5-2010

Hermit Thrush (*Catharus guttatus*) and Veery (*C. fuscescens*) Breeding Habitat Associations in Southern Appalachian High-Elevation Forests.

Andrew J. Laughlin
East Tennessee State University

Recommended Citation

Hermit Thrush (*Catharus guttatus*) and Veery (*C. fuscescens*) Breeding Habitat
Associations in Southern Appalachian High-Elevation Forests

_____

A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for degree

Masters of Science in Biological Sciences

_____

by

Andrew J. Laughlin

May 2010

_____

Dr. Fred J. Alsop III, Chair

Dr. Istvan Karsai

Dr. Thomas F. Laughlin

Keywords: Birds, Habitat Partitioning, Principal Components Analysis

ABSTRACT

Hermit Thrush (*Catharus guttatus*) and Veery (*C. fuscescens*) Breeding Habitat
Associations in Southern Appalachian High-Elevation Forests

by

Andrew J. Laughlin

The Hermit Thrush is a new breeding bird in the Southern Appalachian high-elevation
mountains, having expanded its range southward over the last few decades. Here it is sympatric
with the Veery, a congeneric breeding resident. In order to more fully understand why the range
expansion took place and to understand more about the local ecology of the newly arrived bird, I
measured several habitat variables in 30 Hermit Thrush and 24 Veery territories. Principal
Components Analysis and Cluster Analysis brought to light several patterns of habitat
preferences for these 2 species. Hermit Thrushes prefer territories with more leaf litter on the
ground and less shrub density than Veery territories. Competition between these species should
remain low, as their niche differences brought to light in this study should enable them to breed
in close proximity to each other in these high-elevation mountains.

ACKNOWLEDGMENTS

CONTENTS

LIST OF TABLES

CHAPTER 1

INTRODUCTION

The Spruce-Fir forest type of the Southern Appalachian Mountains is one of the most distinctive and imperiled ecosystems in North America (White 1984; Noss 1995). Ranging from southwestern Virginia, down along the high peaks of the Tennessee / North Carolina border, this forest type is found in island-like stands on the highest mountains and ridges above 1600m in elevation. This ecosystem resembles the boreal forests of the north and northeast, with Red Spruce (*Picea rubens*) and Fraser Fir (*Abies fraseri*) dominating the overstory. These southern forests, though, have been isolated from the northern forests for the last 10,000 years, and have developed their own unique species composition. They have also come under several forms of environmental stress, especially during the last century. These stresses, and the naturally smaller distribution compared to the vast northern forests, have contributed to the steady, and perhaps permanent, decline of this forest type.

The Southern Appalachian high-elevation avifauna is an ecologically important and scientifically interesting assortment of birds (Hubbard 1971; Rabenold 1984). Most of the birds that inhabit these Spruce-Fir or mixed Spruce-deciduous forests are remnant populations of more northerly breeding forest birds. For example, the breeding range of the Red-breasted Nuthatch (*Sitta canadensis*) is concentrated in coniferous forests of Eastern Canada and New England, but also follows the spine of the Appalachians all the way down through West Virginia, eastern Tennessee, and western North Carolina, where high elevation forests resemble forests of more northern latitudes. Some of these disjunct populations are genetically different from more northerly populations. The Red Crossbill (*Loxia curvirostra*) that occurs here may be an endemic species here in the Southern mountains, and the Northern Saw-whet Owl (*Aegolius acaticus*) is

more genetically diverse here than in more northerly populations (Hunter et al. 1999). Other birds that have these peninsular breeding ranges down the spine of the Appalachian high peaks include the Dark-eyed Junco (*Junco hyemalis*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), Brown Creeper (*Certhis americana*), and Common Raven (*Corvus corax*).

The Hermit Thrush (*Catharus guttatus*) has recently expanded its breeding range into these forests (Simpson 1992; Knight 1997), where once the Veery was the only forest thrush that bred here (Noon 1981b; Hall 1988). In June 1979 a male Hermit Thrush was heard singing on Roan Mountain, on the border of east Tennessee and western North Carolina (Potter and LeGrand 1980). A few years later more singing Hermit Thrushes were found on Grandfather Mt. in North Carolina, Mt. Collins in the Great Smoky Mountains National Park, and in the Black Mountains of North Carolina (Simpson 1992; Browning 2003). In 2005 the Hermit Thrush reached the southern limit of Spruce-Fir forests in the Great Balsam Mountains of North Carolina (Westphal et al. 2009). All of these places where the Hermit Thrush was located are above 1550m in elevation and are in the Spruce-Fir forest belt or the mixed Spruce-deciduous forest.

Birds often expand into regions they weren't previously known to breed in, and many bird's breeding ranges are constantly expanding or shrinking due to an abundance or lack of resources. Climate change, human alteration of the landscape, fluctuations in numbers of individuals, and genetic variation within populations are all documented reasons for avian breeding range expansions (Newton 2003). The recent expansion of the Hermit Thrush is perhaps noteworthy because of the scale on which it occurred and the direction. Most studies of avian breeding range expansions have emphasized the northerly direction of the expansion

largely due to changing weather patterns and global warming (Thomas and Lennon 1999, Hitch and Leberg 2007). The expansion south of the Hermit Thrush runs counter to these studies and to the predictions of Matthews et al. (2004), who predicted a northerly movement of birds (including Hermit Thrushes) as suitable habitat shifted north due to climate change.

This range expansion seemed ripe for study and became the basis for this research project. I wanted to find out why this bird was expanding its breeding range so quickly into these forests where they had previously been absent. Are there vegetative characteristics that may be driving this expansion? To answer this question we need to understand what habitat characteristics the Hermit Thrush is drawn to in this area. No study has measured these characteristics (Nicholson 1997) until now. I also decided to bring another species into the study, the Veery (*C. fuscescens*), a closely related, congeneric bird that has been a breeding resident in this forests for many decades and perhaps much longer (Noon 1981b). By comparing the habitat associations between these 2 forest thrushes, we can not only describe the habitat partitioning occurring between them, but can also glean some information about the local ecology of the newly arrived bird.

These 2 species have very similar ecological niches, but there are key differences as well. These differences in niche allocation are habitat partitioning methods that these species have evolved in order to use the same environment (Dilger 1956b; MacArthur 1958). Both of these species seem to require large tracts of uninterrupted forests and are found largely in the interior of these forest tracts. Both are capable of inhabiting coniferous or mixed coniferous / deciduous forests across most of their ranges. Both species spend a lot of time on or near the ground, foraging among the leaf litter and shrub layer for insects during the breeding season. Both species also seem to require some sort of developed shrub or sapling layer as opposed to a

completely open understory environment. This is a requirement for nesting (which takes place on or near the ground), foraging, and concealment from predators. The Hermit Thrush and the Veery are also migratory songbirds that spend the winter season and the summer breeding season in different places.

However, there are some key differences between their habitat preferences and general ecology. Hermit Thrushes generally prefer drier areas of the forest, while the Veery prefers wetter habitat (Bertin 1977; Jones and Donovan 1996; Bevier 2005). The Hermit Thrush sings its breeding song from a much higher perch than the Veery, which usually sings between 2 – 8m off the ground (Bertin 1977; pers. obsv.). The Hermit Thrush seems to be more dependent on the ground layer than the Veery, and the Veery spends more time foraging arboreally than the Hermit Thrush (Paszkowski 1984). The Hermit Thrush usually builds its nest on the ground (though sometimes a meter or so off the ground in a sapling or shrub) in proximity to an interior forest edge, while the Veery usually builds its nest above the ground in a sapling or shrub further away from forest edges (Dellinger et al. 2007; Bevier et al. 2005).

It is important to discern the environmental conditions that affect the distribution and abundance of bird species, and a bird-habitat relationship study is one way to do this (Young and Hutto 2002). How are these birds using the habitat they are in, and what sort of forest structure are they selecting over others? This study may also help us to understand why the Hermit Thrush is expanding its breeding range in this southward manner, if we can link its habitat preferences to any vegetative changes that have been occurring over the last few decades.

It is also important to understand what habitat characteristics animals are selecting in forests that are undergoing major changes in order to predict how they may fare under future scenarios. Several factors are contributing to the overall decline of the Southern Appalachian

Spruce-Fir forest, making it not only one of the rarest but also one of the most endangered ecosystems in North America (Noss et al. 1995). This forest type once covered almost a million acres of land, 95% of which was cut or burned in the 1920s (Korstian 1937). Past logging, acid deposition, climate change, and the accidental introduction of the Balsam Wooly Adelgid (*Adelges piceae*) are all decimating different components of this forest, perhaps irretrievably. The insect infestation has killed nearly 90% of mature Fraser Firs in some areas, leaving whitened stumps still standing or fallen over and creating large openings in a once-thick canopy. These openings have had a large effect on the understory plant and animal composition, and many mature stands of Fraser Fir may be totally eliminated within the next decade (DLIA ATBI 2008).

In summary, the objective of this study was to measure certain topographical and habitat structural variables in both Hermit Thrush and Veery territories. These measurements were compared to delineate niche partitioning between the species in this dynamic forest environment. This is also the first study to quantify the habitat preferences of the Hermit Thrush in the Southern Appalachian high-elevation forests in order to understand why this species is expanding its breeding range into this area.

CHAPTER 2

MATERIALS AND METHODS

Study Area

The Spruce-Fir forests of Southern Appalachia exist as several high-elevation islands in an ocean of lower elevation mixed and deciduous forests. These forests are largely found above 1600m in elevation and extend to peaks as high as 2000m. There is no montane tree-line at this latitude. The Great Smoky Mountains National Park All Taxa Biodiversity Inventory describes at least 6 types of Spruce or Spruce-Fir forests in the Southern Appalachian region (DLIA ATBI 2006), but for our purposes a simpler description will suffice. These forests are dominated in the canopy by Red Spruce and Fraser Fir, an endemic tree species to the Southern Appalachians. At the highest elevations pure stands of Fraser Fir can be found. Several deciduous trees such as Yellow Birch (*Betula alleghaniensis*), Mountain Ash (*Sorbus americana*), and Fire Cherry (*Prunus pensylvanica*) are found in the understory. The shrub layer consists of Catawba Rhododendron (*Rhododendron catawbiense*), Mountain Laurel (*Kalmia latifolia*), and Hobblebush (*Viburnum lantanoides)*. The herb layer is dominated by ferns where present but is generally sparse.

Total acreage of this forest type previous to logging varies widely, from 140,000 acres to almost 1 million acres (Korstian 1937, Hunter et al. 1999). By all accounts most of these forests were logged heavily from 1905 – 1930. Only a few tracts in the current Great Smoky Mountain National Park were spared this fate. Many of these logged stands of Spruce were taken over by Northern hardwood species or Fir, and in some cases were replanted with Spruce seedlings. The

13

current total acreage of Spruce-Fir forest is approximately 85,000 – 90,000 acres (Griep 1998), 80% of which is in the late-successional stage of growth (Hunter et al. 1999).

After the logging ended and the forest started to recover, other indirect human influences have been altering this forest type for several decades. Acid deposition from near-by pollution sites has dramatically reduced the annual radial increment of Spruce trees (White 1984) and has resulted in a higher Spruce mortality. Spruce stands are, however, fairing much better than its coniferous neighbor, the Fraser Fir. The accidental introduction of the exotic aphid the Balsam Wooly Adelgid (*Adelges piceae*) in North America around 1900 has decimated mature stands of Fraser Fir by up to 90%. This insect, which reached the Southern Appalachian Spruce-Fir forests in 1957, feeds on the plant sap of the Fir trees and disrupts nearby cells and tissues causing tree mortality within 2 – 7 years of infestation (Eagar 1984). It is yet unclear whether infested Fir saplings can reach reproductive age (Hunter et al. 1999), and stands of Fraser Fir may be completely extirpated from the peaks within the next few decades if proper control methods are not performed (Rheinhardt 1984, DLIA ATBI 1999).

This study took place in several Spruce-Fir forests of the Southern Appalachian Mountains. The survey sites of the study can be divided into 3 separate sites: 1) The Great Smoky Mountain National Park, 2) Unaka Mt. / Roan Mtn., and 3) Whitetop Mt. / Mt. Rogers. Both the first and second study sites straddle the border between Tennessee and North Carolina, while the third is located in southwestern Virginia.

Bird Finding and Plot Measurements

This study took place between late May and late July 2009 during the breeding season. Study sites were chosen based on known Hermit Thrush and Veery sightings over the years as

described in the ornithological journals of Tennessee, North Carolina, and Virginia (*The Migrant*, *The Chat*, and *The Raven*, respectively). The Atlas of Breeding Birds for each state was also consulted where available. Walking along trails and old logging roads within these forests, I noted each Veery or Hermit Thrush territory as I came to it. Detecting birds during the breeding season is facilitated by knowing the songs and calls that are particular to each species. Male birds have a species-specific advertising song that is sung throughout the breeding season in order to ward off competing males and to attract females. For secretive and skulking species such as forest thrushes, this is the best way to locate breeding territories. Each territory was carefully approached so as not to disturb the bird and to get an accurate point where the bird was first detected.   Once a plot was identified as a breeding territory of either species, an 11.3m radius circle was centered on the bird where it was first located. Many avian microhabitat studies are centered on the nest of the study species, but this protocol was avoided for several reasons. It is notoriously difficult to find forest thrush nests, as they are usually very well hidden, the location of which is not easily given away by the birds themselves. Because I was on a limited time budget, I chose a singing or calling bird to be the center of each plot. This is not an uncommon compromise, as a singing or calling bird during the breeding season is usually within the breeding territory that is to be measured (James 1971, Jones and Robertson 2001).

The individual measurements taken within each plot were chosen based on several factors. Variables that are directly related to the ecology of each species such as foraging location and behavior, nesting location, concealment, and diet are important when trying to discern what habitat variables birds are choosing (Sutherland et al. 2004). Habitat measurement protocols have been developed for birds in general by the Breeding Biology Research and Monitoring Database (BBIRD), a nationwide cooperative program "that uses standardized field

methodologies for studies of nesting success and habitat requirements of breeding birds" (Martin et al. 1997). Variables and measurement protocols were adapted from this program and from other bird-habitat relationship studies of birds in general (James and Shugart 1970, Noon 1981a, Steele 1992, Jones and Robertson 2001, Sutherland et al. 2004) and forest thrushes in particular (Noon 1981b, Paszkowski 1984,Young and Hutto 2002, Dellinger et al. 2007).

The following measurements were taken within each territory. Elevation and Aspect were measured using a GPSmap 60csx handheld GPS unit (Garmin). Slope was calculated using a rangefinder (Bosch DLR165) to measure from the center of the circle to a point 10m distant along the estimated average slope of the plot. The angle was calculated later. Canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Bartlesville, OK). Four readings of the densiometer were taken 5m from the center of the circle in each of the cardinal directions. These readings were put together to calculate the average canopy closure of the plot (Strickler 1995, Jennings et al. 1999). All trees >2.5cm diameter at breast height (DBH) were measured and identified to species and put into 5 size categories: 2.5cm – 7.9cm, 8.0cm – 14.9cm, 15.0cm – 22.9cm, 23cm – 37.9cm, and >38.0cm. Percent cover of the plot was estimated at 5 vertical height intervals: 0.0m – 0.5m, 0.6 – 1.3m, 1.4m – 3.0m, 3.1m – 6.0m, and >6.0m. Percent cover is the amount of ground that has foliage above it in each of the 5 height intervals. This variable was estimated by eye by dividing the plot into 4 sections, estimating percent cover in each section, and taking the average. Ground cover was also estimated by eye, by dividing the circular plot into 4 sections, estimating the percent ground cover of ferns, rock, bare ground, leaf litter, herbs, and moss, and then taking the average among these estimations. All variables that were estimated by eye were measured by the same individual for each plot to try to reduce error. These measurements and those derived from them total 34 different variables

for each species that can be statistically analyzed. For a complete list of variables measured and calculated, see Table 1.

Statistical Analyses

Because many of these variables are not independent of each other, multivariate analyses were performed on the data. Principal Components Analysis (PCA) was used on many of the variables that I felt were not explicitly, but could potentially be, correlated with each other. (See Table 3 for a list of variables that were used in the PCA.) Two tests were used to make sure PCA was an appropriate analysis for the data set. The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy was used to test for linearity of the variables. This index is a ratio of the observed correlation coefficients to the partial correlation coefficients and ranges from 0.0 to 1.0. A value closer to 1.0 means that the observed correlations between pairs of variables can be explained by the other variables. A value less than 0.5 indicates that PCA is not a good procedure to use on the data, because the variables are not linearly related (Norusis 2010). Bartlett's test of sphericity was also used to test the null hypothesis that the correlation coefficients are 0. A nonsignificant value for this test also indicates that PCA should not be used on the data because the variables are uncorrelated (Mertler & Vannatta 2005).

Principal Components Analysis (PCA) is one of several types of multivariate statistical techniques that fall under the heading Factor Analysis. Factor Analysis in general tries to identify a small number of factors or components that can explain the correlations between variables and seeks to discover the shared variance among the variables. Factor Analysis, in other words, tries to take a large number of variables and collapse them to a much smaller set of factors that explain the variation in the data to a large extent. In Principal Components Analysis, perhaps the

simplest method of Factor Analysis (Manly 2005, Norusis 2009), 2 or more linear combinations of the initial variables are produced with each combination being uncorrelated with the previous one. It is possible, and is indeed often the case, to produce as many components as original variables, but in that case you haven't reduced your analysis. There is no rule of thumb for how many components should be kept and analyzed for any given set of variables, but in general it is a good idea to keep those components that explain more than any individual variable explains by itself.

The first step of a PCA is to have all the values of the variables standardized to have a mean of zero and a variance of 1. By doing this, all of the variables have the same influence on the final outcome even though some initial variables may have much larger variances to begin with. For example, the elevational differences between sites in this study will have a much larger variance than tree species richness simply because the numbers are much larger for elevation. By standardizing the variables in such a way, one can be sure that both variables have the same weight or influence on the final outcome. The program that I used, PASW 17.0, performed this step automatically on the data set before computing the components.

I used a Varimax rotation for the PCA procedure in order to maximize the correlation of variables to certain components. Without rotation some variables may by highly correlated with 2 or more components, which makes interpretation of the PCA results much more difficult. An orthogonal rotation such as Varimax simplifies the relationship between variables and components while still maintaining no correlations between the components. (By contrast, oblique rotations of the PCA axes do correlate the components to each other, which is perhaps more realistic but much harder to interpret.) Varimax is the most often used rotation method because it minimizes the number of variables that are highly correlated with each component,

making the components unique and easier to interpret (Norusis 2009). Rotation also seems to increase the amount of variation explained by each component so that a component that only explains 5% of the total variance before rotation might explain 10% of the same variation after rotation. For this reason several iterations of the PCA may need to be run in order to pick up every potentially important component that explains more variance than an individual variable would.

Only a small set of the variables originally measured and calculated were used in the PCA for this project. Some variables were so highly correlated with each other that using them both in the PCA would only complicate the procedure and make dubious the results. For example, the variable Total Number of Trees was not used in the PCA, but the 2 variables Total Number of Deciduous Trees and Total Number of Coniferous Trees were used in the analysis. Total Number of Trees is just the combination of these 2 other variables, and would thus be too highly correlated with them to be of much use in the PCA. Likewise, the variables Percentage of Coniferous or Deciduous Trees was not used in the analysis for the same reason.

The statistical package PASW 17.0 calculates a component score for each case in the data set. By plotting the component scores on an X-Y axis (component 1 on the X-axis and component 2 on the Y-axis), one can visualize how each case (in this study, each bird plot) scores each component. Further, the 2 kinds of cases in this data set (corresponding to the 2 species of birds in the study) can be color coded to see clearly how each species corresponds to each component. The resulting scatter-plots make interpretation of the PCA much more meaningful and can be found in the results section of this paper.

Cluster Analysis is a technique that groups similar cases or variables together into clusters based on similarities. In the simplest form a distance matrix is calculated for all

19

variables. This matrix, usually Euclidean or Squared Euclidean distances between variables, is used as a measure of similarity. Low distances between cases mean they are close to each other and would be in the same cluster. Hierarchical clustering produces a dendrogram, a family tree of sorts that makes clear the clusters that are inherent in the data set.

I used hierarchical agglomerative clustering on 4 sets of data: the habitat variables, all 54 of the bird territories, and on the Hermit Thrush and Veery territories individually. The method of clustering used was centroid, and the interval method was squared Euclidean distance. All values were rescaled to between $0 - 1$ for the analysis. This reduces the effect that very large values have and makes the variables more equally weighted in the analysis. The clustering of habitat variables is used as a comparison with the PCA. Ideally, the clusters formed by the variables would be very similar to the different principal components that are produced on the same data. The clustering of all 54 bird territories should give us an idea of the similarity between the 2 species habitat differences. If there are differences between Hermit Thrush and Veery preferences, then the 2 species territories should end up in different clusters. The last sets of clusters, on the Hermit Thrush and Veery territories individually, will group the territories according to their similarities and should explain a little more about how the birds perceive similar territories.

CHAPTER 3

RESULTS

Pair-Wise Comparisons

A total of 30 Hermit Thrush and 24 Veery territories were surveyed during the study period. (For a complete list of territories surveyed including location, dates, and GPS coordinates see Appendices A and B.) It might be helpful to peek at the pair-wise comparisons that revealed several differences between the breeding habitat preferences of the 2 species in the Southern Appalachian Mountains. The total number of trees per acre differed significantly between them, with an average of 770 in the Hermit Thrush territories and 330 in the Veery territories ($p < 0.001$). The total number of coniferous and deciduous trees also differed slightly but is probably a remnant of the differing total number of trees in general. Both total basal area and coniferous basal area were significantly different ($p < 0.01$ and $p < 0.001$, respectively). The total number of trees in 4 out of the 5 size categories was significantly different between the 2 species, but this again is probably just a remnant of the differing total number of trees. Canopy closure was slightly significantly higher for the Hermit Thrush than for the Veery (70% versus 56%). Percent cover for the lowest 3 height categories were also significantly different between the species, with the Veery preferring higher amount of cover from $0.0 – 0.5$ meters (73% to 32%, $p < 0.001$), 0.5 to 1.3 meters (67% to 20%, $p < 0.001$), and $1.3 – 3.0$ meters (51% to 30%, $p = 0.001$). For a complete table of measurement results for each species, including mean and 95% confidence intervals, see Table 1.

Table 1. Habitat variable mean measurements, confidence intervals, standard deviations, and pair-wise p-values for differences between species

Variable	Hermit Thrush			t-test	Veery		
	mean	95% Conf. Interval	Std. Dev.	p-value	mean	95% Conf. Interval	Std. Dev.
Elevation (m)	1700	1634.2 - 1767.2	178.2	0.205	1640	1570.5 - 1709.7	150.5
Slope (°)	9.34	7.8 - 10.9	4.1	0.231	11	8.5 - 13.5	5.7
Aspect (°)	177.3	132.9 - 221.8	119.1	0.623	150	112.0 - 188.0	85.7
Total # of trees	77.2	61.8 - 92.6	41.2	0.000	33.3	19.7 - 47.0	32.3
# Conifer trees	45.2	30.0 - 60.5	40.9	0.021	20.5	6.4 - 34.6	33.5
% Conifer trees	0.55	0.41 - 0.69	0.38	0.735	0.51	0.34 - 0.68	0.40
# Deciduous trees	31.4	17.1 - 45.6	38.1	0.028	12.8	7.1 - 18.6	13.7
% Deciduous trees	0.45	0.31 - 0.59	0.38	0.712	0.49	0.32 - 0.66	0.40
# of snags	7.4	3.0 - 11.8	11.9	0.091	3	1.2 - 4.8	4.3
Basal Area (m^2/ac)	14.81	11.97 - 17.65	7.6	0.000	6.93	4.37 - 9.48	6.05
Conifer Basal Area	10.18	6.85 - 13.51	8.91	0.007	4.13	1.51 - 6.76	6.22
% Conif. Basal Area	0.59	0.45 - 0.73	0.38	0.583	0.53	0.35 - 0.71	0.42
Decid. Basal Area	4.63	2.81 - 6.44	4.86	0.126	2.79	1.33 - 4.26	3.48
% Decid. Basal Area	0.41	0.27 - 0.55	0.38	0.583	0.47	0.29 - 0.65	0.42
Number of trees:							
dbh 3.0 - 7.9 (cm)	28.7	19.6 - 37.8	24.3	0.002	11.7	5.9 - 17.4	13.7
dbh 8.0 - 14.9 (cm)	22.6	15.9 - 29.3	17.9	0.006	9.7	3.8 - 15.7	14.1
dbh 15.0 - 22.9 (cm)	14.8	11.9 - 17.7	7.8	0.000	7.2	4.0 - 10.4	7.6
dbh 23.0 - 37.9 (cm)	8.4	5.9 - 10.9	6.7	0.001	3.8	1.7 - 5.9	4.9
dbh > 38.0 (cm)	1.7	0.7 - 2.6	2.6	0.000	0.8	0.3 - 1.3	1.2
Percent of trees:							
% 3.0 - 7.9 (cm)	0.34	0.28 - 0.40	0.16	0.908	0.33	0.25 - 0.41	0.18
% 8.0 - 14.9 (cm)	0.29	0.23 - 0.34	0.14	0.632	0.27	0.20 - 0.33	0.16
% 15.0 - 22.9 (cm)	0.23	0.18 - 0.28	0.13	0.727	0.24	0.16 - 0.33	0.21
% 23.0 - 37.9 (cm)	0.11	0.08 - 0.15	0.10	0.783	0.12	0.08 - 0.17	0.11
% > 38.0 (cm)	0.03	0.1 - 0.4	0.04	0.533	0.03	0.01 - 0.06	0.06
% Canopy Closure	0.70	0.62 - 0.79	0.22	0.018	0.54	0.42 - 0.66	0.28
% Cover: 0.0 - 0.5m	0.32	0.21 - 0.44	0.31	0.000	0.73	0.62 - 0.84	0.26
% Cover: 0.5 - 1.3m	0.20	0.13 - 0.26	0.17	0.000	0.67	0.58 - 0.76	0.21
% Cover: 1.3 - 3.0m	0.30	0.23 - 0.38	0.20	0.001	0.51	0.41 - 0.61	0.24
% Cover: 3.0 - 6.0m	0.39	0.30 - 0.48	0.25	0.273	0.32	0.24 - 0.41	0.20
% Cover: > 6.0m	0.58	0.47 - 0.69	0.30	0.214	0.48	0.36 - 0.60	0.29
% Ground: Leaf litter	0.5	0.37 - 0.63	0.36	0.004	0.23	0.11 - 0.35	0.29
% Ground: Fern	0.24	0.12 - 0.36	0.31	0.004	0.04	0.00 - 0.08	0.09
% Ground: Grass	0.13	0.02 - 0.24	0.28	0.041	0.01	0.00 - 0.02	0.03
% Ground: Seedling	0.03	0.00 - 0.07	0.1	0.189	0.09	0.00 - 0.19	0.22
% Ground: Rock	0.01	0.00 - 0.03	0.04	0.282	0.00	0.00 - 0.01	0.02
% Ground: foliage	0.41	0.27 - 0.55	0.37	0.000	0.00	0.00 - 0.01	0.00
% Woody debris	0.05	0.02 - 0.07	0.06	0.439	0.03	0.00 - 0.06	0.07

Habitat variables such as these measured here tend to be highly correlated with one another and it can be hard to tease apart which variables have more of an influence on the birds when they choose a breeding site. Multivariate statistical methods such as ordination and clustering can help group interrelated variables together, thereby shrinking a large number of variables into a more manageable few. Such analyses have been performed for decades on avian habitat-relationship studies (James 1971; Cody 1981; Morrison et al. 2006).

Results of Principal Components Analysis

The result of the Kaiser-Meyer-Olkin measure of sampling adequacy (Table 2.) was mediocre (0.664). Bartlett's test of sphericity was significant ($p = 0.000$), meaning that the data set correlations are significantly different from zero. These results mean that a PCA is an appropriate technique to use on this data set, perhaps in addition to another statistical technique that might explain the variation in the data more completely. For our purposes here the PCA is quite adequate.

Table 2. Kaiser-Meyer-Olkin measure of sampling adequacy and Bartlett's test of sphericity for the principal components analysis

KMO and Bartlett's Test		
Kaiser-Meyer-Olkin Measure of Sampling Adequacy.		.664
Bartlett's Test of Sphericity	Approx. Chi-Square	547.205
	df	105
	Sig.	.000

The Principal Components Analysis results begin with a correlation matrix that displays a measurement of correlation between each variable with all other variables. (See Table 3 for the complete correlation matrix and the significance levels of those correlations.) Here we can see which variables are correlated with each other, and which variables don't seem to explain the variation in the others. In the correlation matrix we see a high correlation between SNAG and ELEV (0.661, p = 0.000), a correlation we may have missed had we not run this PCA. SLOP doesn't seem to be very highly correlated with any of the other variables except perhaps RICH (0.379, p = 0.002), but as we will see later this correlation isn't strong enough to create a new component. There is a high (and perhaps obvious) correlation between CONI and CONB per territory (0.727, p = 0.000). If there were a lot of variation in the sizes of the coniferous trees in these territories, we might not see such a high correlation here, as mentioned earlier. For example, one territory with 30 very large coniferous trees would have a much higher basal area than another territory with 30 small coniferous trees. CONI is also negatively correlated with COV1 (-0.526, p = 0.000) and positively correlated with LEAF (0.529, p = 0.000). DECI is correlated with DECB (0.855, p = 0.000) and also with COV4 (0.403, p = 0.001). SNAG is correlated with CONI (0.368, p = 0.003). RICH (the number of species of trees in each territory) is negatively correlated with ELEV (-0.333, p = 0.007) and slightly correlated with DECI (0.329, p = 0.008), DECB (0.383, p = 0.002), and CANP (0.386, p = 0.002). CONB is negatively correlated with the first 3 horizontal bands of percent cover: COV1 (-0.501, p = 0.000), COV2 (-0.541p = 0.000), COV3 (-0.519, p = 0.000) and positively correlated with LEAF (0.509, p = 0.000). DECB is correlated with CANP (0.426, p = 0.001). COV1 is negatively correlated with CANP (-0.570, p = 0.000) and LEAF (-0.797, p = 0.000) but highly correlated with COV2 (0.757, p = 0.000), which itself is correlated with COV3 (0.622, p = 0.000). COV5 is correlated

with LEAF (0.405, p = 0.001) but negatively correlated with COV1 (-0.485, p = 0.001) and

COV2 (-0.401, p = 0.001). Finally, LEAF is highly correlated with CONI (0.529, p = 0.000) and

CONB (0.509, p = 0.000) and negatively correlated with percent COV1 (-0.797, p = 0.000) and

at COV2 (-0.518, p = 0.000).

Table 4 lists the communalities for each of the variables. The communality of a variable

is the proportion of its variance explained by the PCA. Only one variable (coniferous basal area)

is below 0.9 (though only slightly at 0.896), which indicates that the variation in each variable is

explained very well by the PCA. There is therefore no reason to remove any of these variables

and run the procedure again, as would be the case if a variable had a low communality.

Table 5 displays the total variance explained by each of the components. The total

variance explained by principal component 1 after rotation equals 2.586, which is 17.2% of the

total variance in the data set. In other words, principal component 1 explains the variance in the

data set almost 2.6 times greater than any one variable by itself. The amounts of variance

explained by each of the components are the eigenvalues of the original correlation matrix of

Table 3. Each successive component explains a smaller amount of the total variance. Of the 16

components described by this analysis, the first 9 components explain more of the variance than

just one variable can by itself (after rotation). The first 8 components explain almost 85% of the

variance, again after rotation, essentially halving the number of factors (from the original 16

variables) that help explain the variance in the data. The second principal component explains

almost 14% of the variance, the third component explains 12.7%, while the rest of the

components each explain less than 10% of the variance.

Table 3. Correlation matrix (upper shaded matrix) and significance level (lower unshaded matrix) for variables used in the PCA

	ELEV	SLOP	CONF	DECD	SNAG	RICH	CONB	DECB	CANP	COV1	COV2	COV3	COV4	COV5	LEAF
ELEV		.064	.496	-.303	.661	-.333	.287	-.427	-.503	.173	-.050	-.085	-.047	-.361	-.136
SLOP	.322		-.080	.023	-.092	.379	-.098	.025	.018	.108	.150	.284	.183	-.053	-.127
CONF	.000	.282		-.295	.368	-.069	.727	-.283	.129	-.526	-.497	-.308	-.101	.179	.529
DECD	.013	.434	.015		-.263	.329	-.279	.855	.320	-.102	-.252	.018	.403	.021	-.015
SNAG	.000	.254	.003	.027		-.195	.251	-.310	-.339	.125	-.218	-.255	-.250	-.255	-.099
RICH	.007	.002	.311	.008	.079		-.018	.383	.386	-.213	-.208	-.006	.208	.088	.042
CONB	.018	.241	.000	.021	.034	.448		-.349	.181	-.501	-.541	-.519	-.259	.309	.509
DECB	.001	.428	.019	.000	.011	.002	.005		.426	-.103	-.170	.057	.311	.147	.044
CANP	.000	.448	.176	.009	.006	.002	.095	.001		-.570	-.480	-.163	.374	.782	.442
COV1	.105	.218	.000	.231	.184	.061	.000	.229	.000		.757	.372	-.118	-.485	-.797
COV2	.358	.139	.000	.033	.057	.066	.000	.109	.000	.000		.622	-.126	-.401	-.518
COV3	.270	.019	.012	.449	.031	.482	.000	.340	.120	.003	.000		.337	-.312	-.259
COV4	.368	.093	.233	.001	.034	.065	.029	.011	.003	.198	.182	.006		.137	.021
COV5	.004	.351	.097	.441	.031	.264	.012	.145	.000	.000	.001	.011	.162		.405
LEAF	.163	.180	.000	.458	.237	.381	.000	.377	.000	.000	.000	.000	.029	.441	

Variables are: ELEV = elevation, SLOP = slope of plot, CONF = number of coniferous trees, DECD = number of deciduous trees, SNAG = number of snags, RICH = tree species richness, CONB = coniferous basal area, DECB = deciduous basal area, CANP = percent canopy closure, COV1 = percent cover 0.0 - 0.5m, COV2 = percent cover 0.5 - 1.3m, COV3 = percent cover 1.3m - 3.0m, COV4 = percent cover 3.0 - 6.0m, COV5 = percent cover above 6m, LEAF = percent leaf litter

Table 4. Initial and extracted components of the 15 variables used in the PCA

Communalities

	Initial	Extraction
ELEV	1.000	.951
SLOP	1.000	.996
CONI	1.000	.956
DECI	1.000	.965
SNAG	1.000	.990
RICH	1.000	.984
CONB	1.000	.990
DECB	1.000	.966
CANP	1.000	.939
COV1	1.000	.935
COV2	1.000	.934
COV3	1.000	.960
COV4	1.000	.972
COV5	1.000	.957
LEAF	1.000	.916

Table 5. Variances explained by the components, before and after rotation

Total Variance Explained

Component	Initial Eigenvalues			Rotation Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	4.347	28.982	28.982	2.586	17.239	17.239
2	3.723	24.818	53.801	2.090	13.931	31.171
3	1.510	10.066	63.867	1.904	12.694	43.865
4	1.375	9.166	73.032	1.437	9.579	53.444
5	1.050	7.003	80.035	1.233	8.221	61.664
6	.796	5.307	85.342	1.217	8.115	69.779
7	.509	3.396	88.738	1.132	7.544	77.322
8	.461	3.076	91.814	1.106	7.372	84.694
9	.406	2.707	94.521	1.034	6.891	91.585
10	.234	1.557	96.077	.674	4.492	96.077
11	.213	1.421	97.499			
12	.132	.878	98.377			
13	.095	.631	99.008			
14	.080	.536	99.544			
15	.068	.456	100.000			

The numbers under the "Total" column are the eigenvalues of the correlation matrix. The next column is the percent of variance explained by each component, and the third column is the cumulative variance explained by the component and the preceeding ones.

Figure 1 shows a scree plot of the component number plotted against its eigenvalue for

the unrotated PCA. It shows that after 7 components, the eigenvalues start to level off and

become horizontal. This visual representation helps in the decision of how many components to

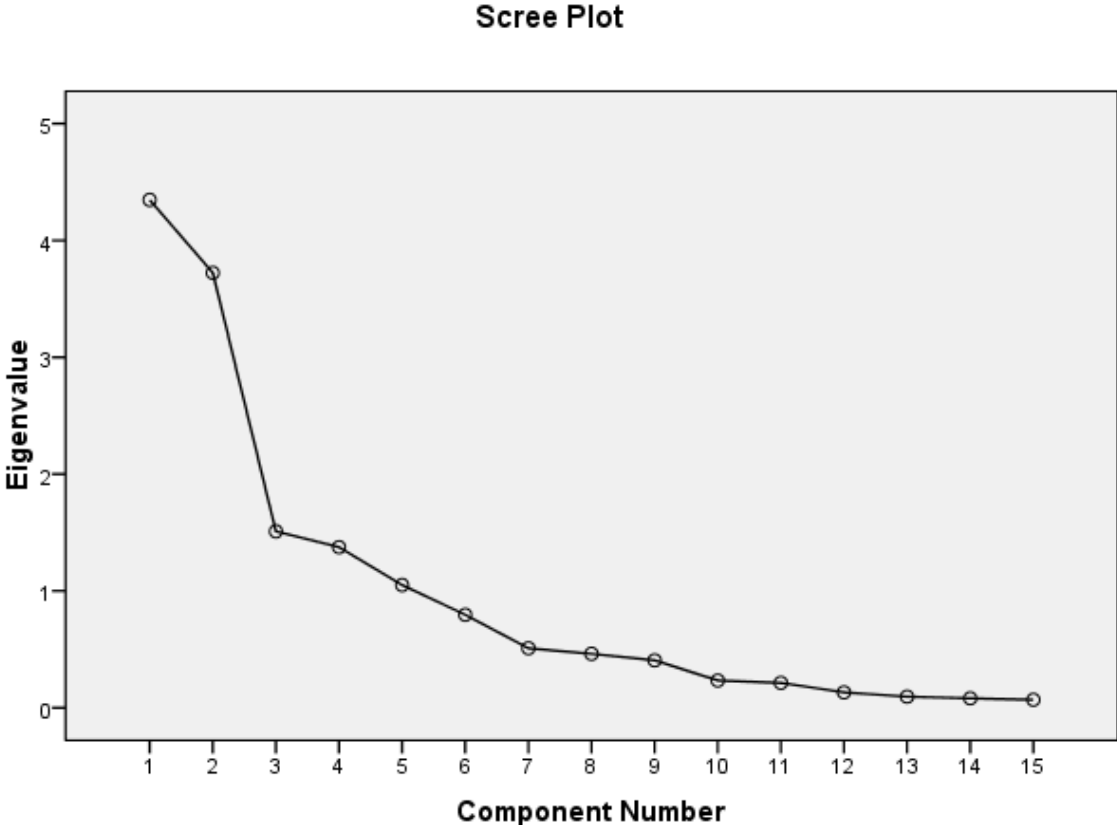keep in the final analysis, and which are less important.

Figure 1. Scree plot showing the eigenvalue (amount of variance explained) for each of the components in the PCA

Table 6 is the rotated component matrix that lists the coefficients of each variable in each of the components. Here we can start naming the components based on which variables have high loadings for each component. A high loading is generally considered to be anything with an absolute value over 0.3, so a variable with a loading of -0.500 is just as important to the component as a variable with a loading of 0.500. The first principal component has high positive loading for LEAF (0.922) and a high negative loading for COV1 (-0.871). Thus, the first

Table 6. Coefficients of each variable for each of the principal components

				Component				
	1	2	3	4	5	6	7	8
LEAF	.922		.196					
COV1	-.871		-.246	.263			-.111	-.138
DECI		.932				-.145	.231	
DECB		.923	.181		-.101			.169
COV5	.221		.922	-.190	-.124			
CNPY	.336	.250	.798		-.102		.207	.247
COV3	-.166		-.148	.898			.238	
COV2	-.575	-.197	-.205	.583	-.274		-.202	-.133
SNAG		-.152	-.173	-.140	.920	.225	-.107	
CONI	.515	-.201			.200	.730		
ELEV	-.117	-.215	-.362	-.117	.434	.676	.134	-.247
COV4		.223	.144	.162			.922	
RICH		.220						.927
SLOP				.131				.193
CONB	.406	-.243	.155	-.297		.337	-.162	

The highlighted coefficients are the ones used to name each component, and the ones on which the discussions are based. Variables are: LEAF = percent leaf litter, COV1 = percent cover at 0.0m - 0.5m, DECD = number of deciduous trees, DECB = deciduous basal area, COV5 = percent cover above 6.0m, CANP = percent canopy closure, CONF = number of coniferous trees, CONB = coniferous basal area, COV3 = percent cover at 1.3m - 3.0m, COV2 - percent cover at 0.5m - 1.3m, SNAG = number of snags (dead trees), ELEV = elevation, COV4 = percent cover at 3.0m - 6.0m, RICH = tree species richness, SLOP = slope of plot.

component explains the cover of foliage on the ground and is called "Ground Cover". The second component has high loadings for both DECI (0.932) and DECB (0.923). The second principal component is called "Deciduous Cover". The third component is called "High Canopy Cover", because it has high loadings for both CANP (0.798) and COV5 (0.922). The fourth component is called "Shrub Density" that has high loadings for COV2 (0.583) and COV3 (0.898). The fifth component is called "Snags", with high loadings only for the variable SNAG (0.920). There is also a high loading for ELEV in the 5th component, but ELEV also has a higher loading for PC6 (0.676), as does CONI (0.730). The 6th component is called "Deciduous / Elevation". The next 4 components have high loadings at only one variable. Component 7 is ("Upper Shrub Density") at COV4 (0.922), and component 8 is "Tree Richness", RICH (0.927). The last 2 components are not shown or discussed in the text because they do not help explain more than a single variable by itself would.

Figures 2 through 6 are scatter-plot graphs of each bird territory scored and plotted between 2 components. The blue circles are Hermit Thrush territories, and the green circles are Veery territories. By graphing the bird territories in this way, we can visualize how each species differs or not for each of the principal components. For example, if most of the green circles lay in one quadrant and most of the blue circles are in another, this is a good indication that the 2 species differ quite markedly in at least one of the principal components.

Figure 2. Scatterplot of PC1 (ground cover) against PC2 (deciduous cover). Species 1 (in blue) = Hermit Thrush, and Species 2 (in green) = Veery. Numbered cases are extreme values and are discussed in the text. This graph shows a clear distinction between Hermit Thrush and Veery preferences for PC1, but not PC2.

Figure 3. Scatterplot of PC3 (canopy closure) against PC4 (shrub density). Species 1 (in blue) = Hermit Thrush, and Species 2 (in green) = Veery. This graph shows a slight difference between species preferences for PC3, with most Hermit Thrushes scoring positive, but no clear pattern for Veeries. PC4, however, shows a clear distinction. Most Hermit Thrushes scored negatively while Veeries scored positively for Low Shrub Density.
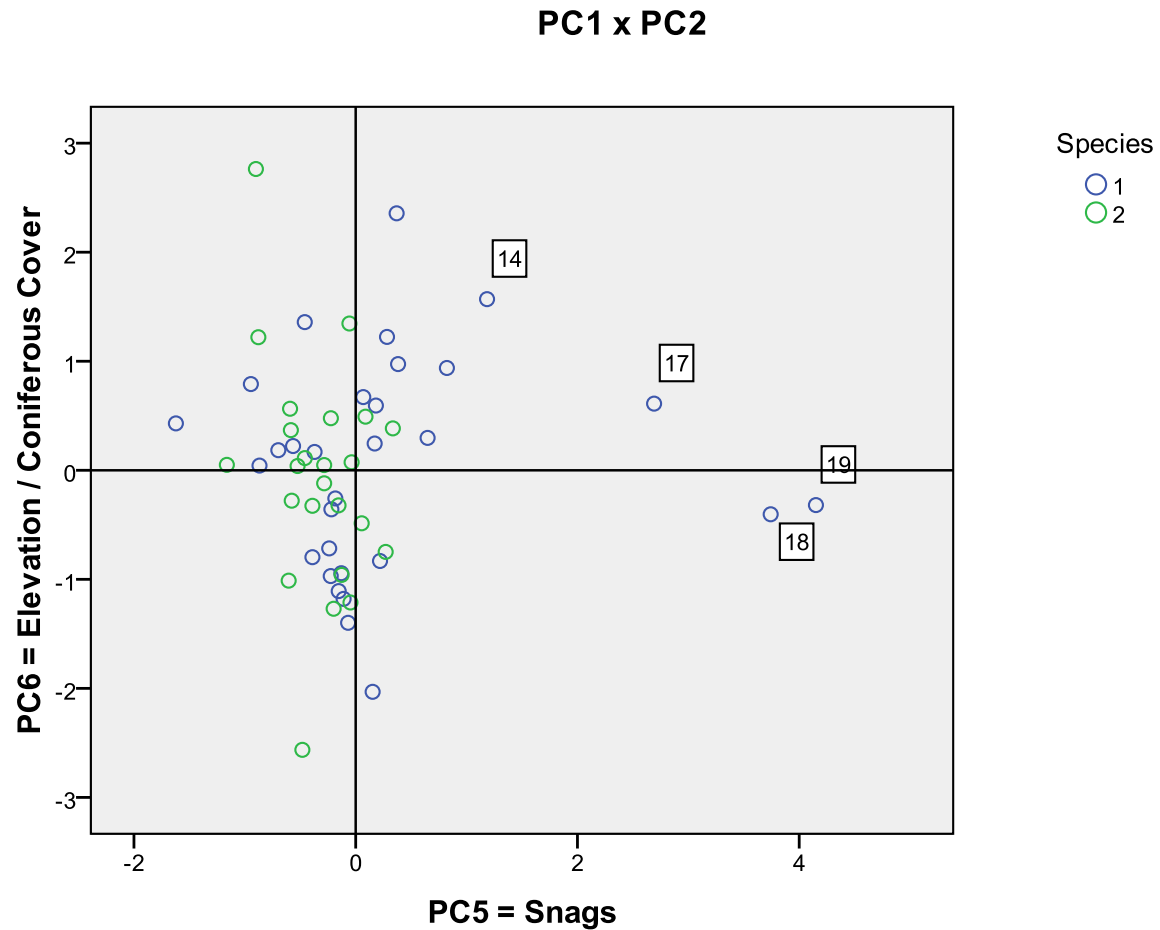
Figure 4. Scatterplot of PC5 (snags) against PC6 (elevation / coniferous cover). Species 1 (in blue) = Hermit Thrush, and Species 2 (in green) = Veery. Numbered cases are extreme values and are discussed in the text. This graph shows a number of extreme cases for Hermit Thrushes on PC5, and a few for Veeries on PC 6, but otherwise no clear distinction between them.
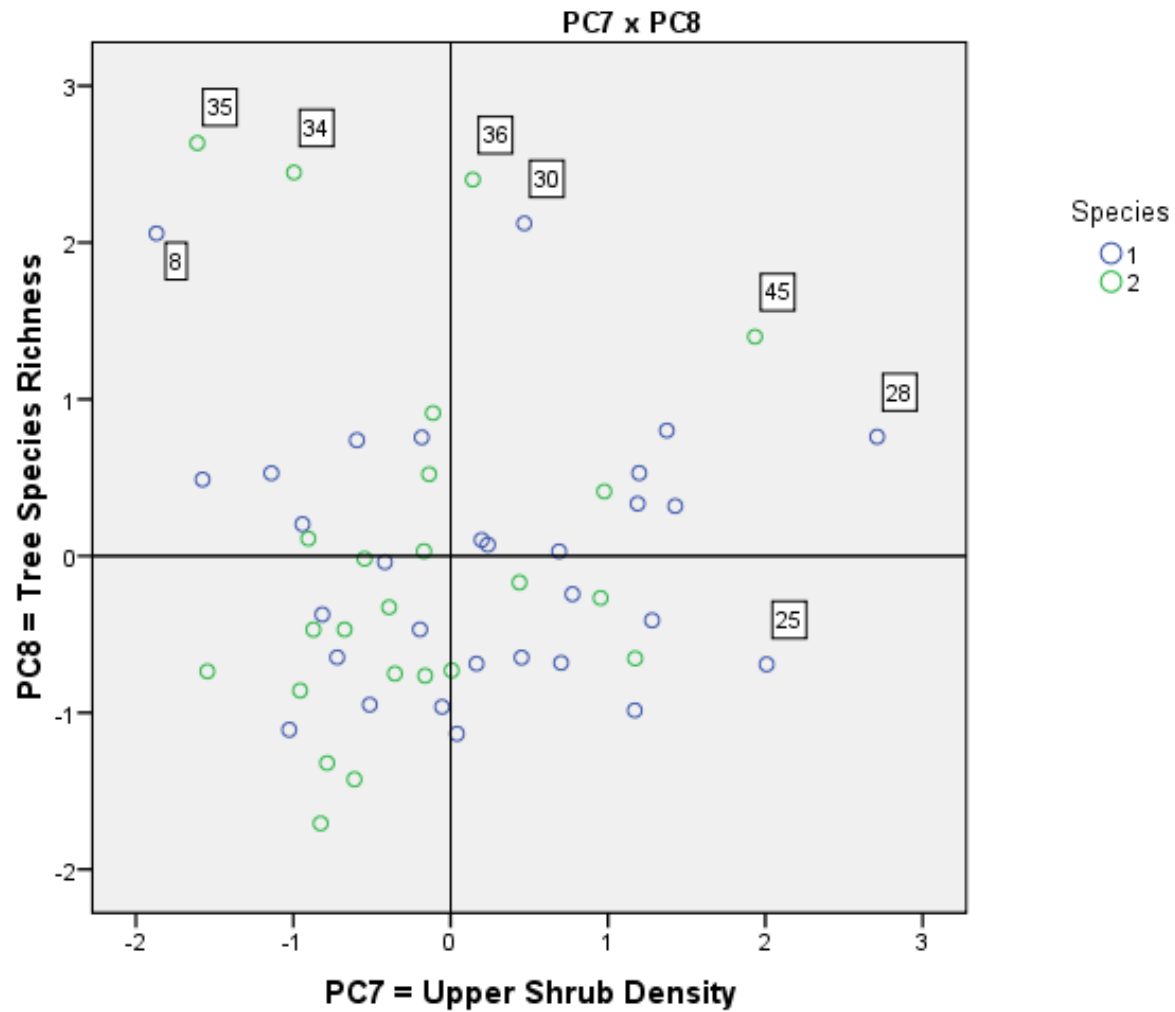
Figure 5. Scatterplot of PC7 (upper shrub density) against PC8 (tree species richness). Species 1 (in blue) = Hermit Thrush, and Species 2 (in green) = Veery. Numbered cases are extreme values and are discussed in the text. Veeries generally score low for PC8, except for the extreme cases 34 – 36.
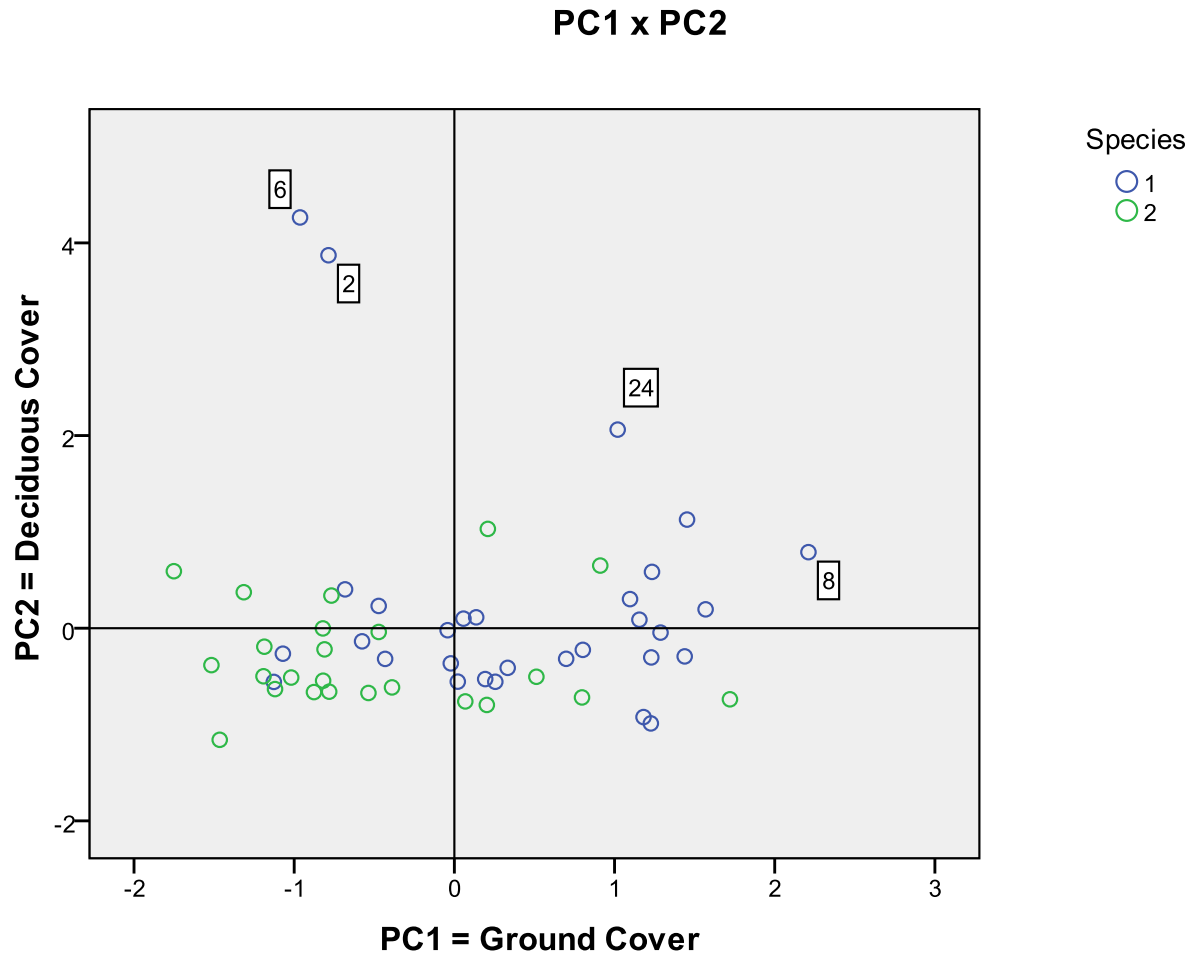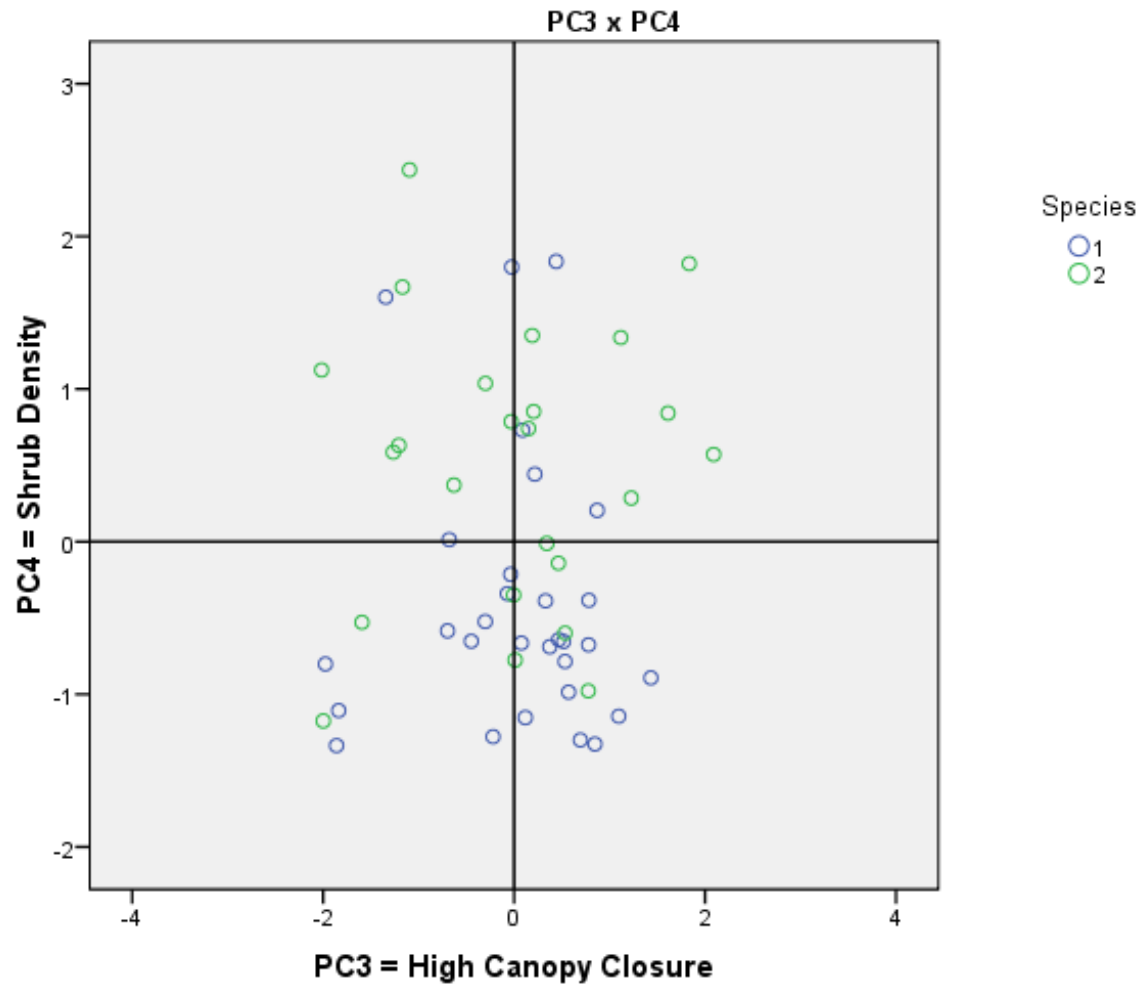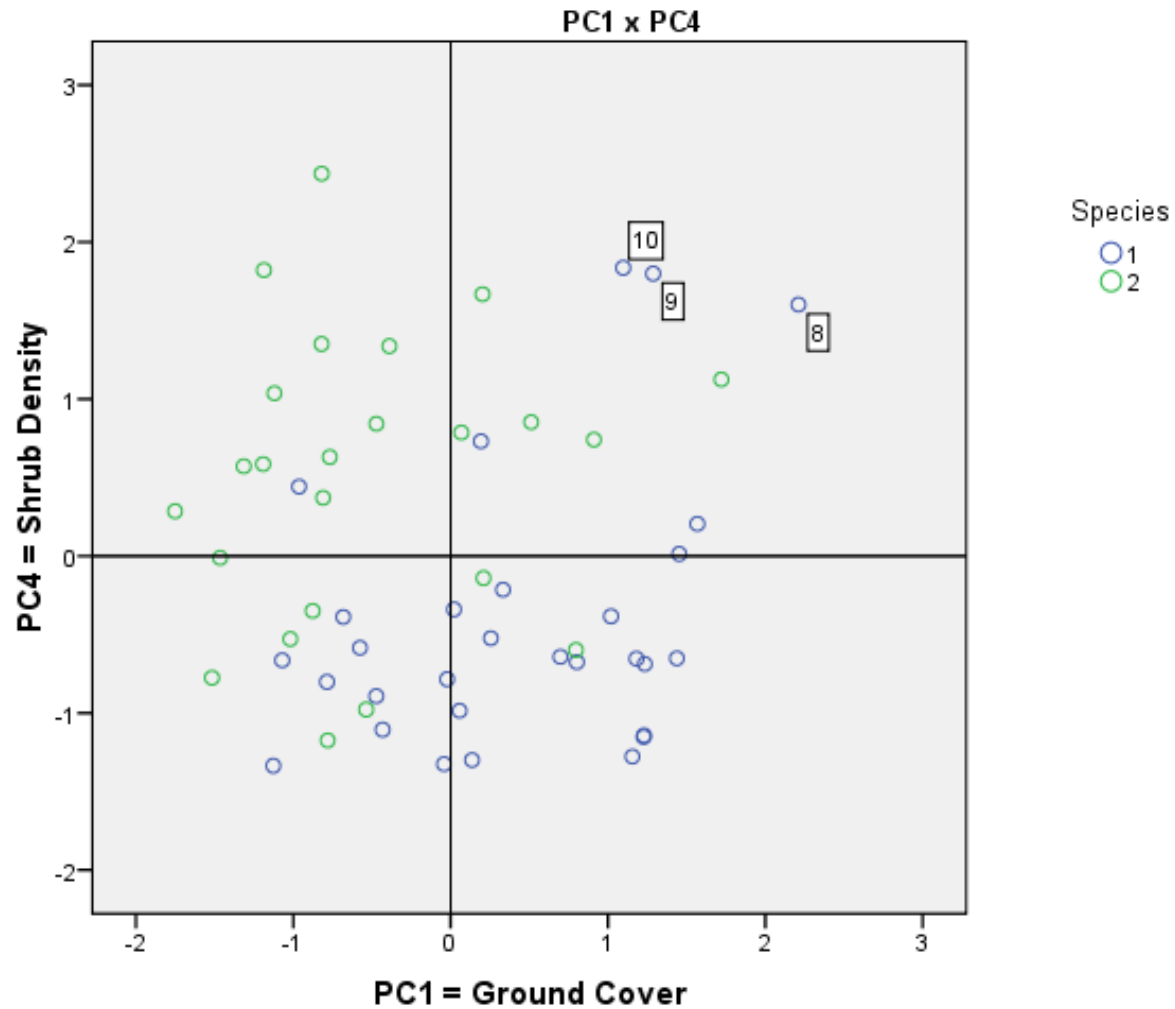
Figure 6. Scatterplot of PC1 (ground cover) against PC4 (shrub density). Species 1 (in blue) = Hermit Thrush, and Species 2 (in green) = Veery. Numbered cases are extreme values and are discussed in the text. This graph shows a clear distinction between species for both PC1 and PC4. Most Hermit Thrush cases are in the lower right quadrant, while most Veery cases are in the upper left.

Results of Cluster Analysis

Four cluster analyses were performed on the same data set that was used in the PCA, above. The first analysis clustered the habitat variables based on their similarities. This cluster agreed well with the Principal Components Analysis, with some of the major clusters being the same combinations that made up the Principal Components 2 - 4. See Figure 7 for the dendrogram.
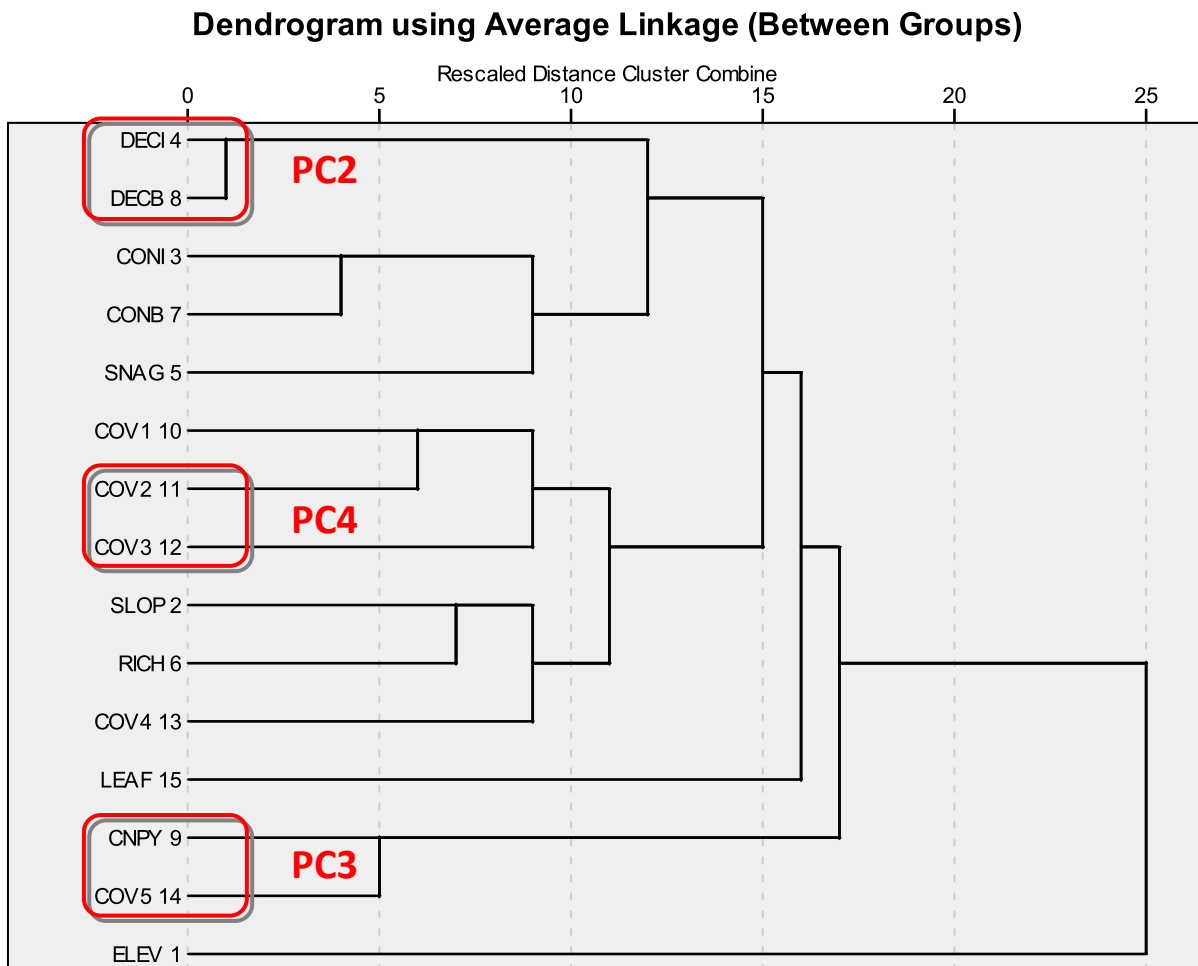
Figure 7. Dendrogram showing the relationships between habitat variables used in the analysis. Red boxes highlight the clusters that are also components from the PCA.

Principal Component 1 consisted of 2 variables, one of which was negatively correlated with PC1 (COV1), the other one was positively correlated (LEAF). These 2 would not be clustered together because they are not similar. Care should thus be taken when performing a cluster analysis to verify principal components, as things at a great distance from each other can make up a strong component but not a cluster.

Figure 8 shows a combination of 2 dendrograms. On the left is a habitat variable dendrogram of only Hermit Thrush territories, and on the right is a similar one for Veery territories. They are facing each other in order to see how clusters of variables for each species compare. There are several clusters that are similar for each species that show up different sections of the tree but are otherwise identical.

Figures 9 and 10 show a dendrogram of Hermit Thrush territories and Veery territories separately, and Figures 11 and 12 split the complete data set dendrogram up into 2 parts. In Figure 9, Hermit Thrush territories seem to be of 2 kinds. Seven territories are separated from the rest as being high in ELEV, CONI, and SNAG. The other 23 territories make up a large cluster that is largely defined by a mixture of DECI and CONI, LEAF, and some COV1 and COV2. In this larger cluster several smaller clusters are defined within these parameters. The largest of these (in dark blue) is a group of plots defined by high CANP and LEAF but low COV1 and COV2. Other clusters are color coded in the Figure. Turning to Figure 10, the cluster of Veery territories, we see something very similar: 2 large clusters defined by ELEV and CONI, the other by DECI and COV1 and COV2. Within these 2 main clusters are smaller ones, color coded as in Figure 8, to represent plots that are defined by more discrete variables. Care has been taken to use the same colors to represent similar plots for both species.

Figure 8. Dendrogram of habitat variables for Hermit Thrush (in large blue box, left) and Veery plots (large green box, right). Smaller colored boxes are clusters of variables that are similarly grouped for both species. Clusters for the Veery territories are much stronger than clusters for Hermit Thrush territories. This seems to indicate that Veeries are more sensitive to these particular variables, and Hermit Thrushes are less sensitive, or more of a habitat generalist than the Veery.

The last cluster analysis is for all 54 bird territories together. Figure 11 is the upper portion of the dendrogram. This branch represents those plots that are largely defined by a mixture of the variables DECI and CONI, and CANP. Further clusters are color coded as in Figures 7 and 8, including plots of both species that are similar. Figure 12 is the lower portion, which is largely defined by CONI and SNAG, and the smaller clusters are also a mixture of the 2 species' plots.

There is only one major cluster of this large dendrogram that contains only one species. This is the first cluster in Figure 12, the light blue box. These plots were defined by high ELEV and SNAG and were also all in the same area geographically.

Figure 9. Dendrogram of Hermit Thrush territories. Two main clusters (orange and green) are broken into smaller clusters with the habitat variables important to each cluster color coded.

Dendrogram using Average Linkage (Between Groups)

Rescaled Distance Cluster Combine
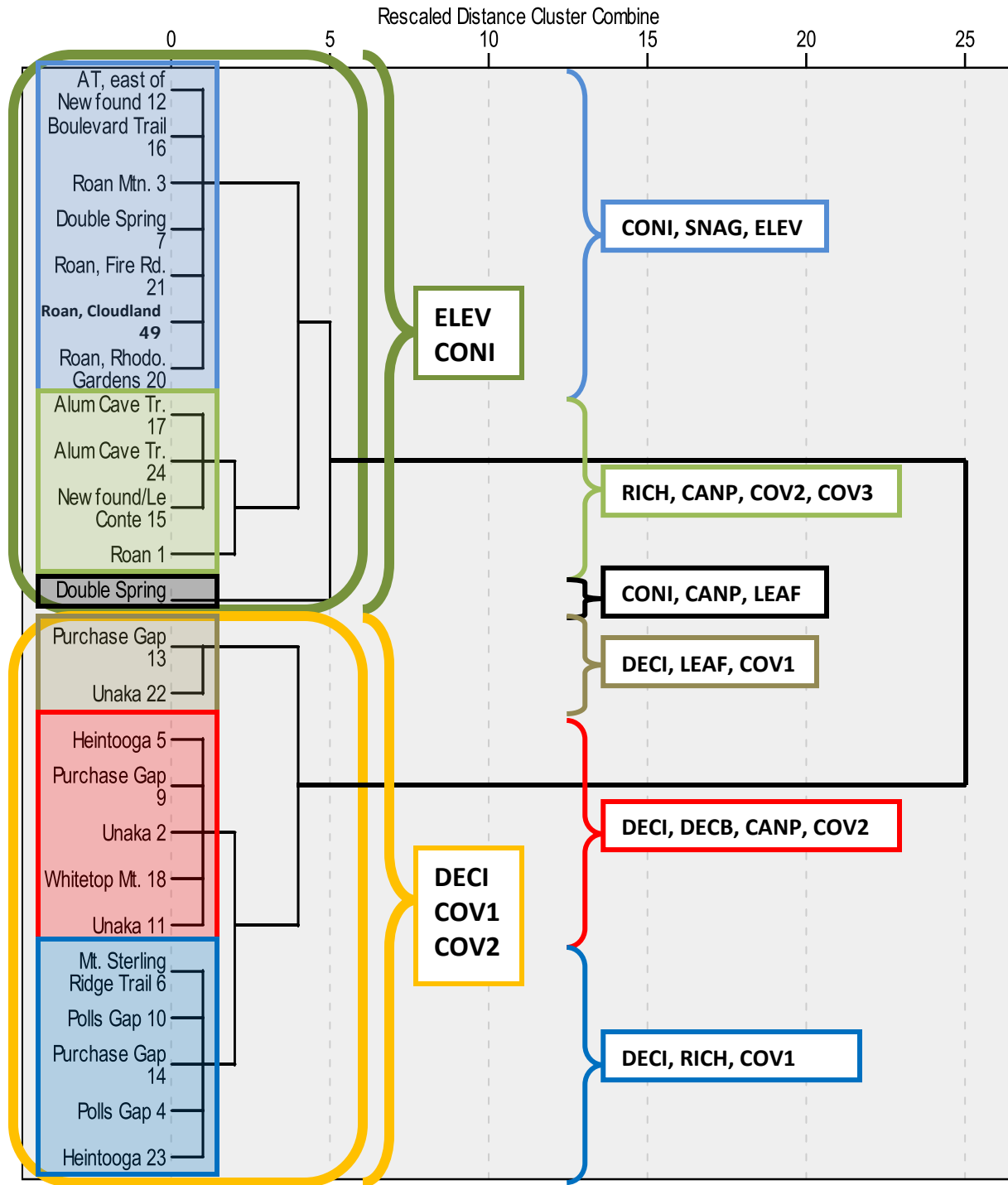
Figure 10. Dendrogram of Veery territories. Two main clusters (orange and green) are broken into smaller clusters with the habitat variables important to each cluster color coded.
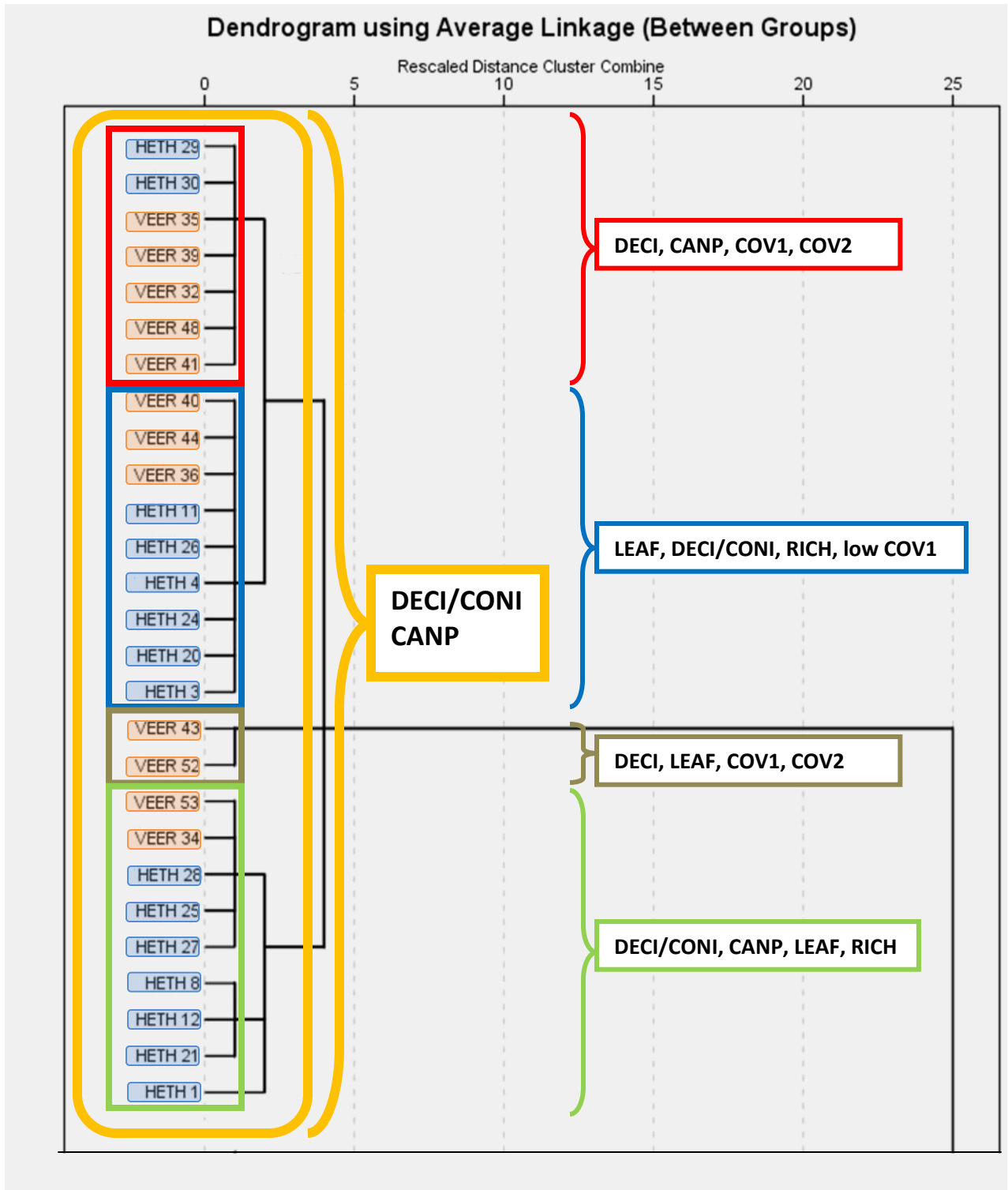
Figure 11. Upper portion of the dendrogram of all territories in the study. The leaves are the different species of birds, Hermit Thrushes in blue boxes, Veeries in red boxes.
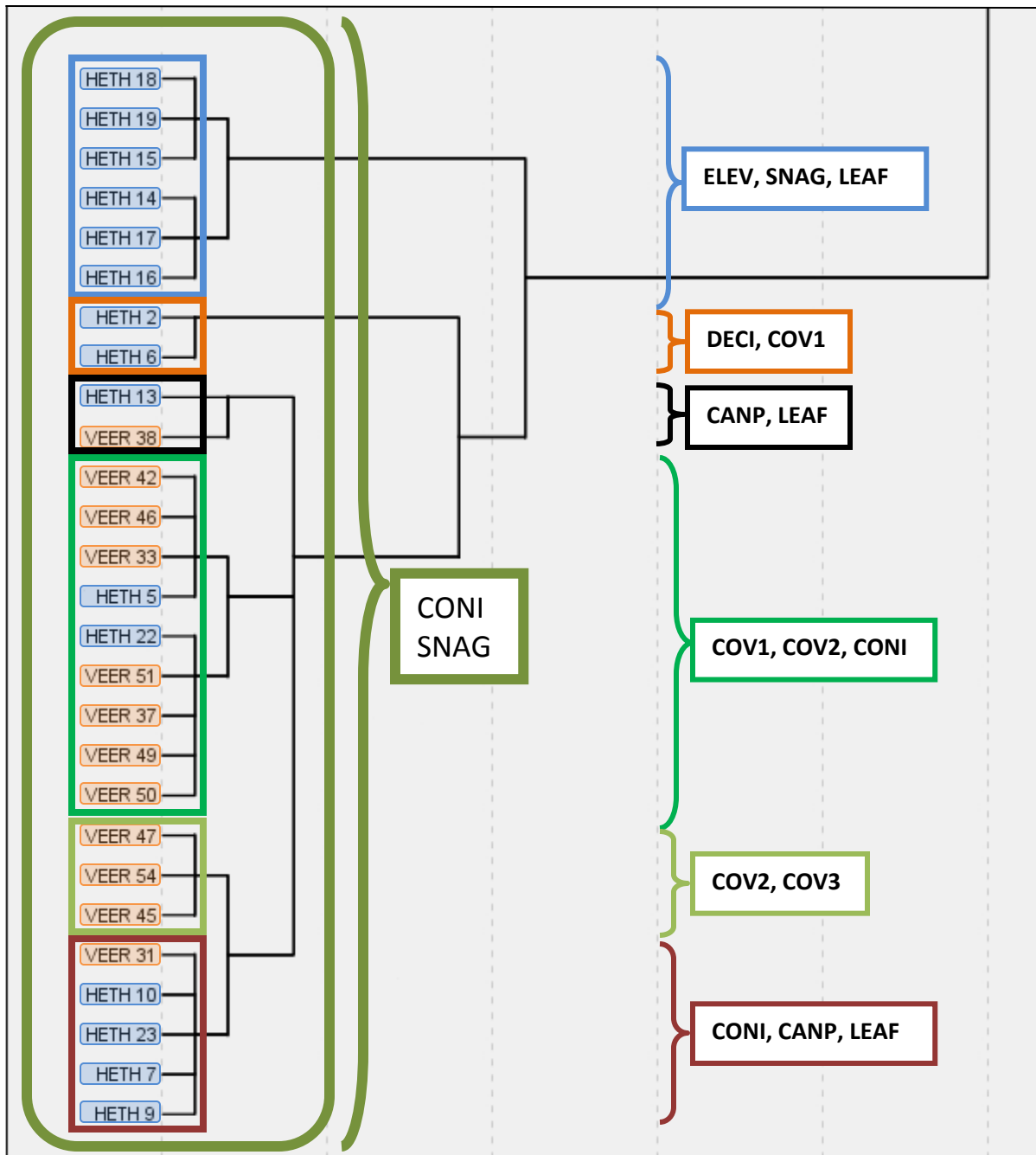
Figure 11. Lower portion of the dendrogram of all territories in the study. The leaves are the different species of birds, Hermit Thrushes in blue boxes, Veeries in red boxes.

CHAPTER 4

DISCUSSION

Description of Hermit Thrush habitat in the Southern Appalachians

Based on data collected in this study, a formal description of Hermit Thrush breeding habitat in its southernmost range can now be reported. First, the topographic measurements did not reveal anything new. We already have a good understanding of the elevational range of this species during the breeding season based on the numerous accounts of birders throughout the Southern Appalachians. This bird seems to be restricted to the Spruce-Fir and mixed Spruce-deciduous forests above 1525 meters (~ 5,000 feet). Where these forest types reach lower elevations, on northern slopes in particular, the bird may also be found. There are a few accounts of this species in areas of little to no Spruce occurrence [Huckleberry Knob, North Carolina (pers. comm Mike Nelson) and Craggy gardens, North Carolina, (pers. observ.)], but not enough reports to easily predict this bird outside of the typical Red Spruce range. The slope of the 30 territories in this project had an average angle of approximately 9.3° but varied widely. Most territories were not on steep slopes. It seemed like more of the Veery territories were steeper, but there was no statistically significant difference. The average Aspect of these territories was 177.3°, almost due south, but with such a high standard deviation (119°) that we cannot claim this to be significant.

Many vegetative characteristics, especially regarding the Veery territories, seem to be more significant than the topographic variables. Hermit Thrush territories were generally full of trees, with an average of 772 trees per acre. These sites had approximately equal numbers of coniferous (55%) and deciduous trees (45%), though a slightly higher percentage of coniferous is

noteworthy. Snags did not seem to be a particularly important part of Hermit Thrush territories (thought see PCA results), which seems to go against my original hypothesis about why this species may be expanding its range to the south. It should be mentioned, however, that the area that had the highest density of Hermit Thrushes in this study (Mt. LeConte, Great Smoky Mountain National Park) had a significantly larger number of snags per territory than any other site ($p < 0.001$). The peak of Mt. LeConte is full of Fraser Fir snags and the understory is full of Fir saplings. It is also full of Hermit Thrushes. Incidentally, here also is where the only Swainson's Thrush (*C. ustulatus*) has been found in Tennessee during the breeding season (2008, per Rick Knight, and 2009, pers. observ.).

Related to the gross number of trees per acre is the Basal Area of each territory. The basal area of a tree is the area of the cross section of that tree at 1.3 meters from the ground (approximately breast height). The basal area of a territory is an indication of how much standing wood there is per acre. Hermit Thrush territories had an average basal area of 14.81 m^2. Veery territories, by contrast, had an average of 6.93 m^2. Though basal area is correlated with the number of trees per acre, it is not always highly correlated. For example, 2 sites can have an equal number of trees on them but different basal areas because the basal area depends on the size of those trees. Hermit Thrush territories had almost 60% coniferous basal area and 40% deciduous basal area, which is similar to the percentages of coniferous and deciduous trees.

I separated the trees into 5 size categories based on their diameter at breast height (DBH), as has been done for other avian habitat descriptive studies (Noon 1981b). Hermit Thrush territories had an average of 287 trees with DBH 3.0cm – 7.9cm (34%), 226 trees with DBH 8.0cm – 14.9cm (29%), 148 trees with DBH 15.0cm – 22.9cm (23%), 84 trees with DBH 23.0cm – 37.9cm (11%), and 17 trees with DBH >38.0cm (3%). Noon (1981) suggested that Hermit

Thrush territories, more so than other forest thrush territories, have a higher number of mid-successional trees. According to my data, 35% of the trees in Hermit Thrush territories are considered mid-successional by Noon's definition, that is between 15.0cm – 37.9cm DBH.

Canopy closure is an indication of how much direct sunlight can penetrate beneath the canopy. A territory with a high percent canopy cover usually has little direct sunlight able to reach the shrub and ground layers. Hermit Thrush territories in this study had an average of 70% canopy closure, which is fairly high compared with the Veery (56%), almost half of which is open canopy. The amount of sunlight that can reach the lower layers of the forest structure has a profound effect on the vegetation that can grow there. The next 5 variables that I measured show this effect quite well.

Percent Cover is a measurement of how much foliage there is in a particular horizontal band throughout the territory. I estimated percent cover in 5 such horizontal bands in each territory: 0.0 – 0.5m, 0.5 – 1.3m, 1.3 – 3.0m, 3.0 – 6.0m, and >6.0m above ground. Hermit Thrush territories generally had low percent cover in the first 3 layers above the ground (32%, 20%, and 30%, respectively). The Veery territories, however, had significantly higher percentages in these three bands (73%, 67%, and 51%). Veery territories generally had a much denser shrub layer ($p < 0.001$) than Hermit Thrushes. This is also reflected in the PCA results below. The upper 2 bands were not significantly different between the species (39% and 58% for the Hermit Thrush, 32% and 48% for the Veery).

Ground cover was the last measurement made in each territory. Hermit Thrush territories had a high percentage of leaf litter (50%), ferns (24%), and grasses (13%). Ground cover is an important component of forest thrush breeding territories because this guild spends a lot of time

on the ground foraging for insects. The Hermit Thrush also uses the ground as a nest site, often placing its nest under foliage or under a small coniferous sapling. Approximately 41% of the ground was covered by some foliage for the 30 territories surveyed in this study. The fact that there is so much ground cover in Hermit Thrush plots correlates well with what is known of their ecology. Hermit Thrushes spend more time on the ground actively searching for insects than do Veeries.

Comparison of Southern Appalachian Hermit Thrush Territories with Other Studies and with Breeding Bird Atlases of States to the North

The breeding territories of the Forest Thrush guild have been studied in many different areas throughout their respective ranges. An interesting phenomenon with these studies is that in different places each Thrush species responds differently to the other members of the guild. For example, in eastern North America the Swainson's Thrush prefers higher elevations than its congeners where they overlap, but in western North America they are found at lower elevations than sympatric congeners (Collar 2005). Many states have also published a Breeding Bird Atlas that describes the habitat structure for each species of bird that breeds within the boundaries of that state. It is interesting to compare the Hermit Thrush breeding territories of these other studies and atlases with the data collected for this present study.

Wood et al. (1999) created a Habitat Suitability Index Model for Hermit Thrushes that breed in west-central Alberta, Canada. They proposed that sites with at least 10% spruce or fir in the canopy, a canopy height of 10m, 60% canopy coverage, and some deciduous trees in the canopy are suitable places for Hermit Thrushes to breed. This model, though based on local data,

has yet to be tested in the field, but it correlates well with the present study. Northern forests are similar in both floristics and physiognomy to the Spruce-Fir forests of the Southern Appalachians, so the high correlation between this model and my study is understandable. The Wood et al. model discusses the need for a high level of shrub or sapling cover for nesting purposes but does not include this component in their final model. The present study found little evidence that Hermit Thrushes prefer areas with high densities of shrubs or saplings but preferred a more open understory, especially compared to the Veery.

Morse (1972) compared Swainson's and Hermit Thrush territories in Spruce forests along the coast of Maine. He found Swainson's Thrushes to prefer forests with a dense understory of young conifers, while Hermit Thrushes preferred forests that were larger and not so dense. These forests are dominated by Spruce, and very few deciduous trees exist here. This is somewhat comparable to the present study, where Veery's were found in areas with a higher density of the shrub layer, while Hermit Thrushes tended to prefer more open understory.

Paszkowski (1984) compared habitat use between Veeries and Hermit Thrushes in northern Wisconsin mixed coniferous – northern hardwood forests. She found no significant differences between the tree types, sizes, overstory structure, or understory structure between the 2 species. Hermit Thrushes did, however, forage on the ground layer 3 times as much as the Veery did, while the Veery used all height strata evenly. Hermit Thrushes foraged in conifers more often than deciduous trees, while the Veery foraged in deciduous trees more than in conifers. According to her study Veeries were more of a habitat generalist, while the Hermit Thrush was a little more specialized. These results don't agree well with the present study, and my data suggest that canopy cover and shrub density are important components that distinguish Hermit Thrush and Veery territories.

Noon (1981) studied the whole Forest Thrush guild in many different gradients along the length of the Appalachian Mountains. During his study Hermit Thrushes were not yet present in the Southern Appalachians, so he was not able to compare them with the Veery here. He did, however, study their habitat structures in the northern portions of his study. He found that Hermit Thrushes prefer midsuccessional forests that had high canopy cover with trees in the intermediate diameter range (15.3 – 38.0cm DBH). The Hermit Thrush also had the broadest niche breadth of the 5 species he studied, which is consistent with other Thrush studies, including the present one.

Dellinger et al. (2007) studied habitat partitioning between 4 Thrush species in West Virginia: Hermit Thrush, Veery, Wood Thrush (*Hylocichla mustelina*), and American Robin (*Turdus migratorius*). They found significant differences between the species at 3 spatial scales (nest substrate, nest site, and territory). Hermit Thrushes nested at the highest mean elevation, their territories were slightly more northeast facing, and tended to be closer to edge situations compared to the other 3 species. The present study agrees with the elevation aspect of the Dellinger study but not with the edge aspect. Veery territories were very close to and sometimes situated within edge-type and disturbed habitats within the forests. The forests in West Virginia are perhaps not as disturbed as the Spruce-Fir forests of the southern mountains, due to their lack of Fraser Fir (a result of the Balsam Wooly Adelgid).

Bucklew and Hall published the West Virginia Breeding Bird Atlas in 1994. Here they discuss the habitat of the Hermit Thrush as having at least some Red Spruce and usually constrained to areas above 1200m. McWilliams et al. (2000) describe the habitat of the Hermit Thrush in Pennsylvania very similarly to Bucklew and Hall. Here they prefer forests with some coniferous cover, generally at the higher elevations throughout the state (> 1800 feet). In Oregon

(Marshall et al. 2003) a different subspecies of the Hermit Thrush (*C. guttatus guttatus*) breeds throughout much of the higher mountains in mature and old-growth forests of all types. Typical Hermit Thrush territories here have a semiopen canopy with an open understory. These descriptions of Hermit Thrush territories in other states agree well with the data collected in the present study. Hermit Thrushes are found generally at higher elevations with some coniferous cover (in Tennessee, mostly coniferous cover) and a relatively open understory.

Principal Components Analysis

There were not too many surprises in the correlation matrix (Table 3.) Most of the variables that should have been correlated were. A few noteworthy correlations are worth further discussion. There is a high correlation between elevation and number of snags (0.661). These snags are mostly Fraser Firs that have been killed by the Balsam Wooly Adelgid. Only at the highest mountain peaks are there relatively pure stands of Fraser Fir, mostly above 1830m in elevation. These high peaks have been hit hard by this infestation, so it makes sense that the higher one goes up the mountain, the more snags one encounters. Percent canopy closure is also negatively correlated with elevation, invariably for the same reason.

Slope and percent cover at 1.3m – 3.0m are positively correlated (0.430). Perhaps in areas with greater slope there is a higher shrub density, but I could not find anything in the literature to support this hypothesis. Tree species richness is negatively correlated with elevation (-0.333), which makes sense, as the higher one goes in elevation, the more pure stands of Spruce and Fir there are, and the northern hardwoods start to decrease. The number of coniferous trees and coniferous basal area are both correlated with percent leaf litter on the ground (0.529 and 0.509,

respectively). Coniferous trees don't allow much sunlight penetration, so the ground foliage is much less in these habitats than in others. For this reason as well coniferous basal area is negatively correlated with percent cover at 0.0m – 0.5m (-0.541), at 0.5m – 1.3m (-0.541), and at 1.3m – 3.0m (-0.519).

Another interesting correlation is between the number of deciduous trees and percent cover at 3.0m – 6.0m (0.403). This is not a very tall canopy. At high elevations, the northern hardwoods don't grow as tall as they do at lower elevations due to extreme temperatures during the winter and shorter growing season in the summer. This correlation seems to be a result of this phenomenon.

The fact that it took 8 components to reach 85% of the explained variance, and that the result of the Kaiser-Meyer-Olkin measure of sampling adequacy was somewhat low (0.634), means that these variables were perhaps not as well correlated with each other as initially thought. A PCA on this data set is therefore a good start but perhaps not the only analysis that can return interesting results. A PCA coupled with a Cluster Analysis was performed for this reason, and is discussed below.

The first 4 components all have high loadings for 2 separate (but correlated) variables, indicating that a combination of variables is necessary to understand the important features of these bird territories. The 5th, 7th, and 8th components have high loadings for only one variable, indicating that they are perhaps only as useful in describing the variance as one variable alone. Ignoring these components, however, might mean missing an important distinguishing characteristic between the species habitat preferences. By examining the scatter-plot graphs in Figures 2 through 6, we can visualize how each species scores for each component. The first

scatter-plot (Figure 3.) shows the scores for PC1 (Ground Cover) plotted against the scores for PC2 (Deciduous Cover). It is clear that as you move from left to right the number of green circles *decreases*, meaning that Veery territories score relatively low for PC1. It is also clear that the number of blue circles *increases* as you move from left to right, meaning that Hermit Thrush territories generally score high for PC1. Principal Component 1 refers to Ground Cover and is the component that describes the highest amount of variance within the data set. It is clear that these 2 species differ markedly in their preference for territories with differing amounts of ground cover. One only needs to look at a high scoring blue territory (number 8, for example) to find out how the component is scored and which species prefers less ground cover and more leaf litter. According to the original data Hermit Thrush territory number 8 has a percent cover at 0.0m – 0.5m of 5% and percent leaf litter of 85%. This means that a high score for PC1 refers to territories with low densities of ground cover and high percentages of leaf litter. These variables seem to be the ones that explain the differences between Hermit Thrush and Veery territories the most. Veery territories tend to have high amounts of ground cover and low levels of leaf litter. On the same graph, principal component number 2 shows some outliers in blue. These outliers (Hermit Thrush territories number 6, 2, and 24) score very high for PC2, which is Deciduous Foliage. These territories are extreme cases where most if not all of the trees were deciduous. Cases 2 and 6 were both on Roan Mountain, straddling the border of TN and NC. Here, thick stands of maturing Yellow Birch (*Betula lutea*) are found, and so were a few Hermit Thrushes. Most of the Veery territories (17 out of the 22 here plotted) have slightly negative scores for PC2, indicating that more often than not Veery territories have low deciduous cover, which seems counterintuitive. Veeries have a much broader elevational range than Hermit Thrushes in the southern mountains, so one would think that the Veeries would have much higher scores for

this PC. However, I did not survey Veery territories in the full elevational range but concentrated on the elevational band in which both species are found. Perhaps this is an isolating mechanism between these species. Hermit Thrushes can use areas with both high coniferous and high deciduous basal areas, while Veeries at least in this elevational range generally prefer areas with lower deciduous basal areas.

Principal Component 3 (Figure 4) shows high scores for most of the Hermit Thrush territories (though no extreme cases) but relatively even scores for Veery territories. Hermit Thrushes prefer areas with high canopy cover, as indicated by the scores of this PC. However, the results can be misleading, as the graph seems to indicate that a third of Hermit Thrush territories have low High Canopy Closure. In certain cases territories can have a low canopy closure but still many trees that are stunted, forming a lower canopy then measured for COV5, which is above 6 meters. If the trees are not above 6m in height, even though canopy closure is high, this territory would score low for PC3 because there is no cover above 6m. In general canopy closure and percent cover above 6m are highly correlated (0.782 in the correlation matrix)\ but are not always perfectly correlated.

Principal Component 4 (Shrub Density) gives almost as striking a result as PC1 (Ground Cover). Most of the Veery territories score high for PC4, and most of the Hermit Thrush territories score low. This variable is significantly different between species according to the MANOVA. In fact, PC1 and PC4 show the largest differences between the species and are thus plotted together in Figure 7, where most of the Hermit Thrush cases (in blue) are in the lower right quadrant, and most of the Veery territories are in the upper left quadrant. See Figure 13 for a scatter plot taken from the original data, showing LEAF plotted against COV2. Here, most of the Hermit Thrush cases are below 0.40 on the Y-axis, while most of the Veery cases are above.

Also evident in this figure is the negative correlation between LEAF and COV2 (-0.518, p = 0.000 in the correlation matrix). Veery territories show a clear pattern of high shrub density, while Hermit Thrush territories show a clear pattern of low shrub density. This finding has been verified in other studies. Veeries are known to sing and forage mostly within the shrub layer (Bertin 1977), while Hermit Thrushes are less dependent on a well-developed shrub layer (Holmes and Robinson 1988) and do most of their foraging on the ground in the leaf litter.

Principal Components 5 and 6 are plotted against each other in Figure 5. Veery territories generally show low scores for PC5 (Snags). Snags do not seem to be an important part of Veery territories. There are, however, a few extreme cases for Hermit Thrush territories. Labeled on the graph are cases 14, 17, 18, and 19. These 4 plots were all on Mt. LeConte, in the Great Smoky Mountains National Park. This particular peak had a very high density of dead Fraser Firs, and also a very high density of Hermit Thrushes. My original hypothesis of a correlation between Hermit Thrush appearance and Fraser Fir die-off seems to have justification on this peak, but not in most other Hermit Thrush territories in general. Principal Component 6 (Elevation / Coniferous Cover) doesn't seem to show any clear distinctions between species. There are 4 extreme cases, 2 of which are Hermit Thrush territories, the other 2 are Veery territories.
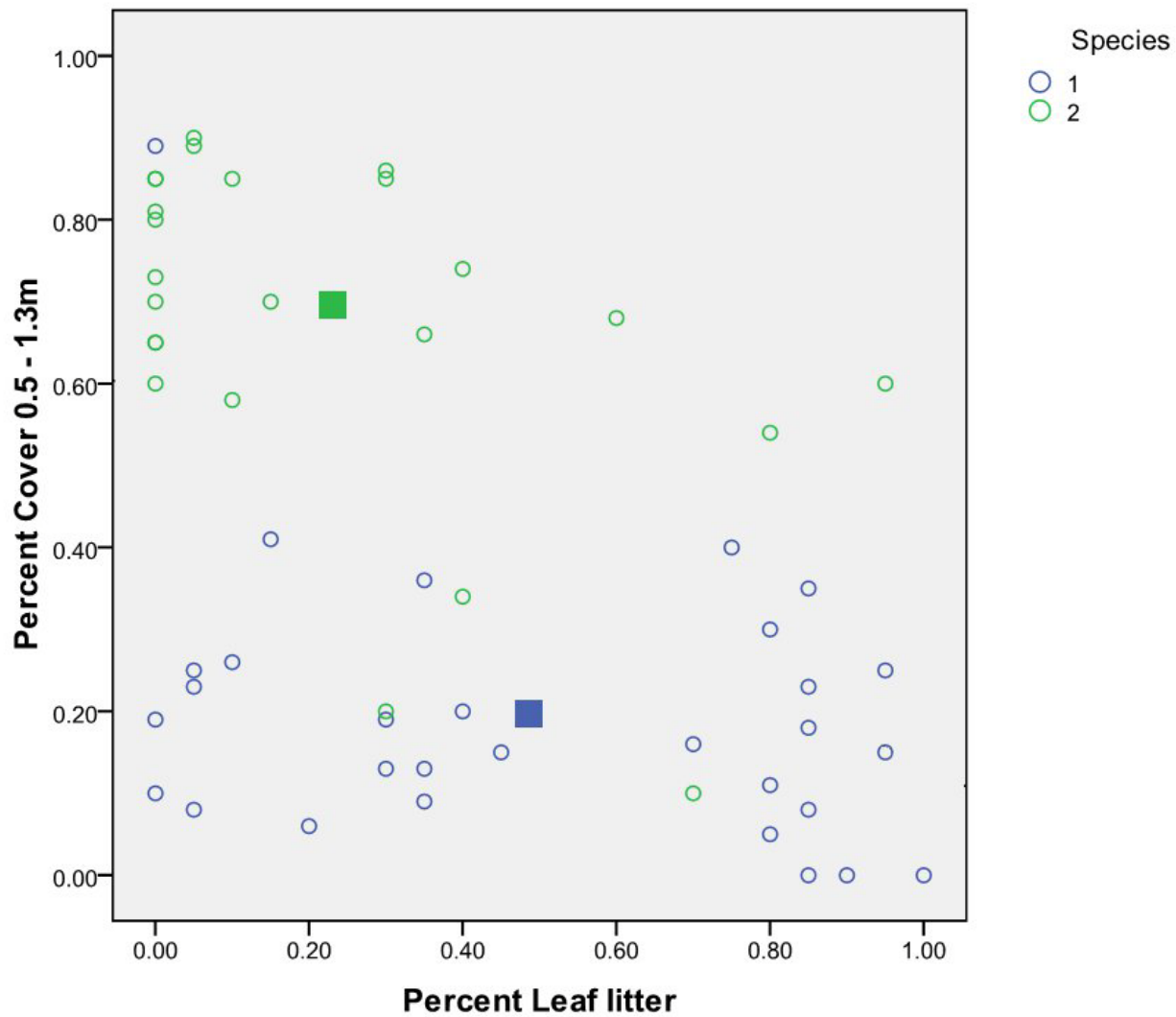
Figure 13. Scatterplot showing LEAF against COV2. Blue circles = Hermit Thrush, green circles = Veery. Squares are mean values for these two variables for Veery (green) and Hermit Thrush (blue).

Principal Components 7 and 8 are plotted against each other in Figure 6. There are no clear patterns of distinction in either of these 2 components between the species. There are extreme cases for PC 8 (Tree Species Richness) for Veeries. These territories all have 7 species of trees within them, the highest number for any of the Veery territories. These are located at the Heintooga / Polls Gap area of Great Smoky Mountains National Park. It is unclear why this area shows the most species richness. High Shrub Density (PC7) has lower scores for Veery territories. It is interesting the Veeries prefer high densities of lower shrubs but lower densities of higher shrubs.

In summary, PC1 and PC4 seem to show the clearest distinctions between the habitat preferences of Hermit Thrushes and Veeries. Ground Cover and Shrub Density seem to be higher for Veeries, while Leaf Litter is high and Shrub Density is low for Hermit Thrushes.

Cluster Analysis

The different cluster analyses were performed to try to simplify the data and to get a visualization of how the habitat variables are important to each species. The first analysis was performed on the habitat variables of both species together (Figure 7). This was done largely to verify the principal components, which it did very well. PC1 did not cluster because the 2 variables are negatively correlated with each other, but PC2, PC3, and PC4 show up as clusters here. A similar analysis was done on habitat variables individually for each species. Figure 8 shows these 2 dendrograms facing each other, with clusters of similar variables in both trees color coded. Here we see that many clusters are the same for both species, which isn't too surprising. What is striking about this comparison is how distinguishable the groups are for

Veery plots compared to the weaker groupings of Hermit Thrush variables. Veeries, it seems, are more sensitive to these variables, and show more habitat specificity than do Hermit Thrushes. This is in agreement with the ecology of both species. Hermit Thrushes, at least among the guild of forest thrushes, are habitat generalists, while the other species are more habitat specific.

The next cluster analysis was on Hermit Thrush territories and Veery territories separately. Both Figures (9 and 10) are divided into 2 sections: one defined by CONI, ELEV, and SNAG, the other by a mixture of DECI/CONI and maybe COV2, LEAF, and CANP. What is striking is the similarities between these dendrograms, which is made more so when putting them together in Figures 11 and 12. The final clusters are largely a mixture of territories, with many plots showing the same defining variables but not separated by species. In other words, there seems to be a lot of overlap between the habitat preferences of the birds, with no really clear distinction between them. For example, in Figure 11 the dark blue box shows a cluster of plots that are defined by LEAF, DECI/CONI, RICH, low COV1. Most of these plots are Hermit Thrushes, but there are 3 Veery plots in here as well. Likewise, in Figure 12, the bright green box surrounds a cluster defined by COV1, COV2, CONI. Most of these plots are Veeries, but there are 2 Hermit Thrush plots that use this habitat as well.

Possibility of double-brooding of Hermit Thrushes in the Southern Appalachians

McWilliams et al. (2000) discuss the possibility of Hermit Thrushes producing more than one brood per breeding season based on the arrival dates of these birds to their breeding grounds in Pennsylvania. Hermit Thrush eggs can be found between May 12 and June 29, and nests have been found as late as August 10 (McWilliams et al. 2000). During the course of this study, I

witnessed and photographed a just-fledged Hermit Thrush being fed by both parents on June 2, very early in the breeding season. If juvenile Hermit Thrushes leave the nest in early June, there is every indication that Hermit Thrushes can produce more than one brood per season in the Southern Appalachians. Other documented evidence of Hermit Thrush breeding comes from Rebecca Browning (2003), who ran across Hermit Thrush parents and fledglings in western North Carolina in mid-June. These and other anecdotes of Hermit Thrush sightings throughout this region (Knight 1997; Browning 2003) give good evidence of the possibility that Hermit Thrushes can produce a second brood each summer.

Range Expansion of the Hermit Thrush and Its Possible Effects on the Veery

This study was undertaken to better understand the expansion of the breeding range southward by the Hermit Thrush. By studying the vegetative characteristics in many of the territories, are we closer to understanding this phenomenon? My original hypothesis was that the Hermit Thrush is moving southwards to take advantage of the changes in the Spruce-Fir forest structure brought about by the Balsam Wooly Adelgid infestation. Great losses of mature Fraser Firs are opening up many canopy gaps and allowing the understory vegetation to grow denser, and it is this feature that I thought the Hermit Thrushes were responding to. However, the relative lack of understory growth in the typical Hermit Thrush territory in this study leads me to believe that my original hypothesis is wrong, and that the Hermit Thrush may be expanding its range here for different reasons. Perhaps the maturation of the Red Spruce forests after having been cleared in the 1920s is making this area more attractive to this species. Hermit Thrushes in

other areas prefer mid-successional to mature forests in which to breed, and these forests are now

quite mature where disturbances other than logging have not had a great impact.

Figure 14. Photograph of a Hermit Thrush fledgling. Heavy dorsal spotting and very short tail indicate this bird as having left the nest within 2 or 3 days of this photo, taken by Andrew Laughlin, June 2, 2009.

There is evidence that forest-breeding birds in eastern North American are experiencing

an increase in population size (Valiela and Martinetto 2007). If this is true for the Hermit Thrush,

we could be witnessing a source/sink population relationship. The eastern population of the

Hermit Thrush is increasing at a steady rate of 1.4% per year (Peterjohn et al. 1994) which lends

some weight to this hypothesis as well. But, as in most ecological processes, a combination of many factors is probably involved in this expansion we are fortunate to witness.

Will the Veery and the Hermit Thrush be able to successfully breed in the same forests here in the Southern Appalachians? Or could the Veery, already pushed up the mountain due to competition at lower elevations by the Wood Thrush, be pushed down the mountain to the belt between the Hermit and Wood Thrushes? Morse (1971) noted the effects of the Wood Thrush when it expanded its range northwards into Maine. Where Veeries and Hermit Thrushes once nested in close proximity to each other, Morse noted in subsequent years some of these territories to be held solely by Wood Thrushes, a larger species by comparison. He concluded that Wood Thrushes were socially dominant over the other species and could therefore set up territories where both species used to inhabit. One interesting question is whether something similar will happen on the Southern Appalachian peaks as well, with the newly arrived Hermit Thrush supplanting the resident breeder. It could be that Hermit Thrushes and Veeries in the Southern Appalachians will still breed in close proximity to each other, especially because the habitat is not as homogeneous as a climax forest generally is. Because there seem to be significant differences between the habitat preferences of the 2 species studied here, and both preferences seem to be in abundance here, further competition between the species that results in one species being forced out of this elevational belt seem unlikely under the present conditions.

Another scenario worth considering is the possibility that the Wood Thrush will move up in elevation as climate change starts shifting its habitat upslope. There is overlap between the Wood Thrush and Veery, but as this overlap increases the Veery may have to shift its range upslope to avoid competition. It will be interesting to see how this competition plays out.

The Hermit Thrush is not the only *Catharus* thrush that is expanding its range southwards into the Southern Appalachians. About 6 Swainson's Thrushes (*C. ustulatus*) have been heard singing regularly at a location near Mt. Mitchell in North Carolina for the past 3 breeding seasons. An individual of this species was also heard singing at Mt. LeConte in the Great Smoky Mountain National Park in 2008 (pers. comm. Rick Knight) and 2010 (pers. observ.). This species generally prefers an even thicker understory shrub layer than the Veery, but habitat analysis in the Southern Appalachian Spruce-Fir forests has not yet been undertaken. There are perhaps too few individuals in this region to study as of yet, and disturbing these birds during the breeding season might be detrimental to their breeding success. Nonetheless, this makes for an interesting pattern of Thrush expansions into this area.

CHAPTER 5

SUMMARY

Habitat and topographical characteristics were measured in 30 Hermit Thrush and 24

Veery territories and compared. Several differences between the species habitat preferences were

discovered using a few multivariate statistical methodologies. Hermit Thrushes preferred

territories with much less shrub density between the ground and 1.3m above ground, while

Veeries preferred a relatively high shrub cover up to 3.0m. Hermit Thrush territories had much

more leaf litter on the ground and higher percent canopy closure than Veery territories did. In

general Veery territories were much denser in foliage in the understory and had a more open

canopy, while Hermit Thrush territories had a more open understory and closed canopy.

However, there is much overlap within these parameters. Some Hermit Thrush plots had

'typical' Veery characteristics and vice versa. These differences reflect the foraging and breeding

ecology of each species. Hermit Thrushes are known in other areas to forage on the ground for

insects more than Veeries, and Veeries tend to nest and forage in low shrub cover more so than

other Forest Thrushes. Hermit Thrushes also nest on the ground under low-lying ferns or

seedlings. It is not known why Hermit Thrushes prefer a more open understory.

These comparisons were made in order to more fully understand the range expansion of

the Hermit Thrush southwards into the Southern Appalachian high-elevation forests. The Hermit

Thrush population is expanding across eastern North America according to Breeding Bird

Survey analysis (Peterjohn et al. 1994), and perhaps this area is serving as a sink area for the

overflowing populations further north. This seems unlikely, as there is no evidence that these

northern populations have fully saturated the available habitat (R. Dellinger, pers. comm.). Based

on the findings of this study, the range expansion does not seem to be due to any environmental changes occurring in the Southern Appalachian forests, although there are indeed many changes occurring there. Hermit Thrushes seem to be drawn to the mature forests that have been here for several decades, although perhaps they are attracted to the continued maturation of these forests. There is, however, a dense area of Hermit Thrush presence at Mt. LeConte in the Great Smoky Mountains National Park. This particular forest has been hit hard by the Balsam Wooly Adelgid infestation and is thus covered in Fraser Fir snags and saplings. It was originally hypothesized that such areas would have higher densities of Hermit Thrushes, but this was not the case for other Fir decimated areas.

BIBLIOGRAPHY

Bertin, RI. 1977. Breeding habitats of the Wood Thrush and Veery. Condor 79:303-311.

Bevier, LR, Poole AF, and Moskoff W. 2005. Veery (*Catharus fuscescens*). In: Poole AF, editor The Birds of North America Online. Ithaca (NY): Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.libproxy.lib.unc.edu/bna/species/142

Browning RB. 2003. Hermit Thrush nesting in North Carolina. Chat 67(1):11-13.

Bucklew A, and Hall GA. 1994. The West Virginia Breeding Bird Atlas, University of Pittsburgh Press, Pittsburgh, Pennsylvania. 215 pp.

Cod, ML. 1981. Habitat Selection in Birds: The Roles of Vegetation Structure, Competitors, and Productivity. BioScience 31(2): 107-113.

Collar N. 2005. Family Turdidae (Thrushes). In: del Hoyo J, Elliott A, Christie D, editors. Handbook of the Birds of the World, v. 10, Lynx Edicions, Barcelona, Spain.

Dellinger RL, Wood PB, Keyser PD, and Seidel G. 2007. Habitat Partitioning of Four Sympatric Thrush Species at Three Spatial Scales on a Managed Forest in West Virginia. The Auk 124(4):1425-1438.

Dilger WC. 1956b. Adaptive modifications and ecological isolating mechanisms in the thrush genera *Catharus* and *Hylocichla*. Wilson Bull. 68: 170–199.

[DLIA] Discover Life in America - All Taxa Biodiversity Inventory. 2008. The ATBI Database. http://tremont22.campus.utk.edu/ATBI_start.cfm. Gatlinburg (TN): Discover Life in America.

Eagar C. 1984. Review of the Biology and Ecology of the Balsam Woolly Aphid in Southern Appalachian Spruce-Fir Forests, In: White PS, editor. The Southern Appalachian Spruce-Fir Ecosystem: Its biology and threats. NPS Southeast Region. Research/Resources Management report SER-71.

Garson GD. 2009. *Multivariate GLM, MANOVA, and MANCOVA* from *Statnotes: Topics in Multivariate Analysis.* Retrieved 03/20/2010 from http://faculty.chass.ncsu.edu/garson/pa765/statnote.htm.

Griep S. Conservation and Management of High Elevation Spruce-Fir Forests in the Southern Appalachians. Information based on 1996 Southern Appalachian Assessment Terrestrial Technical Report. Accessed 26 January, 2010.

Hall GA. 1988. Birds of the Southern Appalachian Subalpine Forest. In: Bird Conservation v. 3. Jackson J, editor. University of Wisconson Press, Madison (WI).

Hitch AT and Leberg PL. 2007. Breeding Distributions of North American Bird Species Moving North as a result of climate change. Conservation Biology 21(2):534-539.

Holme, RT and Robinson SK. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. Wilson Bulletin 100:377-394.

Hunter C, Katz R, Pashley D, Ford B. 1999. Bird Conservation Plan for the Southern Blue Ridge, physiographic region #23. Partners in Flight. Version 1.0 http://www.blm.gov/wildlife/plan/pl_23_10.pdf

Hubbard JP. 1971. The avifauna of the southern Appalachians: past and present. Pp. 197–232 *in* The distributional history of the biota of the southern Appalachians, pt. 3: vertebrates. Virginia Polytechnic Inst. and State Univ., Blacksburg.

James FC. 1971. Ordinations of Habitat Relationships Among Breeding Birds. The Wilson Bulletin 83(3):215-236.

James FC and Shugart HH, A quantitative method of habitat description. *Aud. Field-Notes* **24** (1970), pp. 727–736.

Jennings SB, Brown ND, Sheil D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72(1):59-73.

Jones J. 2001. Habitat Selection Studies in Avian Ecology: A Critical Review. The Auk 188(2):557-562.

Jones J and Robertson RJ. 2001. Territory and nest-site selection of Cerulean Warblers in eastern Ontario. The Auk 118(3):727-735.

Jones PW and Donovan TM. 1996. Hermit Thrush (Catharus guttatus). In: Poole AM, editor. The Birds of North America Online. Ithaca (NY): Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.libproxy.lib.unc.edu/bna/species/261

Korstian CF. 1937. Perpetuation of spruce on cut-over and burned lands in the higher southern Appalachian Mountains. Ecological Monographs 7:125-167.

Knight RL. 1997. Evidence of probably (sic) breeding by the Hermit Thrush on Roan Mountain, Tennessee/North Carolina. The Migrant 68(4):123.

MacArthur RH. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39(4):599-619.

Manly BJ. 2005. Multivariate Statistical Methods: a primer. Chapman & Hall/CRC Press. Boca Raton, FL.

Martin TE, Paine CR, Conway CJ, Hochachka WM, Allen P, and Jenkins W. 1997. **BBIRD Field Protocol**. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.

Marshall DB, Hunter MG, and Contreras AL. 2003. Birds of Oregon. Oregon State University Press. Corvallis, OR.

Matthews S, O'Connor R, Iverson LR, Prasad AM. 2004. Atlas of climate change effects in 150 bird species of the Eastern United States. Gen. Tech. Rep. NE-318. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 340p.

McWilliams GM and Brauning DW. 2000. The Birds of Pennsylvania. Cornell University Press. Ithaca, NY.

Mertler C and Vannatta R. 2005. Advanced and Multivariate Statistical Methods. 3rd ed. Pyrczak Publishing. Glendale, CA.

Morrison ML, Marcot BG, and Mannan RW. 2006. Wildlife-Habitat relationships: concepts and applications. 3rd edition. Island Press. Washington, DC.

Morse DH. 1971. Effects of the arrival of a new species upon habitat utilization by two Forest Thrushes in Maine. The Wilson Bulletin 83(1):57-65.

Morse DH. 1972. Habitat Differences of Swainson's and Hermit Thrushes. The Wilson Bulletin 84(2):206-208.

Newton I. 2003. *The speciation and biogeography of birds*. London: Academic Press. 668 p.

Nicholson CP. 1997. Atlas of the Breeding Birds of Tennessee. The University of Tennessee Press. Knoxville, TN.

Noon BR. 1981a. Techniques for Sampling Avian habitats, *in* The use of multivariate statistics in studies of wildlife habitat, Capen D. E. (ed.) Rocky Mountain Forest and Range Exp. Stat. U.S. For. Serv., Gen. Tech. Rep . RM-87. Fort Collins, Co: US Dep. Agric.

Noon BR. 1981b. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51: 105–124.

Norusis M. 2009. SPSS 17.0 Statistical Procedures Companion. Prentice Hall Press. Upper Saddle River, NJ. 672pp.

Noss RF, LaRoe ET, III, Scott JM. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological report. U.S. Fish and Wildlife Service.

Paszkowski CA. 1984. Microhabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest. Wilson Bulletin 96(2):286-292.

Peterjohn BG, Sauer JR, and Link WA. 1994. The 1992 and 1993 Summary of North American Breeding Bird Survey. Bird Populations 2:46-61.

Potter EF and LeGrand HE Jr. 1980. Bird Finding on Roan Mountain, Mitchell Co., N.C. Chat 44: 32-36.

Rabenold K. 1984. Birds of Appalachian Spruce-Fir Forests: Dynamics of Habitat-Island Communities, *in* White, P.S. (Ed) The Southern Appalachian Spruce-Fir Ecosystem: Its biology and threats. NPS Southeast Region. Research/Resources Management report SER-71.

Rheinhardt RD. 1984. Comparative Study of Composition and Distribution Patterns of Subalpine Forests in the Balsam Mountains of Southwest Virginia and the Great Smoky Mountains, *in* White, P.S. (Ed) The Southern Appalachian Spruce-Fir Ecosystem: Its biology and threats. NPS Southeast Region. Research/Resources Management report SER-71.

Simpson MB. 1992. Birds of the Blue Ridge Mountains. Chapel Hill: The University of North Carolina Press. 354 p.

Steele BB. 1992. Habitat selection by breeding Black-throated Blue Warblers at two spatial scales. Ornis Scandinavica 23(1):33-42.

Strickler GS. 1959. Use of the densiometer to estimate density of canopy on permanent sample plots. USDA Forest Service Research Note No. 180.

Sutherland WJ, Newton I, Green RE. 2004. Bird Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford, England.

Thomas CD, and Lennon JJ. 1999. Birds extend their ranges northwards. Nature 399:213.

Valiela I and Martinetto P. 2007. Changes in Bird Abundance in Eastern North America: Urban Sprawl and Global Footprint? BioScience 57(4):360-370.

Westphal MJ, Simpson MB, Murdock N, Laughlin AJ. (in press) Range expansion of Hermit and Swainson's Thrushes in the Southern Appalachians. The Chat.

White PS. 1984. The southern Appalachian spruce-fir ecosystem: an introduction, in P.S. White, ed., *The Southern Appalachian spruce-fir ecosystem: its biology and threats*. USDI, National Park Service, Res./Resour. Manage. Rep. SER-71, Atlanta, GA.

Wood L, Beck B, Beck J, Todd M, Bonar R, Quinlan R. 1999. Hermit Thrush Reproductive Habitat: Habitat Suitability Index Model, Version 5. Weldwood of Canada Integrated Resource management Steering Committee.

Young JS and Hutto RL. 2002. Use of regional-scale exploratory studies to determine bird-habitat relationships, *in* Scott, J. M., P.J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Hall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covello, CA.

APPENDICES

APPENDIX A. A COMPLETE LIST OF HERMIT THRUSH TERRITORIES SURVEYED
DURING THE 2009 BREEDING SEASON, INCLUDING DATE SURVEYED,
COORDINATES, AND ELEVATION

	Location	Date	Latitude	Longitude	Elevation(m)
1	Unaka/Roan Mtn.	5/26/2009	36° 08.097'	82° 17.830'	1570
2	Unaka/Roan Mtn.	6/1/2009	36° 06.317'	82° 06.432'	1703
3	Unaka/Roan Mtn.	6/6/2009	36° 07.833'	82° 18.176'	1521
4	Unaka/Roan Mtn.	6/6/2009	36° 08.156'	82° 17.369'	1516
5	Unaka/Roan Mtn.	6/9/2009	36° 06.339'	82° 04.974'	1789
6	Unaka/Roan Mtn.	6/8/2009	36° 06.290'	82° 05.840'	1698
7	Unaka/Roan Mtn.	6/15/2009	36° 06.480'	82° 06.520'	1715
8	GSMNP	6/22/2009	35° 33.947'	83° 09.818'	1607
9	GSMNP	6/23/2009	35° 33.048'	83° 29.521'	1766
10	GSMNP	6/23/2009	35° 32.891'	83° 29.501'	1751
11	Unaka/Roan Mtn.	7/3/2009	36° 07.866'	82° 17.909'	1526
12	GSMNP	7/5/2009	35° 34.424'	83° 10.806'	1618
13	GSMNP	7/6/2009	35° 37.940'	83° 23.350'	1860
14	GSMNP	7/13/2009	35° 39.221'	83° 26.082'	1999
15	GSMNP	7/14/2009	35° 39.195'	83° 26.507'	1982
16	GSMNP	7/13/2009	35° 39.244'	83° 26.401'	1957
17	GSMNP	7/13/2009	35° 39.209'	83° 26.288'	1979
18	GSMNP	7/14/2009	35° 39.220'	83° 26.370'	1961
19	GSMNP	7/14/2009	35° 39.239'	83° 26.546'	1973
20	Mt. Rogers	7/20/2009	36° 38.286'	81° 35.432'	1512
21	Mt. Rogers	7/20/2009	36° 38.200'	81° 36.172'	1644
22	Unaka/Roan Mtn.	7/21/2009	36° 05.591'	82° 08.551'	1880
23	Unaka/Roan Mtn.	7/21/2009	36° 06.399'	82° 06.933'	1737
24	Mt. Rogers	7/26/2009	36° 39.484'	81° 33.928'	1529
25	Mt. Rogers	7/27/2009	36° 39.172'	81° 33.017'	1623
26	Mt. Rogers	7/27/2009	36° 38.694'	81° 30.791'	1529
27	Mt. Rogers	7/27/2009	36° 39.426'	81° 31.476'	1626
28	Mt. Rogers	7/27/2009	36° 39.926'	81° 31.019'	1571
29	Mt. Rogers	7/27/2009	36° 38.061'	81° 30.927'	1443
30	Mt. Rogers	7/27/2009	36° 38.092'	81° 30.986'	1434

APPENDIX B. A COMPLETE LIST OF VEERY TERRITORIES SURVEYED DURING THE 2009 BREEDING SEASON, INCLUDING DATE SURVEYED, COORDINATES, AND ELEVATION

	Location	Date	Latitude	Longitude	Elevation(m)
1	Unaka/Roan Mtn.	6/1/2009	36° 06.325'	82° 06.751'	1706
2	Unaka/Roan Mtn.	6/6/2009	36° 08.031'	82° 17.335'	1453
3	Unaka/Roan Mtn.	6/15/2009	36° 06.069'	82° 07.660'	1780
4	GSMNP	6/22/2009	35° 33.836'	83° 09.689'	1587
5	GSMNP	6/23/2009	35° 33.147'	83° 10.398'	1479
6	GSMNP	6/28/2009	35° 42.154'	83° 06.810'	1542
7	GSMNP	6/29/2009	35° 33.874'	83° 31.172'	1846
8	GSMNP	6/29/2009	35° 33.896'	83° 31.524'	1793
9	GSMNP	6/29/2009	35° 35.270'	83° 04.388'	1475
10	GSMNP	6/30/2009	35° 34.365'	83° 09.640'	1524
11	Unaka/Roan Mtn.	7/3/2009	36° 07.838'	82° 17.837'	1483
12	GSMNP	7/6/2009	35° 37.304'	83° 23.947'	1818
13	GSMNP	7/12/2009	35° 34.729'	83° 04.129'	1404
14	GSMNP	7/12/2009	35° 35.275'	83° 04.514'	1514
15	GSMNP	7/13/2009	35° 37.005'	83° 24.756'	1687
16	GSMNP	7/13/2009	35° 38.557'	83° 25.386'	1807
17	GSMNP	7/14/2009	35° 38.983'	83° 26.201'	1743
18	Mt. Rogers	7/20/2009	36° 38.348'	81° 35.539'	1469
19	Unaka/Roan Mtn.	7/21/2009	36° 05.652'	82° 08.511'	1881
20	Unaka/Roan Mtn.	7/21/2009	36° 05.995'	82° 08.080'	1845
21	Unaka/Roan Mtn.	7/21/2009	36° 06.164'	82° 07.831'	1855
22	Unaka/Roan Mtn.	7/28/2009	36° 08.867'	82° 17.033'	1384
23	GSMNP	6/22/2009	35° 33.937'	83° 10.897'	1568
24	GSMNP	7/14/2009	35° 39.020'	83° 26.133'	1718

VITA

ANDREW J. LAUGHLIN

Personal Data:	Date of Birth: September 26, 1975 Place of Birth: Pittsburgh, PA

Education:	M.S. Biological Sciences, East Tennessee State University,
	     Johnson City, Tennessee, 2010
	B.A. English/Classics, Calvin College, Grand Rapids, Michigan
	     1997

Publications:	Laughlin, Andrew J. 2007. *Hermit Thrush Breeding Range Expansion in Western North Carolina*. UNC Asheville Journal of Undergraduate Research. Westphal, M., Simpson, M. Murdock, N., Laughlin, A. 2008. *Hermit and Swainson's Thrush Breeding Range Expansion in the Southern Appalachians*. The Chat 72(4):126-132
Presentations:	Oral: Hermit Thrush Breeding Range Expansion in the Southern Appalachians. April 21, 2008, Sigma Xi local NC chapter. Hermit Thrush and Veery Habitat Associations in Southern Appalachian Spruce-Fir Forests. April, 2010. Association of Southeastern Biologists, Annual Meeting. Asheville, NC. Poster: "Hermit Thrush Breeding Range Expansion and Habitat Associations in Southern Appalachian High-Elevation Forests". May 2009. Conference on Ecology and Management of High-Elevation Forests of the Central and Southern Appalachian Mountains
Memberships:	Sigma Xi, The Scientific Research Society. Inducted April, 2008.