007b. Species interactions and population density mediate the use of social cues for habitat selection. *The Journal of animal ecology* **76**:598-606.
- Fletcher, R. J. and K. E. Sieving. 2010. SOCIAL-INFORMATION USE IN HETEROGENEOUS LANDSCAPES: A PROSPECTUS. *Condor* **112**:225-234.
- Forsman, J. T., J. Seppanen, and M. Monkkonen. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings. Biological sciences / The Royal Society* **269**:1619-1623.
- Forstmeier, W. and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* **104**:487-499.
- Frank R. Thompson, I. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**:98-109.

- Goodale, E., G. Beauchamp, R. D. Magrath, J. C. Nieh, and G. D. Ruxton. 2010. Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution* **25**:354-361.
- Greenlaw, J. S. 1996. Eastern Towhee (*Pipilo erythrophthalmus*). *in* A. Poole, editor. *The Birds of North America Online* Cornell Lab of Ornithology, Ithaca.
- Hamilton, W. D. 1971. Geometry for the Selfish Herd. *Journal of Theoretical Biology* **31**:295-311.
- Harrison, H. H., National Audubon Society., and National Wildlife Federation. 1975. A field guide to birds' nests of 285 species found breeding in the United States east of the Mississippi River. Houghton Mifflin, Boston.
- Kleindorfer, S. and R. Y. Dudaniec. 2009. Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches. *Behavioral Ecology and Sociobiology* **63**:731-739.
- Kleindorfer, S., F. J. Sulloway, and J. O'Connor. 2009. Mixed species nesting associations in Darwin's tree finches: nesting pattern predicts predation outcome. *Biological Journal of the Linnean Society* **98**:313-324.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* **84**:485-513.
- Martin, T. E. 1991. Breeding productivity considerations: what are the appropriate habitat features for management? Pages xiii, 609 p. *in* J. M. Hagan, D. W. Johnston, and Manomet Bird Observatory (Mass.), editors. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington.
- Martin, T. E. 1993. Nest Predation and Nest Sites. *BioScience* **43**:523-532.
- Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. *Nature* **380**:338-340.
- Martin, T. E., C. Paine, C. J. Conway, W. M. Hochachka, P. Allen, and W. Jenkins. 1997. BBird Field Protocol. *in* M. C. W. R. Unit, editor. *Breeding Biology Research and Monitoring Database*. University of Montana, Missoula.
- Miller, C. W., R. J. Fletcher, Jr., and S. R. Gillespie. 2013. Conspecific and heterospecific cues override resource quality to influence offspring production. *Plos One* **8**:e70268.
- Monkkonen, M. and J. T. Forsman. 2002. Heterospecific attraction among forest birds: A review. *Ornithological Science* **1**:41-51.
- Mönkkönen, M., P. Helle, G. J. Niemi, and K. Montgomery. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology* **75**:2077-2083.
- Morales, M., I. Guerrero, J. Oñate, and L. Meléndez. 2012. Inter-specific association and habitat use in a farmland passerine assemblage. *Ecological Research* **27**:691-700.
- Mowbray, T. B. 1999. Scarlet Tanager (*Piranga olivacea*). *in* A. Poole, editor. *The Birds of North America Online* Cornell Lab of Ornithology, Ithaca.
- Newell, F. L. and M. S. Kostalos. 2007. Wood Thrush Nests in Dense Understory May Be Vulnerable to Predators. *The Wilson Journal of Ornithology* **119**:693-702.
- Nocera, J. J. and M. G. Betts. 2010. The Role of Social Information in Avian Habitat Selection. *The Condor* **112**:222-224.

- Nocera, J. J., G. J. Forbes, and L. A. Giraldeau. 2009. Aggregations from using inadvertent social information: a form of ideal habitat selection. *Ecography* **32**:143-152.
- Petrides, G. A. 1973. *A Field Guide to Trees and Shrubs: Northeastern and north-central United States and southeastern and south-central Canada*. 2nd edition. Houghton Mifflin Harcourt, New York.
- Quinn, J. L. and M. Ueta. 2008. Protective nesting associations in birds. *Ibis* **150**:146-167.
- R Core, T. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reiter, M. E. and D. E. Andersen. 2013. Evidence of Territoriality and Species Interactions from Spatial Point-Pattern Analyses of Subarctic-Nesting Geese. *Plos One* **8**:1-10.
- Richardson, T. W., T. Gardali, and S. H. Jenkins. 2009. Review and Meta-Analysis of Camera Effects on Avian Success. *Journal of Wildlife Management* **73**:287-293.
- Robinson, S. K. and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. *Conservation International* **4**:233-249.
- RStudio. 2012. RStudio: Integrated development environment for R. Boston, MA.
- Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Population Ecology* **148**:22-29.
- Schmidt, K. A., S. A. Rush, and R. S. Ostfeld. 2008. Wood Thrush nest success and post-fledgling survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology* **77**:830-837.
- Schmidt, K. A. and C. J. Whelan. 1999. Nest predation on woodland songbirds: when is nest predation density dependent? *Oikos* **87**:65-74.
- Sebastian-Gonzalez, E., J. A. Sanchez-Zapata, F. Botella, and O. Ovaskainen. 2010. Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. *Proceedings. Biological sciences / The Royal Society* **277**:2983-2990.
- Seppanen, J. T. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**:2950-2950.
- Seppanen, J. T., J. T. Forsman, M. Monkkonen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* **88**:1622-1633.
- Slagsvold, T. 1980. Habitat Selection in Birds: On the presence of other bird species with special regard to *Turdus pilaris*. *Journal of Animal Ecology* **49**:523-536.
- Tekiela, S. 2004. *Trees of Pennsylvania Field Guide*. Adventure Publications, Cambridge, MN.
- Varela, S. A. M., E. Danchin, and R. H. Wagner. 2007. Does predation select for or against avian coloniality? A comparative analysis. *Journal of Evolutionary Biology* **20**:1490-1503.
- Villard, M.-A. and T. Part. 2004. Don't put all your eggs in real nests: a sequel to Faaborg. *Conservation Biology* **18**:371-372.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:S120-S139.

- Whitehead, D. R. and T. Taylor. 2002. Acadian Flycatcher. *in* A. Poole, editor. The Birds of North America Online Cornell Lab of Ornithology, Ithaca.
- Windsor, D. M. 1972. Nesting Association Between Two Neotropical Polybiine Wasps (Hymenoptera, Vespidae). *Biotropica* **4**:1-3.
- Young, B. E., M. Kaspari, and T. E. Martin. 1990. Species-Specific Nest Selection by Birds in Ant-Acacia Trees. *Biotropica* **22**:310-315.