Climate, Resource Phenology, and Demographic Population Structure Impacts on Songbird Habitat Quality

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Climate, resource phenology, and demographic population structure impacts on songbird habitat quality

By

Ashley Ozelski

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract
Climate, resource phenology, and demographic population structure impacts on songbird habitat quality

By: Ashley Ozelski
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Monitoring bird populations becomes more complex as climate change alters species’ relationships with their habitats. The presence of a species does not necessarily indicate a thriving population; in fact, we expect to see changes in demography and nest success before extinction at a site. Here, I first model aspects of demography as a proxy for habitat quality across a large portion of a species’ range, using land cover and climate predictors. I show a gradient of high to low habitat quality from north to south within the range for the Yellow Warbler (*Setophaga petechia*), with summer temperature and amount of habitat cover being important predictors. However, these relationships with habitat are not fixed across time, especially as climate alters the phenology of trees and important insects that these birds rely on to feed their nestlings. Little is known about the phenology of caterpillar biomass availability in North America, and since many birds have specific breeding habitat and foraging niches, the phenology and caterpillar biomass availability from specific tree species may be important to the persistence of certain bird species. In Chapter III, I model caterpillar biomass curves through time for eight tree species using random intercept mixed-effects models and find differences in the availability of caterpillar biomass among tree species. In addition, I test for differences in caterpillar biomass availability during the breeding period for four species of long-distance migratory warblers with different nesting and foraging niches, finding that tree species such as Red Oak (*Quercus rubra*) provide the majority of caterpillar biomass to these birds. However, species assemblages, species phenology, and species’ phenological responses to climate change vary across large spatial scales, so extrapolating caterpillar biomass availability across these large scales is problematic. Chapter IV tests how well a remotely-sensed measure of
greenness commonly used as a measure of tree phenology, the Normalized Difference Vegetation Index (NDVI), correlates with caterpillar biomass in each of these tree species. Interestingly, the caterpillar biomass from most tree species correlates synchronously with NDVI in 2014, but lags NDVI in a year with anomalously warm spring temperatures. This suggests that although NDVI may be a good proxy for caterpillar biomass in some years, caterpillars and their trees are likely to be susceptible to phenological mismatches as climate anomalies become more common. My dissertation chapters highlight the importance of monitoring phenology range-wide in as many taxa as possible in order predict how interspecific relationships will change with changing climate.
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# Table of Contents

**Abstract**  iv  

**Acknowledgements**  vi  

**Chapter I - Introduction**  1  

**Chapter II – Predicting demography across landscapes: regional-scale models of recruitment**  7  

**Chapter III – Characterizing caterpillar biomass phenology: differences among host trees and implications for climate change**  33  

**Chapter IV – The use of MODIS NDVI as a proxy for food abundance available to breeding birds**  57  

**Chapter V – Conclusion**  69  

**Literature Cited**  75
List of Figures

◊ Figure 1.1: Map of the study region and MAPS stations used in this analysis 13
◊ Figure 1.2: Density plots of PABC and PASY 15
◊ Table 1.1: Model summaries for PABC models 20
◊ Table 1.2: Model summaries for PASY models 20
◊ Figure 1.3: Predictive maps of the models 22
◊ Figures 1.4a-c: Regressions of model predictions and population trends 24
◊ Table 2.1a-d: ANOVA tables for models 42
◊ Table 2.2: Model orders and r² values 44
◊ Figure 2.1: Biomass availability curves and models in 2013 and 2014 45
◊ Figure 2.2: Scaled caterpillar biomass curves and bird breeding dates 47
◊ Table 2.3: ANOVA tables for food availability models 48
◊ Table 2.4: Available biomass laying to fledging 49
◊ Table 3.1: Lag with highest correlation coefficient by tree and year 61
◊ Table 3.2: Correlation coefficients of median tree biomass and predicted NDVI 62
◊ Figure 3.1: Average daily temperatures for 2013 and 2014 64
◊ Figure 3.2: NDVI models for 2013 and 2014 64
CHAPTER I – Introduction

Bird-habitat interactions, including habitat selection and habitat quality, have been studied frequently in North America (Chalfoun and Schmidt 2012). Which habitat characteristics bird species choose and which predict high reproductive success are commonly used for managing habitats for particular species. However, there are two precautions to consider when extrapolating results from these studies: first, the presence of a species at a site does not reliably predict reproductive success. Even when preference is shown for particular habitat characteristics, reproductive success only occasionally accompanies this preference (Chalfoun and Schmidt 2012). This means that the habitat characteristics used to manage habitats may fail to capture the requirements for species persistence. The second precaution to consider when extrapolating the results of habitat selection studies is that habitat quality is not fixed in time. Intrinsic properties of habitat, such as structure or species assemblages, change over time, both naturally due to processes such as ecological succession, or due to anthropogenically-facilitated changes such as the introduction of exotic species, land cover use changes, or climate change. Improving methods of monitoring and predicting high-quality habitat over large temporal and spatial scales is crucial to addressing both our understanding of how change impacts habitat quality and mitigating major anthropogenic damage to populations.

Habitat Selection in Birds

Studies on bird occupancy patterns show that bird species have distinct preferences at both the landscape and local scales. Habitat amount and spatial arrangement within the landscape governs whether and where birds will settle locally within the landscape (Cornell and Donovan 2010; Zurita and Bellocq 2010). Locally, birds select breeding habitat based on structural factors such as shrub density (Steele 1992) or forest composition (Hunt 1996). For many bird species, there is a linear relationship between the amount of habitat in the landscape and the probability of
occupancy or persistence; however, some species exhibit a "threshold" response: below a pivotal point in habitat amount, the probability of persistence within the landscape declines rapidly (Betts et al. 2010; Zuckerberg and Porter 2010; Andrén 1999). As anthropogenic land cover such as concrete, lawns, and cropland replaces natural land cover, species disappear from local habitats in which they used to reside (Zuckerberg and Porter 2010; Andrén 1999; Betts et al. 2010).

Before local extinction occurs, there are likely to be decreases in reproductive output for individuals at a site (Miller-Rushing et al. 2010). The alteration of landscape from natural habitat to anthropogenic habitat has shown to decrease nest success for several bird species nesting in remnant forests (Rodewald et al. 2013). A 2012 meta-analysis showed that only 23.3% of North American studies find support that bird habitat choices are congruent with nest success (Chalfoun and Schmidt 2012). In fact, in a population of song sparrows, reproductive success is better predicted by individual female quality than by habitat structure (Germain and Arcese 2013).

Thus, reproductive success per se would be the ideal metric to use for modeling habitat quality. The problem with this is the labor intensity needed for accurate estimates, even at a single site. Chapter II of this dissertation addresses this problem via predictive modeling of two demographic values: the proportion of birds captured at a site aged to after-second-year and the proportion of birds in breeding condition. I use these demographic values as proxies for reproductive success, with climate and land cover variables as predictors. With these predictions, I extrapolate and map expected reproductive success across a portion of the species’ range.

Understanding how the reproductive success of a species responds to predictors across its entire range is important for identifying areas at high risk and understanding the fundamental ecology of the species. The reason this is important is also the reason that it is difficult – both species’ responses to predictors and the predictors themselves vary across their geographic range (Visser et al. 2010). For example, birds respond to landscape-level habitat loss linearly in some US states, but exhibit a threshold response in others (van der Hoek et al. 2013). Further, the amount of
habitat at which these thresholds occur varies spatially as well. Using large-scale and generic predictors such as “amount of forest cover” tends to be inconsistent for local processes such as persistence, likely due to variation in local environmental resources, local vegetation structure and diversity, and climate will vary across large spatial scales. Additionally, species show local genetic adaptations across their ranges to coincide with differences in local habitat metrics (Virginie et al. 2009).

Habitat preferences themselves are also shown to change across the geographical range of a species (Carbonell et al. 2003; Petrides 1942; Whittingham et al. 2007), making generalizations and estimations of habitat amount difficult on large scales. Additionally, small-scale studies may not extrapolate across an entire population due to differences in selection pressures and phenotypes across a wide geographical range. For this reason, monitoring the entire distribution of a species is important for detecting and understanding responses to change caused by habitat alteration and climate change.

Phenology, climate change, and birds

Habitat characteristics are unlikely to remain consistent over time. In particular, climate change can alter abiotic factors such as temperature and precipitation patterns and consequently alter biotic characteristics within a patch (Walther et al. 2002). This can cause the spatial distribution of species to shift as patches once unsuitable become suitable, and vice-versa. Latitudinal range shifts have already been observed in some North American bird species (Rodenhouse et al. 2008; Zuckerberg et al. 2009; but see Zuckerberg et al. 2009; Kujala et al. 2013).

Changes in climate have also been shown to disrupt or alter phenology cues for many taxa, including plants and insects that birds rely on (Visser et al. 2004). The timing of biological events is regulated by accumulated warm temperatures for plants and insects (van Asch and Visser 2007; Richardson et al. 2006). Thus, as local climates warm, plants accumulate these required degree days...
earlier, spurring early phenological events such as bud burst or first leaf date. For North American lilacs, first leaf date advanced an average of 5.4 days from 1959 to 1973 (Schwartz and Reiter 2000). However, the amount the date shifted varied by region, with the largest shifts occurring in the Pacific Northwest and the Northeast.

Since caterpillars eat plants, and birds eat caterpillars, this sudden change in climate has the potential to de-couple trophic relationships (Both et al. 2009). Insects, such as the Lepidopteran larva (caterpillars), which make up a large proportion of the nestling diet, rely on temporal synchrony with their host plants (van Asch and Visser 2007). Because caterpillars regulate phenology via temperature and photoperiod, it is predicted that the phenology of caterpillars will closely track their host plants. This results in the primary food source for breeding birds shifting temporally as climate change continues. It follows that birds need to shift their breeding dates to compensate.

Complications arise when birds’ reproductive fitness is determined in the breeding habitat, while some cues that trigger phenology occur in the winter habitat. This is the case for migratory birds, meaning adapting phenologically to climate change is less straightforward (Visser et al. 2010). In Europe, studies have shown that bird populations that do not shift migration and breeding dates have become mismatched with their primary prey source – caterpillars. Populations which have become mismatched with caterpillars show decreases in abundance. This mechanism for the population decline is supported by research that shows decreased chick weight and fledging success in birds that are less synchronous with caterpillar peaks (Visser et al. 2006).

Whether phenological mismatches are occurring and causing population declines in North America is currently unknown. With such high diversity of migratory species spread over such a large continent, testing mismatches using similar methods to the European studies would be quite costly and labor-intensive. The first step to approaching this problem, and the subject of Chapter III, is characterizing caterpillar biomass availability curves in North America. In Europe, deciduous tree
species have shown high, narrow peaks which birds must match in order to have enough food for their offspring (Veen et al. 2010). Coniferous trees, on the other hand, have low, gradual increases in caterpillar biomass. Little is known about the phenology of caterpillar biomass availability in North America, and since many bird species have specific breeding habitat and foraging niches, the phenology and caterpillar biomass availability from specific tree species may be important to the persistence of different bird species. In Chapter III, I model caterpillar biomass curves for eight tree species using random intercept mixed-effects models and test for differences in the availability of caterpillar biomass among tree species. In addition, I test for differences in caterpillar biomass availability during the breeding period for four species of long-distance migratory warblers with different nesting and foraging niches.

However, as shown by the lilac study, phenological responses differ across a species’ range (Schwartz and Reiter 2000; Visser et al. 2010). This observation is due to local selection of genes controlling the physiological responses to phenology cues such as temperature and photoperiod (Visser et al. 2010). Thus, extrapolating the phenological relationships between taxa across space will be problematic. Furthermore, North America lacks long-term caterpillar biomass phenology datasets like those used in the European studies. As a substitute, large-scale datasets are available from government-funded sources, such as the United States Geological Survey (USGS) and NASA. Bird occurrence, abundance, phenology and productivity datasets are available from programs such as the North American Breeding Bird Survey (BBS) and the Monitoring Avian Productivity and Survivorship program (MAPS). Utilizing these data, we can potentially test for phenological shifts, phenological mismatches, and spatial or ecological predictors of shifts and mismatches. However, it is unknown whether remotely sensed data can substitute for locally collected data. To facilitate the use of these data, Chapter IV tests the use of a satellite-derived metric of plant productivity, the Normalized Difference Vegetation Index (NDVI) as a proxy for local food availability for birds. This
would greatly facilitate the ease with which researchers can monitor and detect phenological mismatches between birds and insects as well as phenological shifts as climate change progresses.

Overall, this dissertation focuses on expanding the uses for these datasets in order to facilitate new uses for them to address emerging problems. In Chapter II, I use bird demographic data as obtained from the MAPS program and land cover data from the USGS to model how the productivity of a migratory bird species, *Setophaga petechia* (the Yellow Warbler) is distributed across a wide region and what factors affect this productivity. Warblers and other migratory passerines are currently at risk of population declines and range shifts due to climate change. One particular concern for migratory breeding birds is the risk of declines due to phenological mismatches between the birds and their prey. However, little is known about how caterpillar abundance is distributed through time in relation to tree species. Chapter III tests the hypothesis that different tree species provide different phenological landscapes of resource availability for reproducing birds and I characterize the phenology curves of caterpillar biomass for eight tree species. I then test whether different tree species provide different amounts of caterpillar biomass to birds during their breeding period. However, caterpillar biomass phenology likely varies regionally, and the ability to detect this on a regional scale using pre-collected available data would be invaluable. For this reason, Chapter IV tests whether the Normalized Difference Vegetation Index (NDVI) available from NASA is able to accurately predict food resources for breeding birds in upstate New York. The analyses in this dissertation promote and expand upon the knowledge and methods available for detecting and understanding the impacts of climate change range-wide.
Habitat suitability models have diverse uses in ecology, from testing specific hypotheses about biogeography to use in applied fields such as wildlife management. They have been paramount to predicting responses to climate change (Ralston and Kirchman 2013; Reside et al. 2012) and managing biodiversity for conservation (Guisan et al. 2013). These habitat suitability models use the presence, presence/absence, or abundance of a species at a location as predictors (Franklin 2010; Boyce et al. 2015). Such models assume that all presences are equally valuable to the population. In reality, occupied habitats may vary in quality, with the majority of metapopulation growth occurring in only a portion of the range (Foppen et al. 2000). Thus, the area of occupancy is likely larger than the area in which a species is experiencing population growth. For many bird species with dynamic occupancy patterns (such as migratory and territorial species), the inclusion of demographic response variables, over and above presence-absence information, may provide more insight on metapopulation dynamics and identifying critical habitat for species’ reproduction and continued persistence.

In this study, I used land cover data to predict two demographic variables: the proportion of adult birds in breeding condition (PABC) and the proportion of after-second-year birds (PASY), used here as a proxy for mature birds that are likely to have higher rates of fecundity and/or nest success. I then created predictive maps depicting the suitability of landscapes across the study region. My goal is to evaluate the potential of including supplementary data (such as demographic data) in species distribution models, results that should generalize to any species likely to show spatially-varying reproductive success.
Proportion of Birds in Breeding Condition

After fledging, many territorial songbirds fly to winter habitat. The following spring, the first-year male will migrate back to the breeding grounds to claim a breeding territory. However, as this is his first experience with migration and breeding territory selection, he may arrive later to the breeding grounds than more experienced males (Ficken and Ficken 1967). This puts him at a disadvantage as the best territories are acquired by early-arriving, older, more experienced and more aggressive males (Ficken and Ficken 1967; Sherry and Holmes 1989). For this reason, it is thought to be adaptive for the less experienced male to a) spend his first breeding season as a “floater” (non-territory holding males) (Brown 1969) or b) attempt to attract a female to a sub-optimal breeding territory (Ficken and Ficken 1967; Hunt 1996). This may protect the younger male from being killed in a territorial conflict with a stronger, more experienced male armed with higher testosterone levels and experience (Ficken and Ficken 1967). Instead, a young male can spend the summer scouting territories for future breeding seasons or attempting low-risk breeding on a territory he perceives as potentially suitable. For example, Hunt (1996) found that compared to mature deciduous and mature coniferous forests, early successional forests had higher abundance of American Redstart males (Setophaga ruticilla) and higher proportions of older males. This suggests primary habitat occupied by high quality individuals and “overflow” or suboptimal habitat for less competitive/younger males. In the young male’s subsequent breeding seasons, he is likely to attempt to “move up” to higher quality territory. Here, I use a proportion of adult birds in breeding condition (relative to the total number of adults) as a measure of “percent non-floaters” in the population. While floaters are expected even in high quality habitat, a high percentage of floaters may indicate primarily non-breeding habitat for young, inexperienced, or low-quality individuals. These may also be birds that hold a territory, but have failed to attract a female.
Proportion of After-Second-Year Birds

I used the proportion of after-second-year birds (PASY, or the proportion of birds aged to be at least in their second breeding season) as an indicator of reproductive potential. In many passerine species, older, more dominant individuals occupy the best territories (Fretwell 1969). Individuals in these higher-quality territories typically have higher reproductive output, while populations made up of lower quality individuals may need to be sustained by repeated colonization (Pulliam 1988). Due to the combination of territoriality and variation in patch quality, birds in lower quality patches may occur at higher densities than birds in optimal patches, while simultaneously producing fewer offspring. Thus, density may be a poor predictor of habitat quality in species exhibiting territorial and transient traits (Skagen and Yackel Adams 2011; van Horne 1983). Low density in a patch may be due to competitive exclusion by a few dominant individuals which produce a large number of offspring, perhaps even producing more net offspring in a given area than a more densely populated patch. Distributions regulated by intraspecific competitive exclusion (coined “despotic distributions” by Fretwell and Lucas (1969)) have been documented in warblers (Holmes et al. 1996; Petit and Petit 1996) and other groups (Andrén 1990; Huhta et al. 1998; Oro 2008). While density and abundance are both shown to be better predictors of population persistence than occupancy alone (Grouios and Manne 2009), predictions of persistence can be improved by incorporating reproductive success data.

Warbler species such as the Black-throated Blue Warbler (Setophaga caerulescens) have been shown to have habitat-specific demography (Holmes et al. 1996). Habitat containing younger or unpaired males may be suboptimal overflows. Habitats in which the number of deaths exceeds the number of births are known as population “sinks” in theoretical studies (Pulliam 1988) but are difficult to identify in the field (Watkinson and Sutherland 1995). It is important to note that sink habitat should be distinguished from an “ecological trap” in that birds occupying the sink habitat do so because they are not competitive enough to obtain “source” or preferred habitat, whereas in an
ecological trap, birds mistake low quality habitat as high quality and preferentially seek out territories there (Battin 2004). Birds holding territories in suboptimal habitat will likely attempt to “move up” to the “source” habitat (in which births exceed deaths) in subsequent breeding seasons (Ficken and Ficken 1967). This idea of “moving up” is supported by studies that show younger birds (Hallworth et al. 2008) and birds with lower reproductive success (Hoover 2003) also exhibit less nest site fidelity than older birds with higher reproductive success.

True sources and sinks are nearly impossible to identify empirically due to the possible presence of a “pseudo-sink”, a population which appears as a sink due to density-dependence or high immigration rates between populations (Watkinson and Sutherland 1995). For this reason, I instead model desirability as a proxy for per capita reproduction rate. For this, I assume a despotic distribution (Fretwell 1969) in which population density is limited not by resource availability, but by territorial individuals. This may result in high population density in less desirable areas due to the local absence of aggressive, territorial despots who can maintain large, high-quality territories and exclude less competitive individuals from settling.

In this study, I distinguish primary habitat used by mature, breeding birds from sub-optimal habitat used by floaters or subordinate/young males attempting to breed. This has three important implications. First, it will allow us to further identify the habitat “preferences” of my focal species, the Yellow Warbler (*Setophaga petechia*). Second, it allows for more informed decisions when faced with land purchase or protection decisions for conservation efforts. However, suboptimal overflow habitat should ideally not be destroyed, as it serves as a reserve for young future despots, high-quality habitat should be the primary conservation target when funding resources are limited, provided that models show consistent positive reproductive rates across years. The destruction of habitat in which most recruitment occurs is likely to be catastrophic to metapopulation persistence. Third, information regarding landscape composition of high-quality sites could inform restoration decisions when attempting to establish a self-sustaining population within a region. Using
landscape-level indices (rather than smaller-scale factors such as shrub density) may help attract and sustain high-quality populations and support the local metapopulation.

Here, I explore a method for assessing bird habitat quality that provides more information on true habitat quality than abundance or occupancy using land cover and climate data to predict two responses: proportion of adults in breeding condition (PABC) and proportion of after-second-year adults (PASY), indicating reproductive maturity and experience (Ficken and Ficken 1967) as indicators of habitat quality and true persistence. Although a meta-analysis by Bock and Jones (2004) showed that 72% of studies published on the relationship between density and reproductive success in North American birds showed a positive relationship, many habitats that showed a negative relationship were in anthropogenically disturbed habitats. This suggests that in an increasingly anthropogenic landscape, density may become a misleading signal for persistence unless populations adapt to changing environmental cues.

**METHODS**

**Focal Species and Data Acquisition**

I modeled the demography of the Yellow Warbler (*Setophaga petechia*), a common neotropical migrant that nests in riparian landscapes, specifically in willows (*Salix*) or shrubs (Lowther et al. 1999). Reproductive success in Yellow Warblers has been shown to increase with age. Additionally, reproductive success is an indicator for site fidelity in breeding habitat (Lozano and Lemon 1999). Male Yellow Warblers may also exhibit dominance or attractiveness via the prominence of their brown breast streaks (Studd and Robertson 1985a; Yezerinac and Weatherhead 1997), so male age and condition likely play a large factor in female mate selection.

I acquired mist-netting data for 29 populations of Yellow Warblers across the Midwest United States (US Fish and Wildlife Service Region 3) from the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante et al. 2010), which collects long-term, multi-species
demographic data from mist-netting stations across the US and Canada (see Figure 1.1 for the study region and station locations). The MAPS protocols are strictly monitored and standardized for ease of statistical analyses (see Desante et al. 2010 for full protocol). I used two potential indicators of breeding habitat quality: The proportion of adult birds in breeding condition (PABC) and the proportion of birds aged to be at least in their second breeding season (PASY).

**Sampling Locations**

To control for local habitat preferences and availability, I only analyzed stations within the Midwest United States Eastern Forest Ecoregion. Stations in which the focal species was present were removed if 1) the number of years the station was operated was less than five, 2) the station operation period was more than two years from 1999 – 2001, the period which the land cover satellite images were taken; 3) fewer than five adults were captured during the station lifetime (which would reduce the precision of the ratios), 4) the number of adults captured was greater than 1, but PASY was 0, indicating a possible lack of aging effort by the station (for PABC, this was not an issue and these stations were retained).

For absence stations, (where Yellow Warblers had not been captured, and PABC and PASY were assigned a value of 0), stations were removed if 1) the number of years the station was operated was less than five; 2) the station operation period was more than two years from 1999 – 2001; 3) they fell outside the known range of Yellow Warblers. For stations in which a five-kilometer landscape radius overlapped that of another station, I used a random number generator to select which station to remove. These methods resulted in 21 and 19 presence stations for PABC and PASY respectively and 39 absence stations. To account for the large number of absence stations, I used a script which randomly selected 16 absence stations and combine them with the presence stations. This selection process was for each of 10,000 iterations during both predictor variable correlation tests and running the actual models.
Figure 1.1: Map of the study region and MAPS stations used in this analysis. Study region is outlined in grey. Green points represent MAPS stations in which Yellow Warblers were captured; red points represent stations in which Yellow Warblers were absent.
Proportion of Adults in Breeding Condition

I compiled the proportion of adult birds considered to be in breeding condition to form the dependent variable PABC (proportion of adults in breeding condition). Birds were identified as in “breeding condition” by the station operators who scored the probability of breeding condition by observing a brood patch or cloacal protuberance in netted birds. PABC was calculated as the number of adults in breeding condition/number of adults not in breeding condition over the lifetime of the station. Both males and females were included in this calculation.

Proportion of Older Birds

Since nearly all species can be aged to second-year (SY) and after-second-year (ASY) using mean wing chord length or the presence/absence of juvenile or first alternate feathers (Pyle et al. 1987), first time breeders in their second year of life (SY) can be separated from those with at least one year of breeding experience (ASY). The ratio used in this analysis was calculated as the number of ASY individuals captured over the lifetime of the station divided by the total number of adult birds (ASY+SY) captured over the lifetime of the station. This calculation included both males and females. Age ratio values did not correlate with station lifetime productivity (the number of hatch-year birds divided by the number of after-hatch-year birds caught over a station’s lifetime, Pearson’s correlation, p = 0.6956, cor = 0.0908). However, other measures of age that required recaptures to accurately assess, such as maximum age of birds, did correlate with station lifetime productivity (for maximum recorded age, p = 0.001913, cor = 0.637).
Predictor Variables

For land cover values, I used data from the Gap Analysis Program (GAP) available at http://gapanalysis.usgs.gov/gaplandcover. GAP rasters categorize land cover by ecological community at a 30-m resolution (US Geological Survey 2011). I also included the NLCD 2006 Percent Developed Imperviousness layer from http://www.mrlc.gov (Xian et al. 2009). Each land cover variable was extracted to a separate raster in ArcGIS 10.0 and cell values were reclassified to 1. I then used the Focal Statistics in the Spatial Analyst extension to calculate the sum of cells within a 2-km radius. This gives a count of cells for each land cover type, which can then be divided by the total number of cells in that landscape to provide a proportion of land cover. These values were extracted to the MAPS station points.

I also included layers of the average temperature and amount of precipitation data for the months of June, July, and August from the PRISM Climate Group at Oregon State University (PRISM Climate Group 2008; Daly et al. 2008) which I obtained from databasin.org.
To select land cover predictors for the model, I ran a model which selected 16 random absence stations, combined those land cover values with those of the presence stations, and created a correlation matrix of land cover types. This ran for 10,000 iterations, selecting a random set of absence stations each time. For each combination of land cover and climate variables, I then calculated the proportion of iterations in which the correlation coefficient was greater than 0.5. If more than 50% of iterations were correlated, one of the offending variables was removed. The final model included the following predictor variables: mean summer temperature (June, July, August 1992 – 2008), mean summer precipitation (June, July, August 1992 – 2008), proportion of open water within 2-km, proportion of wet meadow within 2-km, proportion of swamp forest within 2-km, and percent impervious ground cover within 2-km.

**Model Building**

I again 1) sampled 16 absence stations, combining them with presence stations; 2) performed a binomial regression of the demographic variable of interest (PASY and PABC were modeled separately) and the land cover/climate predictors, and 3) wrote the coefficients and p-values of each predictor variable to a file. This ran for 10,000 iterations, resulting in a .csv file with 10,000 p-values and coefficients for each predictor variable. I then calculated the p-value for a linear model of the predicted demographic variable vs the actual values and correlation coefficients of the predicted vs observed values.

For the 10,000 model iterations, I calculated the proportion of iterations in which each independent variable was significant. If fewer than 50% of the models were significant for a given variable, that variable was removed and the models re-run. In order to create a consensus model, I first trimmed all model iterations using the following steps: 1) removed iterations in which the p-value for the linear model vs predicted values was not significant or the correlation coefficient was below 0.7; 2) removed iterations in which a predictor variable was not significant; and 3) removed
iterations in which coefficient signs were contrary to the majority of that predictor. Once I had removed all of these defecting models, I calculated the mean coefficient for each variable and the intercept. This method of using multiple iterations with different input stations allowed me to analyze and combine different model results while preventing bias in station selection and providing a better idea of typical and abnormal model results (Araújo and New 2007).

Model Validation

I regressed model predicted values against an independent data source — 1966 - 2012 population trend data from the North American Breeding Bird Survey, hereafter BBS (Sauer et al. 2014, http://www.mbr-pwrc.usgs.gov/bbs). These data formed of a grid of 21,475 meter blocks containing the estimated weighted average of Yellow Warbler population from 1966 - 2012 as obtained and estimated from Breeding Bird Survey routes. I extracted trend values for each MAPS station and regressed these values with the predicted PABC and PASY values obtained from the consensus models.

Predictive Maps

The predictive maps were created using both ArcGIS 10.0 and the R packages raster (Hijmans and Etten 2012) and rgdal (Bivand et al. 2014). The focal statistics raster for each land cover type in the final model was multiplied by the consensus model coefficient in R. These rasters were then summed and the intercept added. These rasters were then transformed so that all values fell between 0 and 1 as proportions, log transforming the PASY raster beforehand. Using the writeRaster function, I wrote the predictive model to a raster compatible with ArcGIS. To display the data, I applied a “Histogram Equalize” stretch.
Testing For Density-Dependence

As territoriality may prevent severe density-dependent declines in per-capita fecundity (Fretwell 1969), I assume that these populations are unaffected by extreme declines in reproductive rate due to high density. To test this in my dataset, I regressed the number of adult birds captured per unit suitable area (as considered to be “habitat” by the models) against the number of hatch-year birds per adult bird captured as an estimate of individual fecundity. I calculated adult bird density by dividing the mean number of adults captured at a station annually by the proportion of open water and wet meadow land cover (the area considered to be “habitat” by the models) within the 2-km landscape. Assuming carrying capacity, I hypothesized a neutral relationship between these variables under an ideal-free distribution (lack of density-dependence) and negative relationship if under the ideal-despotic distribution (density dependence or ecological trap, (Skagen and Yackel Adams 2011)). A positive relationship between these variables would suggest a lack of density dependence, possibly due to the population not reaching carrying capacity. For my Yellow Warblers, there was not a significant relationship between the number of hatch-year birds captured during the lifetime of a station divided by the number of adult (after hatch-year) birds and log-transformed adult bird density (p = 0.374). This suggests that density-dependence is not influencing these models.
RESULTS

Proportion of Breeding Adults

All 10,000 models predicted PABC to the 0.05 significance level (highest p-value = 9.2E⁻⁵). Temperature and precipitation were both negative predictors (100% of iterations for both) and all had significant p-values (see Table 1.1). The proportion of wet meadow and proportion of water within 2-km were positive predictors of PABC, both with 100% positive coefficients and 100% of p-values below 0.05. Swamp forest was found to be a negative predictor in 100% of the models, with 100% of the iterations being significant. Percent impervious was significant in only 27.1% of models; therefore, I re-ran the models with %imperviousness removed. For the consensus model, I removed model iterations in which the correlation coefficient between the actual vs predicted values was below 0.7, resulting in the removal of 2,504 of the 10,000 models (minimum correlation coefficient = 0.595). One more model was removed in which %water was not significant. The consensus model contained the mean coefficient values of the remaining 7,495 model iterations.

Proportion of Older Birds

As in the PABC models, %impervious was not significant and the models were re-run without it. In the new models, all 10,000 models predicted PASY to the 0.05 significance level (highest p-value was 8.89E⁻⁵). However, after the removal of models with correlation coefficients less than 0.7, 50.1% of the remaining models reported the p-value of the %swamp forest variable to be insignificant (p > 0.05). I created a consensus model with the remaining iterations, of this model, cutting iterations in which %swamp forest was not significant, naming this model PASY-A. I then reran the models, removing %swamp forest as a predictor, naming this model PASY-B. PASY-A resulted in 2,496 of the 10,000 iterations remaining in the consensus model, while PASY-B retained 5,642.
For both PASY-A and PASY-B, temperature and precipitation were negative predictors and most had significant p-values (see Table 1.2 for proportions). The proportion of wet meadow and proportion of water within 2-km were both positive predictors of PASY (100% of iterations for both predictors were positive). Wet meadow was significant for all models (100%) and open water was significant for nearly all models (all but one of 10,000). For swamp forest in PASY-A, only 52% of iterations were significant, with 81.6% of coefficients being positive.

Table 1.1: Model Summaries for PABC. For each variable, the sign (positive or negative) of each coefficient, and what percent of the 10,000 iterations were of that sign. The fourth column shows the percent of model iterations with p-value of <0.05 for a linear model of predicted vs actual values. The last two columns show the coefficient of the consensus model (after trimming) and a description of what an increase in the variable predicts.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coef. Sign</th>
<th>% +/−</th>
<th>% p &lt;0.05</th>
<th>Coefficient Consensus</th>
<th>Predicts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>-</td>
<td>100%</td>
<td>100%</td>
<td>-36.8</td>
<td>Fewer birds in breeding condition</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-</td>
<td>100%</td>
<td>100%</td>
<td>-20.1</td>
<td>Fewer birds in breeding condition</td>
</tr>
<tr>
<td>%Wet Meadow</td>
<td>+</td>
<td>100%</td>
<td>100%</td>
<td>7.1</td>
<td>More birds in breeding condition</td>
</tr>
<tr>
<td>%Open Water</td>
<td>+</td>
<td>100%</td>
<td>100%</td>
<td>12.8</td>
<td>More birds in breeding condition</td>
</tr>
<tr>
<td>%Swamp Forest</td>
<td>-</td>
<td>100%</td>
<td>100%</td>
<td>-5.5</td>
<td>Fewer birds in breeding condition</td>
</tr>
<tr>
<td>%Impervious</td>
<td>+</td>
<td>58.2%</td>
<td>27.1%</td>
<td>NA</td>
<td>Not significant</td>
</tr>
</tbody>
</table>

Table 1.2: Model Summaries for PASY: For each variable, the sign (positive or negative) of each coefficient, and what percent of the 10,000 iterations were of that sign. The fourth column shows the percent of model iterations with p-value of <0.05 for a linear model of predicted vs actual values. The last two columns show the coefficient of the consensus model (after trimming) and a description of what an increase in the variable predicts. This is given for model A, which includes swamp forest as a predictor, and model B, which excludes swamp forest.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coef. Sign</th>
<th>% +/−</th>
<th>% p &lt;0.05</th>
<th>Coefficient Consensus</th>
<th>Predicts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>-</td>
<td>100%</td>
<td>100%</td>
<td>-25.43</td>
<td>Fewer ASY birds</td>
</tr>
<tr>
<td>Precipitation</td>
<td>-</td>
<td>92.4%</td>
<td>75.6%</td>
<td>-4.47</td>
<td>Fewer ASY birds</td>
</tr>
<tr>
<td>%Wet Meadow</td>
<td>+</td>
<td>100%</td>
<td>100%</td>
<td>12.27</td>
<td>More ASY birds</td>
</tr>
<tr>
<td>%Open Water</td>
<td>+</td>
<td>100%</td>
<td>100%</td>
<td>7.8</td>
<td>More ASY birds</td>
</tr>
<tr>
<td>%Swamp Forest</td>
<td>+</td>
<td>81.6%</td>
<td>NA</td>
<td>3.98</td>
<td>More ASY birds</td>
</tr>
<tr>
<td>%Impervious</td>
<td>-</td>
<td>58.1%</td>
<td>NA</td>
<td>NA</td>
<td>Not significant</td>
</tr>
</tbody>
</table>
Predictive Mapping

The predictive maps (Figure 1.2) show high PABC and PASY (green, interpreted here as high-quality habitat) in high abundance in the northern part of the study region. In the mid-to-lower portion of the study region – which approaches the lower boundary of the breeding range of this species – showed primarily red, which is interpreted as predicted absences. The vast area of predicted absences contains scattered patches of suboptimal overflow habitat (yellow) and patches of high-quality. This is especially striking in the PASY model, where the suboptimal overflow and high-quality habitat closely follow the major rivers.

Model Validation

Both models (PABC and PASY) successfully predicted Yellow Warbler population trends as obtained from the BBS. For PABC, $p = 0.0176$ without removing a cluster of four outliers from Fort Leonard Wood, Missouri and $p = 0.00749$ (adjusted $r^2 = 0.1108$) with these stations removed (Figure 1.3a). For PASY, model A (which included swamp forest), $p = 0.00932$ (adjusted $r^2 = 0.1081$) (Figure 1.3b). For PASY model B (swamp forest removed), $p = 0.0183$ and adjusted $r^2 = 0.01827$ (Figure 1.3c).
a) PABC: Proportion of Adults in Breeding Condition

Figure 1.3: Predictive maps of the a) PABC and b) PASY model A (no swamp forest). Green indicates a high predicted value and red indicates a low predicted value; interpreted as a gradient from highly productive (green) to suboptimal overflow (yellow) to absence (red). Blue indicates cells with high proportions of water for which climate data were missing.
b) PASY: Proportion of After-Second-Year Birds
Figures 1.4a – c: Regression analyses of model predictions against Breeding Bird Survey population trend. All three models successfully predicted Yellow Warbler population trends as obtained from the North American Breeding Bird Survey (BBS). For PABC, $p = 0.00749$ (a). For PASY model A (which included swamp forest), $p = 0.00932$ (b). For PASY model B (swamp forest removed), $p = 0.0183$ (c).
DISCUSSION

The model results support the use of age ratios and breeding status ratios to predict the fecundity of a species across a portion of its breeding range. These demographic proxies were successfully able to predict population trends as estimated from an independent data source. This supports the use of these methods as a more accurate predictor of reproductive success and therefore habitat quality than abundance and occupancy data. In addition to being a more informative measure, these data are also more easily obtained than long-term trend data and individual fecundity data.

The proportion of birds in breeding condition and the proportion of after-second-year birds both predict population trend due to what these values suggest about the populations. A higher proportion of birds with cloacal protuberances suggests high pairing success and thus a high proportion of high quality individuals. These high quality individuals likely produce more offspring over the course of their lifetime as well as obtain territories that contribute to increased nest success. The relationship between PABC and population trend had a higher $r^2$ value than the relationship between PASY and population trend. This may be due to the numerous other factors influencing age ratios at a particular site. It is possible that higher reproductive success and increasing population trends may cause a higher proportion of second-year birds to be captured at a site as they return to their natal breeding grounds. MAPS stations are required to monitor an area of approximately 20 hectares (0.01 square kilometers), and compared to the scale used in this study (2 kilometer diameter radius from the given MAPS station point) segregation between older and younger birds may be less identifiable.

In addition, Yellow Warblers specialize in successional habitats. Work on another successional specialist, the Prairie Warbler (*Setophaga discolor*) shows that newly created early successional patches of habitat are typically colonized by second-year males. Although these
second-year males still had slightly lower pairing success than after-second-year males (an assumption in my study), those that were paired shared similar nest success with older males (Akresh et al. 2015). This suggests that age ratios may be misleading in successional habitat specialist bird species. Further work should investigate whether this bias towards colonization by younger males holds for Yellow Warblers and whether age ratios as predictors of population trends and reproductive success are better predictors in birds specializing in more stable habitat types.

For the Yellow Warbler, my predictive maps showed more high-quality habitat available in the northern part of the study region, in Michigan, Wisconsin, and Minnesota, as well as eastern New York, eastern Pennsylvania and northern Ohio. High-quality habitat was available, but less abundant, in the southern portion of the study region, which borders the southern limit of the breeding distribution of this species. The high-quality habitat in the south appeared to be focused around major rivers. These predicted distributions of high-quality habitats are consistent with previous research findings on both Yellow Warbler habitat preferences (Knopf and Sedgwick 1992; Olechnowski and Debinski 2008; Riffell et al. 2003) and, more generally, the variability of population dynamics across the range of a species. Both theoretical and empirical studies consistently find that populations on the periphery of the range tend to have lower abundance and density as well as higher temporal variability of these measures (Brown 1984; Vucetich and Waite 2003). However, age structure has been primarily studied on a local scale. To my knowledge, this is only the second study to support the presence of age structure at the landscape scale (see Graves 1997). Graves’ study on Black-throated Blue Warblers (Setophaga caerulescens) demonstrated that age structure varies across the species’ range. From this, Graves hypothesized that the higher proportions of first-year breeders in peripheral areas are due to emigration from more central source populations. My work supports the use of age structure in more accurately detecting these “source” populations at a landscape scale. Although short-term occupancy and abundance data are regarded as easier and less expensive to collect, incorporating age structure data can provide
crucial additional insights to predictions of persistence. The proportion of ASY birds was not
correlated with the abundance (average number of Yellow Warblers captured per year, Pearson’s
product-moment correlation: \( p = 0.973, \text{cor} = -0.00787 \)); however, incorporating age structure data
into a model may provide information about the population that occupancy and abundance omit.

Analyses of all the MAPS stations by David F. DeSante, Danielle R. Kaschube, and James F.
Saracco from the Institute for Bird Populations found that between 1992 and 2006, temporal
variability of productivity for Yellow Warblers was very low (14.1%), while spatial variability was
higher (33.7%). This suggests that the consolidation of PABC and PASY across years into single
values for a station, as done in my analyses, likely did not influence the results. In addition, these
authors found that population trend values were not correlated with productivity spatially, and
suggested that “spatial and temporal variation in weather conditions, perhaps driven by climate
change” may influence population trends. This is supported by my models, which show that climate
variables influence the demographic values PABC and PASY. Although the authors from the
Institute for Bird Populations did not include analyses of age ratios or breeding proportion
measures, spatial analyses of productivity (as young per adult) show predicted absences in the
southern regions, with moderate productivity through Illinois, Indiana, and Ohio. Into the southern
portion of the Michigan’s Lower Peninsula and most of Wisconsin, there is a band of lower
productivity in between areas of this moderate productivity. This is in contrast to the results in my
study, which predicted an increase in productivity. These differences may be due to the large
spatial scale that my models cover; the region used in my study encompassed multiple “Bird
Conservation Regions” as defined by the North American Bird Conservation Initiative. The authors
cautions the interpretation of their spatial results as MAPS stations are not randomly distributed, so
variation in the distribution of station habitat type may exist among regions.
Interpreting MAPS Data – Data Quality and Error Potential

When interpreting the values obtained from MAPS, especially ratios of age and breeding status as used in this study, there are some potential sources of error in these values, especially since migrants will not be in breeding condition. However, many of these concerns have been addressed via the MAPS protocol (DeSante et al. 2010). For example, capture data are corrected for variation in annual mist-netting effort (Desante et al. 2015). In addition, the MAPS protocol prevents migrating individuals from being counted in the data by operating only after migrants have moved through the area, although some late migrants may be counted. Migrants and transient individuals in the dataset may decrease the PASY and PABC ratios based on non-residents, as these birds will not be in breeding condition and late migrants are more likely to be young individuals.

Errors in aging or lack of aging effort are an additional concern with the use of age ratios as a predictor for reproductive success. Although male yellow warblers vary in their plumage intensity, this is not considered to be a case of delayed plumage maturation (Studd and Robertson 1985b, 1989). Males with less intense plumage are not more likely to be young, nor are they inexperienced or have lower nest success. In fact, they are more attentive parents and feed more often than brightly colored males. They do, however, occupy less “desirable” territories. This suggests that, similarly to Germain and Arcese’s 2013 study on a population of song sparrows, individual quality is a better predictor of nest success than habitat quality. Using age ratios as a predictor of habitat quality accounts for this, without the biases of habitat structure. A problem may arise in the lack of delayed plumage maturation in this species if it makes identification of age more difficult for MAPS station operators. Although Yellow Warblers are reliably aged to second-year and after-second-year using mean wing chord length or the presence/absence of juvenile or first alternate feathers (Pyle et al. 1987), these methods require an experienced operator. For this
reason, I attempted to remove any stations which appeared to have erroneous or incomplete data collected on age metrics.

**Ideal Habitat Selection**

Compared to presence and abundance, I consider the proxies used for reproductive success in this study (the proportion of ASY birds and the proportion of adults in breeding condition) to be less susceptible to biases caused by assuming a “free” distribution, in which individuals are free to settle in the best habitat they can find. However, using these proxies instead assumes “ideal” habitat selection, in which individuals have perfect knowledge of the habitats available. Most studies support the assumption that birds select breeding habitat based on environmental cues. However, without a measure of reproductive success per se (such as number of chicks fledged per nest), it is impossible to know with certainty whether the MAPS stations used here have high or low individual or population fecundity. My models do show habitat preferences of the species, although in non-ideal habitat selection (in which an organism has perfect knowledge about the habitat it has selected), preference can be a misleading factor. For instance, these cues may become misleading in cases of anthropogenic habitat alteration if the cues fail to accurately predict habitat quality (Bock and Jones 2004). Anthropogenically altered habitats that birds perceive as high quality breeding habitat may have fewer resources or more predators than the natural habitats the species is adapted to recognize. This results in a preference for a habitat in which individuals may have lowered reproductive success, or an ecological trap. Unlike population sinks, ecological traps are selected over habitats that would provide higher reproductive success (Battin 2004). Because of this, age and breeding status ratios in ecological traps would be similar to those in high quality habitats, and may only be differentiated by reproductive success. Further work is needed to compare reproductive output between these sites to determine whether an ecological trap exists, and what indicators might be used to elucidate traps from sources. Habitat types preferred and
secured by dominant, experienced breeders should be monitored especially closely for ecological traps, since these individuals tend to contribute more offspring to the population than their more naïve counterparts. I suggest that proxies such as fledgling abundance may be useful indicators if post-fledging habitat shifts are taken into account.

The Impact of Large Spatial Scales

A spatial scale this large introduces three potential problems. First, we must ask whether habitat preference of the species changes across the study area—local adaptation to different breeding microhabitats, for example (Petrides 1942). This may be driven or accelerated by a second problem: changes in community composition across the study region. This includes species assemblages that influence habitat structure, food availability, competition, and predators. I accounted for these issues by limiting this study to a single ecoregion (eastern forest) at relatively uniform elevations. However, my results show latitudinal differences, implying that habitat across the species range is not uniform; rather, some parts of the range contain more areas in which we predict to find more older birds and more individuals breeding. The third issue is the possibility of cryptic species. On larger spatial scales, this increases the chance of encountering unidentified species and modeling two or more species as one (Bickford et al. 2007). Unidentified cryptic species, when grouped together in these types of analyses, will give inaccurate results and cause an overestimation of population numbers and habitat available. These erroneous models would be considering data from two or more species as one, skewing the results if each cryptic species had different ecological preferences. I recommend that, resources permitting, any work on large spatial scales prioritize testing for both evolutionary and ecological divergence prior to predicting habitat preferences.
Climate Predictors

Understanding where distinct species exist and their distinct ecological preferences is also vital for predicting responses to climate change. The importance of climate variables (mean summer temperature and mean summer precipitation) in these models suggest that changes in climate will likely shift the locations of high-quality habitat. Although abundance and occupancy shifts have already been noted (Hitch and Leberg 2007; Zuckerberg et al. 2009), changes in demography may have occurred well beforehand. Changes in temperature and precipitation patterns may cause the productive (central) part of the species range to shift northwards before extinction takes place in the south. The negative relationship found between Yellow Warbler fecundity predictors and temperature/precipitation may be due to physiological constraints, as clutch size is known to correlate with latitudinal increases (Cooper et al. 2005). The two leading hypotheses on latitudinal increases in clutch size both predict that cooler temperatures make larger clutch sizes physiologically possible. The Clutch-Cooling Hypothesis (Reid et al. 1999) predicts that since larger clutches possess more mass, they cool more slowly, allowing the female to take longer bouts away from incubating eggs to forage. The Egg Viability Hypothesis predicts that birds in the north are simply less constrained to smaller clutch sizes due to cooler temperatures (Stoleson and Beissinger 1999). During the egg laying period, the embryo is less likely to be exposed to sub-optimal incubation temperatures or premature incubation temperatures, allowing the female to prolong the onset of incubation without risking hatching asynchrony and deformities. As temperatures increase in this region, we may see changes in local fecundity through clutch size decreases alone.
**Temporal Variation**

As climate change may impact local fecundity over time, testing for temporal variation in model predictions may help predict areas of instability. Future studies should prioritize the variability of age ratios and breeding status ratios over time. In particular, research should focus on whether variability is local or in particular parts of the range. Some sites, especially those near the periphery of the range, may show ample nesting success for many individuals one year, and become a population sink in the following year. Resource and climate fluctuations may be stronger in these regions or in low-quality habitat. Variability in particular areas may also be part of long-term trends. Identifying and monitoring habitats with increasing or decreasing age ratios and breeding status ratios would allow for predictions of future range shifts and conservation requirements.

Temporal change is particularly an issue for birds such the Yellow Warbler, which nests primarily in successional habitats. Warblers have been known to display high levels of site fidelity, especially for territories in which they have raised successful broods (Knopf and Sedgwick 1992; Studd and Robertson 1989); however, it is unknown whether site fidelity in Yellow Warblers correlates with previously experienced nest success. Hypothetically, an older bird may continue returning to the same site even as habitat quality decreases. Canada Warblers (*Cardellina canadensis*), for example, exhibit site fidelity regardless of nest success (Hallworth et al. 2008), while site fidelity increases in Prothonatary Warblers (*Protonotaria citrea*) with increased nest success (Hoover 2003). Thus, more work is needed to determine whether nest success influences site fidelity in Yellow Warblers, as this may influence quality predictions when using age as a predictor of quality in species that use successional habitat.
Summary

Age ratios and breeding status ratios successfully predicted long-term population trends consistent with known habitat preferences (Knopf and Sedgwick 1992) and studies which found decreased proportions of older birds along the outer margins of the species’ range (Graves 1997). By mapping my model predictions, I show areas of high productivity in the northern part of the study region (toward the center of the breeding range) and small areas of high quality scattered throughout the southern edge of the range. My model predictions were validated by long-term population trend models, although $r^2$ values show higher support for PABC models over PASY models. I conclude that this modeling technique is effective at predicting productivity and population trends across the range and recommend further research to improve and implement this method at varying temporal scales and across taxa (especially non-successional specialists) as well as the continuance of collecting large-scale demographic data.
CHAPTER III - Characterizing caterpillar biomass phenology: differences among host trees and implications for climate change

Lepidoptera larvae – better known as caterpillars – serve as a crucial food source for many species of birds, reptiles, amphibians, insects, and spiders. Caterpillars are hosts to parasitic wasps and flies (Tanaka and Ohsaki 2006), while most other predators simply consume sometimes large quantities of caterpillars (Mitchell 1952). In particular, many species of passerine birds specialize on caterpillars during the breeding season, feeding these larvae to their nestlings. Caterpillars are shown to have high fat content while being relatively low in chitin found in exoskeletons of many insect taxa, which is indigestible (Redford and Dorea 1984). The importance of caterpillars as a staple of the nestling diet has been demonstrated in that birds are shown to time their breeding with peak caterpillar abundance (Dunn et al. 2010) and show decreased nest success and chick mass when food resources are lower (Visser et al. 2006).

Although experimental reductions of caterpillars in North American studies tend to show slight, but insignificant effects on reproductive output for birds (Holmes 1998; Marshall et al. 2002), habitat-influenced differences in food abundance via plant species composition does appear to decrease productivity (Marshall et al. 2013). Because Lepidoptera species can be host-specific, plant species composition may easily predict food abundance at a site. Coupled with preferred nesting and foraging niches for many passerine species, there may be only a select few plant species that provide the majority of food for a particular bird species during the nesting season (Holmes and Robinson 1981).

Tree species have independently regulated phenologies (Richardson et al. 2006), and it follows that each of the many caterpillar species which feed on them do as well. In temperate regions, tree phenology tends to be triggered by accumulating warm temperatures in the spring, or
“degree days”. However, caterpillar phenology is less sensitive to temperature and may rely partially on photoperiod (Schwartzberg et al. 2014). For these reasons, I predict that each tree species has its own unique “seasonal food availability curve” which is dictated by Lepidoptera species composition, relative species richness, and their phenologies (Veen et al. 2010). Veen (2010) discovered that deciduous trees in Europe had tall, narrow peaks of caterpillar biomass, while coniferous species had low, gradual increases in caterpillar biomass. Depending on the shape of the curve (e.g., tall, narrow peaks or wide, low peaks) food abundance itself may be less important than the timing of food availability (Martin 1987). If food is not in high abundance when nestlings most need it, smaller clutches may be attempted, higher chick mortality may occur, or lower quality offspring may be produced (Visser et al. 2006). Both et al. (2006) discovered that populations of Pied Flycatchers (Ficedula hypoleuca) in Europe decreased at faster rates at sites with earlier insect abundance peaks, despite these peaks being higher overall. This suggests that temporal synchrony between bird reproduction and insect abundances may be crucial to nesting success, and birds should aim to breed when food is most available to the nestlings.

Reproductive phenology is controlled physiologically via environmental cues which trigger hormone production (Visser et al. 2010). This is made more complex for migratory species that rely on environmental cues in the winter habitat to predict conditions in the breeding habitat (Miller-Rushing et al. 2010). In recent years, climate change has led to phenological mismatches between birds and Lepidoptera, causing population declines in European populations (Both et al. 2006). Although no studies have tested for phenological mismatches in North American species, shifts in migratory arrival dates have been noted in some species (Macmynowski et al. 2007; Vitale and Schlesinger 2011), which supports the idea that changes in phenology are occurring in North America. Whether population declines due to phenological mismatches are occurring depends on a few contingencies: 1) Are birds that are shifting dates shifting along with their prey? 2) Is overall prey abundance low enough to cause a food shortage? 3) Are bird species that are not shifting
breeding dates doing so because their prey isn’t shifting or is this causing a mismatch between the birds and their prey? Under my hypothesis, it is likely that not all bird species will be equally affected by climate change depending on foraging niche, breeding habitat, and local food abundance. Understanding how caterpillar phenology differs between tree species in North American is crucial for predicting if bird species will be impacted by phenology shifts and which species may be more at risk. As Veen et al. (2010) showed, some tree species may show high, but narrow, peaks in caterpillar biomass. Trees with these types of food availability curves may be important food sources for birds due to high peaks, but food peaks may be easily missed. In this study, I test the hypothesis that caterpillar availability for birds differs between eight tree species, including three coniferous (Eastern Hemlock, Tsuga Canadensis; White Pine, Pinus strobus; and White Spruce, Picea glauca) and five deciduous (White Ash, Fraxinus americana; Sugar Maple, Acer saccharum; Red Oak, Quercus rubra; American Beech, Fagus grandifolia; and Paper Birch, Betula papyrifera) and characterize their caterpillar availability curves.

**METHODS**

**Site and Species Selection**

In 2013 and 2014, I conducted field work at the Huyck Preserve in Rensselaerville, New York. I selected eight focal tree species, prominent in the landscape and of potential ecological importance to the focal bird species: *Tsuga canadensis* (Eastern Hemlock, N=6), *Fagus grandifolia* (American Beech, N=6), *Betula papyrifera* (Paper Birch, N=5), *Fraxinus americana* (White Ash, N=6), *Quercus rubra* (Red Oak, N=6), *Acer saccharum* (Sugar Maple, N=7), *Pinus strobus* (White Pine, N=5), and *Picea glauca* (White Spruce, N=4). I selected sample trees if they were more than 100 meters from another sample tree of the same species and had canopies which were not overlapped by a canopy of any other tree. I estimated crown height for the trees using an inclinometer, but due to potential inaccuracy caused by dense canopy and difficulty observing the tops of many tree crowns,
I discarded these measurements. To account for differences in tree sizes, I instead used diameter at breast height (DBH). For trees with forks below breast height, I calculated the DBH as the square root of the sum of the squared DBH measurement of each trunk.

**Data Collection and Caterpillar Biomass Estimation**

From 28 May – 30 July in 2013 (63 days) and 26 May – 20 July in 2014 (55 days), I collected caterpillar feces (frass) using frass nets made of 0.25 m² pieces of 90 grade cheesecloth attached to metal stakes and were placed under the unobstructed tree canopy. A small weight (either a stone, glass bead, or stainless steel hexnut) is placed in the middle of the trap to create a slight funnel shape so the frass collects in the trap (stones were eventually used for every trap due to the price of the hexnuts and the light weight and attractiveness of glass beads to animals). I placed nets under their respective trees roughly once per week and collected them at least 24 hours later in the same sequence in which they were distributed. Upon collection, frass on the trap was brushed towards the center of the trap to prevent loss, and the trap was folded up neatly and the four corners twisted together. The entire piece of cloth was then placed in a labeled bag for transportation back to the lab.

In the lab, I emptied frass nets individually into a #40 Hubbard Scientific sieve (mesh opening 0.422 mm). I did this over a large sheet of construction paper in case of any pieces missing the sieve. I then poured the contents from the construction paper through the sieve. After shaking the debris through the sieve, I used a brush to empty the remaining frass and debris into a small class petri dish. In this petri dish I sorted debris from frass using a dissecting microscope, moving frass with a fine-tipped paintbrush to microcentrifuge tubes for storage. Leaving the caps open on the tubes, I placed them in an oven at 60° Celsius for 24 hours to remove moisture.

One sorted and dried, I weighed the frass using an analytical balance to the 0.01 mg. To produce an estimate of frass per square meter, I multiplied the measured mass by four. Using
Tinbergen and Dietz’ equation, I calculated the estimated caterpillar biomass from the frass mass. This equation accounts for the effect of ambient temperature on caterpillar metabolism (Tinbergen and Dietz 1994) and resulted in a measure of biomass/m²/day (Veen et al. 2010). I calculated the mean temperature from the mean trap deployment time to the mean trap collection time. I prioritized the use of temperature values from the Huyck Preserve’s weather station if available. If data were missing, I used data from local weather stations available from the Weather Underground website (www.wunderground.com), which were highly correlated with the Huyck Preserve weather data (p < 2.2e-16, adjusted r-squared = 0.9383). If neither of these were available, I used data from the Albany International Airport weather station, also available from Weather Underground. I was unable to deploy frass nets during periods of rainfall as frass is sensitive to dissolving and losing mass during rainfall (Mizutani and Hijii 2001). Due to trap failure caused by animals, wind, or human error, some samples were discarded or unavailable. I performed all analyses first using the biomass value calculated from the Tinbergen equation, and again correcting for tree size by dividing the biomass value by the diameter at breast height (DBH).

**ANOVA**

In R Studio Version 0.98.501, I used an ANOVA to test a linear model predicting caterpillar biomass using an adjusted date (days since 01 January for both years), tree species, and interaction terms between date and species as predictors (biomass=date*species). These ANOVAs were performed for all tree species together. To test for differences in biomass between years, I performed a second ANOVA which included year as a predictor instead of date (biomass=year*species).

**Mixed Effects Models of Caterpillar Phenology**
I fitted order 1 – 6 polynomial random intercept mixed effects models for the caterpillar biomass of each tree species separately using the R package lme4 (Bates et al. 2014), with date as the fixed effect and individual tree as the random effect. Using an ANOVA, I selected the model with the lowest AIC with a significant p-value. I graphed the best models using ggplot2 (Wickham 2009). When AIC values were within two units of one another, I considered the models to be equivalent (Burnham and Anderson 2002); and selected the least complex of the models. Outliers were included in the analyses as they were considered an important part of the curve, in that I expected large changes in caterpillar biomass over time.

Biomass Availability

I calculated the amount of available caterpillar biomass during the nesting period for four Neotropical migrant warblers: American Redstart (Setophaga ruticilla, N=3), Blackburnian Warbler (Setophaga fusca N=3), Black-throated Green Warbler (Setophaga virens N=3), and Chestnut-sided Warbler (Setophaga pensylvanica N=4). These four species were chosen as they are known to consume and feed large amounts of Lepidoptera to their nestlings, raise one brood per year, and are abundant and easily detected at the Huyck Preserve. They are closely related which reduces the impact of evolutionary history as a confounding factor, but they have different breeding and foraging niches. I performed a Birds of North America Online review of habitat, foraging, and breeding niches for these four species (Rodewald 2015). Blackburnian Warblers and Black-throated Green Warblers both nest in forests containing Eastern Hemlocks, however, Black-throated Green Warblers focus foraging activity on deciduous trees and spruce while Blackburnian Warblers primarily forage on conifers (Morse 2004; Morse and Poole 2005). American Redstarts preferred nesting in Sugar Maple and Yellow Birch, and seem to prefer foraging on Yellow Birch (Sherry and Holmes 1997). Chestnut-sided Warblers show affinity towards nesting in Sugar Maple (but commonly nest in shrubs) and feed on hardwood species (Byers et al. 2013).
I observed these four species at the Huyck Preserve in 2014 to obtain key breeding dates (laying, hatching, fledging) via frequent territory monitoring. I monitored, mapped, and took detailed notes on the behaviors and songs of these four species at the preserve, attempting to visit and locate each bird multiple times per week. I noted behaviors such as song type, which is known to be indicative of pairing status, nest building, and other behaviors such as carrying food, which was interpreted as an indicator of feeding nestlings, and therefore signaled that hatching had occurred. As these birds can be difficult to observe, especially in dense-canopy hemlock forests such as those at the Huyck Preserve, observed evidence of dates was supplemented with the known incubation and nestling durations for the four species to forward and back-calculate estimates of the laying, hatching, and fledging dates (Byers et al. 2013; Morse 2004; Morse and Poole 2005; Sherry and Holmes 1997). In total, I successfully acquired dates for four of each species.

For each bird species, I calculated the average laying, hatching, and fledging dates. I also averaged the intercepts of the models, since the intercepts differed for each tree in the mixed effect model. I used this average intercept and the extracted coefficients for each term to determine the function defining the predicted biomass curve. Using this function, I calculated the area under the curve for each tree species and bird species. This produced a metric of biomass available from each tree during the breeding period. With these values, I performed two ANOVAS, grouping the data first by tree species and then bird species, to test if biomass availability varied by tree species or if bird species varied in how much biomass was available for them. This tells us whether some trees provide more or less food during the breeding period, which may elucidate crucial tree species for maintaining high quality breeding habitat for these birds. By grouping by bird species, I seek evidence for birds specializing on particular tree species by timing reproduction with that tree’s biomass peak.
RESULTS

ANOVA

The ANOVAs showed that the date, species, and the date:species interaction term were important factors in predicting caterpillar biomass (Table 2.1a-b) in the biomass model. However, species alone was not significant for the DBH-adjusted model. This is likely due to the significant differences among the DBH of tree species sampled (ANOVA F-value = 27.71, p < 2.2e-16). Thus, the DBH-adjusted model shows that biomass does differ among tree species, but phenologically rather than overall. Due to the relationship between tree size and caterpillar biomass, I recommend other studies use a size correction when analyzing caterpillar biomass as well.

In the year:species models, only the biomass model showed significant differences among tree species (p = 2.809e-06) and near-significant differences for the year:species interaction (p = 0.0886). However, the DBH-adjusted model showed no significant differences for any predictor (Table 2.1d). Thus, it is unclear whether caterpillar biomass truly differed between years by species, or if this is an artifact of tree size.

Adjusted r-squared values were low for all models. The highest adjusted r-squared value was found for the biomass~species*date model, at r² = 0.1217. Both biomass models had higher r-squared values than the adjusted biomass.dbh models. The low r-squared values indicate that there are other factors determining caterpillar biomass which were not included in these models. These may include factors such as canopy volume, wind speed, or any number of factors governing local caterpillar abundance.
Tables 2.1a-d: ANOVA tables and r-squared values for the four linear models predicting biomass or DBH-adjusted biomass. In both the biomass model (a) and DBH-adjusted model (b), tree species, date, and the tree species:date interactions were significant predictors of biomass. Year was not a significant predictor of biomass in either the biomass model (c) or DBH-adjusted model (d), and tree species was only a significant predictor.

Table 2.1a: lm(biomass~species*date) adjusted $r^2 = 0.1217$

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Table 2.1b: lm(biomass.dbh~species*date) adjusted $r^2 = 0.05875$

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Table 2.1c: lm(biomass~species*year) adjusted $r^2 = 0.03662$

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Table 2.1d: lm(biomass.dbh~species*year) adjusted $r^2 = 0.006594$

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Biomass Phenology Models

Overall, most tree species best fit a higher order polynomial in 2013 than in 2014 (see Table 2.2). The adjusted $r^2$ values of the predicted vs. actual values ranged from 0.025 for Hemlock in 2014 to 0.857 for Hemlock in 2013. Models generally had a higher $r^2$ for model fit in 2013, except for Sugar Maple and White Spruce. Unadjusted biomass models had higher $r^2$ values in 2013 (7 of 8 models), but in 2014, DBH-adjusted models showed higher $r^2$ values (5 of 8 models).

For most trees, the polynomial order was the same between the biomass and DBH-adjusted biomass models, with the exception of 2013 Hemlock and Sugar Maple and 2014 American Beech. However, in instances in which model orders differed, DBH-adjusted models had lower order polynomials. This suggests that DBH-adjustment helps simplify the data, but may also remove some important variation among trees sampled within a species.

For many of the models, a D’Agostino’s K-squared test (R package moments (Komsta and Novomestky 2011)) showed that the residuals were non-normal. Visual examination of the residual distribution revealed that the non-normality was typically due to single-sided tails, or outliers of three or fewer points on one or both sides. In order to preserve interpretability of the model predictions, I decided not to remove outliers or transform data in order to preserve interpretability of the models. The differences in residuals were likely simply due to variation in local caterpillar abundance, such as the Notodontidae outbreak observed for one Sugar Maple tree in 2013, where during collection, frass could be heard falling onto the leaf litter from the surrounding Maple trees.

Graphs of the biomass values (see Figure 2.1) show that the modeled results (dotted and dashed lines for 2013 and 2014, respectively) appear to capture the main effects of the curves generated directly from the data (blue and red). Deciduous species appeared to have a “double peak” biomass curve, with an initial peak in biomass early in the season followed by a second peak later in the summer, especially in 2013. For American Ash, the earlier peak appeared higher both in 2013 and 2014, although the sampling period may have ended before the maximum peak was
recorded. Trees such as Sugar Maple show a small early peak, followed by a higher summer peak. White Pine also had a slight double peak as well as White Spruce in 2013. These peaks are likely due to double-brooding species of Lepidopterans which contribute to biomass curves twice.

<table>
<thead>
<tr>
<th>Table 2.2: Model Orders and $r^2$ Values.</th>
<th>Polynomial Order of Best Model</th>
<th>$r^2$ Best Model</th>
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<tr>
<td>American Beech</td>
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</tr>
<tr>
<td>Paper Birch</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Hemlock</td>
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<td>5</td>
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<tr>
<td>Sugar Maple</td>
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<tr>
<td>White Spruce</td>
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Differences in Food Availability

The two ANOVAs of the area under the curve of biomass during the bird breeding periods showed significant differences in available biomass between tree species ($p < 2e^{-16}$) but no significant differences in biomass availability for the different bird species ($p = 0.972$), (Table 2.3). Hemlock provided more biomass for Hemlock-nesting birds Blackburnian Warblers and Black-throated Green Warblers, but this relationship was not significant (Table 2.4). Blackburnian Warblers, which are noted to feed on spruce, had the highest biomass value for spruce of the four species, but this was also not significant. Graphs show high abundance of food from tree species such as Maple post-fledging, but between egg laying and fledging, Oak, Birch, and Spruce provided the most biomass for nesting warblers (Figure 2.2).
Figure 2.1: Unscaled Caterpillar biomass curves for 2013 and 2014. Each tree species is graphed twice; once with the biomass data (red for 2013, blue for 2014) and models (dotted for 2013 and dashed for 2014) and again with the DBH-adjusted values (pink for 2013, cyan for 2014). Models appeared to fit well, with the exception of 2013 DBH-adjusted data.
Figure 2.2: Scaled DBH-adjusted caterpillar biomass curves and bird breeding dates. Red lines represent 2013 values and blue lines represent 2014 values. Graphs are scaled for comparison of caterpillar biomass availability among trees for breeding warbler species. Green arrows mark the approximate 2014 laying and fledging dates for the four warbler species in this study. Birch, Beech, Oak, and Spruce appeared to produce the most caterpillar biomass during the nesting period.
Table 2.3: ANOVA Tables for Food Availability Models

Analysis of variance tables for the models of food availability by bird species and tree species for adjusted and unadjusted caterpillar biomass values. Bold values denote statistical significance. Tree species differed in the amount of caterpillar biomass available during the average bird breeding period, but bird species did not differ.

<table>
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<tr>
<th>Analysis of Variance Table: biomass~bird species</th>
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<tr>
<td>Residuals</td>
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</table>

<table>
<thead>
<tr>
<th>Analysis of Variance Table: biomass~tree species</th>
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</thead>
<tbody>
<tr>
<td></td>
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<tr>
<td>Tree</td>
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<table>
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<th>Analysis of Variance Table: biomass.dbh~bird species</th>
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<td>Bird</td>
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<th>Analysis of Variance Table: biomass.dbh~tree species</th>
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<tr>
<td>Tree</td>
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<td>Residuals</td>
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**Table 2.4: Available Biomass Laying to Fledging**

Biomass and DBH-adjusted biomass (in mg) available to birds during their observed average breeding period from each tree species. The highest biomass for a bird species is black bolded; the lowest values are red bolded. Red Oak provided the highest caterpillar biomass, followed by Paper Birch and White Spruce, while Eastern Hemlock provided the least caterpillar biomass to birds.

<table>
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<tr>
<th>Available Biomass Laying to Fledging – Biomass – in mg</th>
<th>American Redstart</th>
<th>Blackburnian Warbler</th>
<th>Black-throated Green Warbler</th>
<th>Chestnut-sided Warbler</th>
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<tr>
<td>White Ash</td>
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<td>White Spruce</td>
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<table>
<thead>
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DISCUSSION

The eight tree species studied at the Huyck Preserve have significantly different biomass phenology. In addition, the amount of biomass available during the bird breeding period was found to differ significantly between tree species. The birds observed in this study had very similar breeding dates to one another, and thus I found no evidence of differences between the biomass available for different bird species. Red Oak provided the most biomass for birds during the breeding period, followed by Paper Birch and American Beech. Eastern Hemlock provided the least, along with White Pine and Sugar Maple. My results show the importance of forest heterogeneity for birds. Species such as Blackburnian and Black-throated Green Warblers tend to select habitats in Hemlock forests, placing nests in Hemlock trees. However, I show that Eastern Hemlock produces the least biomass for breeding birds, illustrating the importance of foraging trees within the territory. I observed that the forest with the densest Blackburnian and Black-throated Green Warbler territories was primarily old Hemlock or Hemlock-Beech association with scattered Sugar Maple, Yellow Birch, and Red Oak and was also the most mature forest surveyed (Odum 1943).

Birds need to find breeding habitat in which food will be in high abundance during the correct periods. High quality habitat for an early nesting bird may be poor habitat for a late nesting bird, and habitat managers should take this into account. Birds have likely evolved either to time their breeding dates to match peak food dates, or evolved habitat choices based on their breeding dates.

In a study of foraging tree preferences of these birds in Hubbard Brook, a local field station (roughly 220 miles Northeast from the Huyck Preserve), two of my focal species, the Blackburnian Warbler and Black-throated Green Warbler, were shown to strongly prefer foraging on Yellow Birch or conifers over American Beech and Sugar Maple (Holmes and Robinson 1981). My work confirms that birch (albeit Paper Birch) and spruce provide more caterpillar biomass for birds during the breeding period than Sugar Maple, which appears to have its highest peak later in the season. However, the Holmes 1981 study showed that American Redstarts had a slight preference...
for Sugar Maple long with Yellow Birch. However, since American Redstarts nest in and around Sugar Maples, this observation may be due to Sugar Maples being more available than other tree species. Further, American Redstarts feed via hovering rather than gleaning, which may alter foraging efficiency on different tree species and the types of prey captured. Caterpillars, while still a large part of the nestling diet, may be supplemented by flying insects due to the foraging strategy of American Redstarts. Yellow Birch was also shown to have a higher number of caterpillars than Sugar Maple or Beech, suggesting that birds are at least in part selecting trees based on the amount of food a tree species provides. Preference may also be based on foraging strategy and how well a particular tree species’ leaf arrangement facilitates efficient foraging (Holmes and Robinson 1981).

**Implications for Climate Change**

Climate change has caused overall advancement in spring phenology of plants and insects triggered by temperature cues (Menzel 2003; Schwartz et al. 2006; Visser and Holleman 2001; Wielgolaski 1999). Phenology has been well-studied, especially in plants, and is known to be genetically controlled and heritable (Wilczek et al. 2010). Cues such as photoperiod and accumulated warm temperatures trigger the genes controlling phenological events such as bud burst or follicle maturation. These cues differ latitudinally, and as such, species and populations within a species vary in the amount of light or temperatures required to stimulate these genes (Hall et al. 2007). Across this latitudinal gradient, climate change also varies in its effects (Schwartz and Reiter 2000). Species reliant on matching phenology with other species must both adapt rapidly. Many caterpillars emerge in the spring just as their host trees being to leaf out (van Asch and Visser 2007; Visser and Holleman 2001) in order to take advantage of the soft, new leaves. Many late-season caterpillars, such as some Notodontidae species, may have evolved enlarged mouthparts for eating thicker leaves that occur later in the summer (Kunikichi and Masashi 2012). Caterpillar species less adapted to early season leaves may fare poorly if their host emerges too early, leaving
them unable to forage efficiently. A lack of synchrony between caterpillar and host plant may also result in increased predation mortality (Parry et al. 1998). Conversely, climate change may also increase synchrony between caterpillar and host plant to a detrimental degree – repeated outbreaks of the western spruce budworm (*Choristoneura occidentalis*) due to synchronous phenology between the caterpillars and their host (*Douglas Fir - Pseudotsuga menziesii*) have resulted in mass die-offs of the trees (Chen et al. 2003). Although the high abundance of food may benefit birds in the short term (Morse 1978), the long-term effects are likely to alter community dynamics.

Different species within the same site also vary in their phenological responses to climate change. In Ohio, for example, flowering date significantly advanced over the twentieth century for American Elms (*Ulmus americana*) but did not change for White Ash (*Fraxinus americana*) or Black Oak (*Quercus velutina*) (Chuine et al. 2000). For generalist caterpillars which can use any of these tree species as a host, this may result in directional selection towards specialization if trees with once similar bud burst dates suddenly diverge. This would alter the characteristics of the caterpillar biomass curves described in this study.

Whether birds can and will adapt to shifts in the phenology of their food source is an area of concern for ornithologists (Miller-Rushing et al. 2010). While changes in temperature cues can influence phenology in plants and insects, the same may not be so simple for migratory birds. Bird gonadal development is primarily regulated by photoperiod (Dawson et al. 2001). As the climate-photoperiod relationship in the breeding habitat shifts, current bird phenology cues may become maladaptive. Further, conditions in the winter habitat may fail to provide a reliable cue for conditions in the breeding habitat (Visser et al. 2010). In other words, the phenological phenotype is determined by the conditions in the winter habitat, while reproductive fitness is determined in the breeding habitat. There is evidence for this occurring: some migratory birds have been shown to suffer population declines due to mis-timing their reproduction with their food supply (Burger et
al. 2012; Visser et al. 1998). For example, in Great Tits (*Parus major*), the number of chicks fledged and mean chick weight were both correlated with synchrony of the hatch date with the caterpillar peak (Visser et al. 2006). Thus, the further mismatched a bird is from its primary prey source, the less reproductive success it attains.

Several studies have documented that migration dates have indeed shifted in several North American bird species (Bradley et al. 1999; Butler 2003; Dunn and Winkler 1999; Strode 2003) and some have shifted breeding dates (Dunn and Winkler 1999; Townsend et al. 2013) to align with food abundance. Phenological shifts in birds have been shown to vary across regions (Both et al. 2006; Roetzer et al. 2000), and one source of variation may be forest tree species composition and variation in trees’ responses to climate change. European tree species appear to have much narrower caterpillar biomass peaks than North American trees (Veen et al. 2010). Wider caterpillar biomass peaks allow for more “wiggle room” for birds in the case of a differential shift in phenology. Studies on experimental reductions in Lepidopterans in the eastern United States have shown little effects on bird reproductive output, even in cases of 90% caterpillar reduction (Holmes 1998). However, even within North America, birds specializing their foraging on trees with narrow food abundance peaks may be more susceptible to phenological mismatches, as the lack of synchrony with these peaks could result in lower food abundance than in habitats with wide-peaked trees.

The breeding dates of my focal species, the Blackburnian Warbler, Black-throated Green Warbler, Chestnut-sided Warbler, and American Redstart, were also observed by Charles Kendeigh at the Huyck Preserve from 1942 – 1944 (Kendeigh 1945). Comparing breeding dates across the period, it appears that little or no change has occurred, with the possible exception of the Blackburnian Warbler. For Blackburnian Warblers, breeding dates were 14 – 16 days earlier in 2014 than in the 1940s. However, Kendeigh’s Blackburnian Warbler breeding date record was from a single observation and may have been a second nest attempt or outlier. Although I lack climate or food abundance data from the 1940s, comparison suggests that most of these species may not be
shifting their breeding dates significantly. A lack of breeding date shift may indicate that climate change is not impacting food abundance to a degree that necessitates a shift in breeding date; however, it may also be a warning sign that these birds are unable to undergo selection needed to make these phenological shifts. Future studies should include measures of chick mass and nesting success, as in Visser et al. (2006). This would help determine whether the amount of biomass available during the breeding period impacts these bird populations.

Notes on Methodology and Correction for Tree Size

In caterpillar biomass estimations, the decision of whether to correct for tree size depends on the question being asked. Uncorrected caterpillar biomass estimates give a per-tree value of relative caterpillar biomass in the canopy, while size-corrected values provide a density measure. When looking for differences among individual trees and testing for differences in site-specific caterpillar biomass, uncorrected biomass is likely the better option.

When characterizing caterpillar biomass curves among trees species, however, the goal is to determine a general comparative value of how much caterpillar biomass these trees contain at any given time compared to other tree species. To this end, correcting for tree size standardizes the results and controls for variation in tree size. Although it may be argued that a standardized frass net controls for tree size, this fails to account for the fact that trees with taller crown height have more leaf surface area situated over a frass trap than a tree with less crown height. In addition, caterpillar frass is lightweight and subject to some movement via wind. In fact, some species of caterpillars are known “poop flingers” and scatter frass away from themselves (Weiss 2003).

Including a metric of tree size as an independent variable is one method of accounting for tree size. Although Visser et al. (2006) found that tree height and diameter at breast height were not significant explanatory variables for caterpillar biomass, the diameter at breast height was significant in an ANOVA model run on my data (not shown in this study). If needed, I suggest that
metrics such as leaf area index or crown height (see Veen et al. 2010) are likely to produce the best correction if accurate measures can be obtained.

**Future Priorities**

Future work should focus on characterizing these biomass curves for different tree species at more northern latitudes than those in this study. Not only are more northern latitudes shown to experience more extreme effects from climate change, but due to the shorter summers, caterpillar biomass peaks are likely much more narrow. The European studies in which population declines due to phenological mismatches were observed occurred at a latitude of about 52.1 for Visser et al. (2006), ranged from roughly 51.5 to 52.6 for Both et al. (2006), while my study took place at a latitude of 42.5. In addition, Veen et al. (2010) showed narrow caterpillar peaks on the Gotland and Öland islands of Sweden at latitudes around 57. It may be that more northern populations of birds in North America are experiencing mismatches due to differences in season length and caterpillar peak width.

In addition to caterpillars, studies have found that spiders may be a critical part of the nestling diet. Species such as the Great Tit (*Parus major*) and Blue Tit (*Cyanistes caeruleus*) are shown to supplement the typical diet of caterpillars with high proportions of spiders early in the nestling period (García-Navas et al. 2013). This provisioning of spiders occurs at specific periods during development (around days 5 and 6) irrespective of spider abundance, suggesting a nonrandom selection for these spiders in the diet (Arnold et al. 2007). Compared to caterpillars, spiders have been shown to contain higher levels of the amino acid taurine (Ramsay and Houston 2003). In birds, taurine is thought to influence bone, brain, and retinal development. For example, the proportion of spiders in the diet of Great Tits and Blue Tits predicted nestling tarsus length (García-Navas et al. 2013) and the supplemental taurine in the diet of Blue Tits increased risk-taking behavior and spatial learning ability (Arnold et al. 2007). Thus, supplemental foods may play
a role in nest success and nestling quality. More work is needed in North American to identify supplemental foods for birds and whether climate change threatens their availability.

Summary

The results from this study show that climate change will potentially impact caterpillar availability differently depending on forest composition and foraging niche. Among the risk factors for phenological mismatches and decreased food availability are 1) the bird species being long-distance migrants and not adjusting migration and breeding dates to track changes in phenology of caterpillars and/or trees; 2) narrow foraging niche; 3) breeding habitat with low tree species diversity; and 3) trees with narrow or low food peaks. These risk factors require a more complex and nuanced view of conservation needs when managing habitats for multiple species.
CHAPTER IV – The use of MODIS NDVI as a proxy for food abundance available to breeding birds

Recent studies on phenological shifts occurring due to climate change have yielded non-unifying results. Phenological responses in North American plant species appear to vary within and between taxa (Bradley et al. 1999; Butler 2003; Gibbs and Breisch 2001; Ledneva et al. 2004; MacMynowski and Root 2007; Macmynowski et al. 2007; Strode 2003; van Buskirk et al. 2009; Vitale and Schlesinger 2011) and location (Jason et al. 2013; Jones and Cresswell 2010; Schwartz and Reiter 2000; Zelt et al. 2012). Some bird species appear to exhibit phenotypic plasticity in migration and breeding timing in response to climate variables in their winter habitat (Mazerolle et al. 2011). At the same time, both their lepidopteran prey and their host plants vary in their responses to shifting climates as well. In turn, we have a complex situation with eight different outcomes, seven of which could result in a phenological mismatch between birds and Lepidopterans.

These differing responses to climate change highlight the need for large-scale, long-term, and multi-species studies. The use of continuously collected datasets such as the MAPS program (used in Chapter II) would allow estimation of breeding dates of many bird species across the United States. For estimating phenology of photosynthetic species such as trees, a measure of “greenness” called the Normalized Difference Vegetation Index, or NDVI, has the potential to be used to predict resource abundance. NDVI is a satellite-derived, reflectance-based calculation that compares the wavelengths of light reflected and absorbed by the satellite. Scientists have used it to study growing season dynamics since the NDVI value increases throughout the growing season; however, it has been shown to vary in usefulness among habitat types (Fu et al. 2014). In the face of climate change, a remotely collected, large scale measure such as this would be a huge asset to estimating how organisms such as plants and, potentially, caterpillars, respond phenologically.
NDVI is potentially a valuable proxy for food availability due to its accessibility, but it needs to be verified, as plants and caterpillars potentially respond to different cues to stimulate phenology. Tree phenology is regulated primarily by an accumulation of warm temperatures, called “degree days”. Caterpillar phenology is also regulated by degree days, but to a lesser degree (Schwartzberg et al. 2014). Thus, there is potential for mismatches as climate cues change. The relationship between NDVI and caterpillar biomass must be tested before it can be used to predict food resource availability for birds. As I showed in the previous chapter, tree species vary in their caterpillar biomass phenology. Thus, it can be expected that the caterpillar biomass from not all of these tree species will correlate with NDVI to the same degree. In this chapter, I test the hypothesis that phenology obtained via NDVI measurements correlate with caterpillar biomass obtained from eight different tree species in upstate New York.

METHODS

MODIS NDVI

Healthy plants undergoing photosynthesis absorb wavelengths of visible light and reflect near-infrared light. Knowing this, scientists can compare the amount of each type of light reflected in order to produce a relative measure of photosynthesis. This measure is called the Normalized Difference Vegetation Index, or NDVI. The NDVI is a ratio of the difference between the amounts of reflected visible (0.67 µm) and near-infrared (0.86 µm) light and the sum of these reflected. These data are collected by NASA through a Moderate Resolution Imaging Spectroradiometer (MODIS) on the satellites Terra and Aqua. A high NDVI suggests more photosynthesis is occurring, and as such, this measure has been used to track spring phenology as plants begin producing chlorophyll and undergoing photosynthesis.
NDVI data from the MODIS instrument on NASA’s Terra satellite are available as far back as 2000. I acquired 6-day, 250-m resolution NDVI layers via the USGS Earth Explorer (http://earthexplorer.usgs.gov). I downloaded NDVI data from mid-May to early August. If the data quality layer indicated anything besides a value of “0” (indicating no quality issues), I discarded the data from that period. I extracted the image acquisition dates and the NDVI values from the layers. As per the data use instructions, I multiplied the NDVI values by 0.0001. Due to the way NDVI works, errors are nearly always low (Pettorelli et al. 2005). One main source of error, cloud cover, reduces the reflectance values of near-infrared light, resulting in a lower NDVI calculation. In my data, values lower than expected (outliers) occurred for some dates in 2013, and upon matching them up with local weather station data, I found that these days had precipitation. I removed these values, as clouds will bias NDVI values to be lower (Pettorelli et al. 2005). However, precipitation did not appear to cause outliers in the 2014 data, so I retained values from days with precipitation.

I compared five polynomial GLMs of NDVI, and image acquisition date, using model selection methods (Burnham and Anderson 2002). I selected the model with the lowest AIC – a fifth order polynomial for both 2013 and 2014. With these models, I interpolated the NDVI and caterpillar biomass values (original and DBH-adjusted) to nine Julian dates, seven days apart, from 145 to 201 for both years. With these predicted values, I ran a cross correlation function analysis in RStudio for each tree species, year, and model type. This produced a correlation coefficient between NDVI and caterpillar biomass compared to the correlation coefficient when the data points are shifted in time to create different "lags". In this case, the lag distance was seven days as it was the approximate sampling period of both the frass and NDVI.
RESULTS

NDVI curves differed slightly between 2013 and 2014 (see Figure 3.1). In 2014, NDVI appears to peak between 7 – 16 June (Julian date = 158 – 167). The 2013 NDVI model showed a plateau beginning around May 29 (Julian date = 149), followed by another gradual increase. This erratic behavior is likely a reflection of higher March temperatures in 2013; average daily temperatures were significantly higher in 2013, especially in the early spring (see Figure 3.2).

NDVI correlation with caterpillar biomass was strikingly different between 2013 and 2014. In 2013, the highest correlation coefficient values ($r > 0.6$) were found for Beech, Hemlock, Maple, and Pine (see Tables 3.2a – 3.2b), all at a lag of 1. No tree species had their highest correlation coefficient at lag 0 in 2013. Ash and Oak had the lowest maximum correlation coefficient (for Ash, $r = 0.423$ at lag -3 and for Oak, $r = 0.256$ at lag 1).

In 2014, I found high (>0.6), zero-lag correlations for Ash, Beech, Birch, Oak, and Spruce. The highest correlation coefficients for Maple and Pine in 2014 were 0.408 and 0.571 respectively at lag 3. Maple and Pine were the only two tree species that had higher and more synchronous (lag 0) correlation coefficients in 2013.

I found strong, synchronous correlations between 5 of 8 tree species in 2014 as opposed to 0 of 8 in 2013. However, 7 of 8 tree species correlated best with NDVI at lag position 1 in 2013, while only 6 of 8 correlated at lag 0 in 2014. It appears as though caterpillar biomass on Ash peaked earlier even than NDVI, indicating that Ash tree caterpillar productivity does not correlate with NDVI and thus, caterpillars specializing on Ash will also not correlate well with NDVI. This may be partially due to Ash being poorly represented in the canopy, and thus the NDVI value does not reflect the phenology of this tree species. Alternatively, Ash may serve as a host to specialized caterpillars that happen to be early emerging species, or avoided by late-season caterpillars or second broods.
Table 3.1a: Lag with highest correlation coefficient by tree and year (biomass models). Italic values denote low ($r < 0.6$) correlation coefficients.

<table>
<thead>
<tr>
<th>Tree</th>
<th>2013 Lag</th>
<th>$r$</th>
<th>2014 Lag</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td>4</td>
<td>0.286</td>
<td>0</td>
<td>0.805</td>
</tr>
<tr>
<td>Beech</td>
<td>1</td>
<td>0.648</td>
<td>0</td>
<td>0.675</td>
</tr>
<tr>
<td>Birch</td>
<td>1</td>
<td>0.612</td>
<td>0</td>
<td>0.747</td>
</tr>
<tr>
<td>Hemlock</td>
<td>0</td>
<td>0.671</td>
<td>4</td>
<td>0.368</td>
</tr>
<tr>
<td>Maple</td>
<td>1</td>
<td>0.651</td>
<td>4</td>
<td>0.368</td>
</tr>
<tr>
<td>Oak</td>
<td>0</td>
<td>0.705</td>
<td>0</td>
<td>0.786</td>
</tr>
<tr>
<td>Pine</td>
<td>1</td>
<td>0.678</td>
<td>2</td>
<td>0.487</td>
</tr>
<tr>
<td>Spruce</td>
<td>0</td>
<td>0.888</td>
<td>0</td>
<td>0.675</td>
</tr>
</tbody>
</table>

Table 3.1b: Lag with highest correlation coefficient by tree and year (DBH-adjusted models). Italic values denote low ($r < 0.6$) correlation coefficients.

<table>
<thead>
<tr>
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<th>$r$</th>
<th>2014 Lag</th>
<th>$r$</th>
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<td>4</td>
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<tr>
<td>Oak</td>
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<td>0.408</td>
<td>0</td>
<td>0.796</td>
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<td>Pine</td>
<td>0</td>
<td>0.805</td>
<td>3</td>
<td>0.502</td>
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<tr>
<td>Spruce</td>
<td>-4</td>
<td>0.387</td>
<td>3</td>
<td>0.670</td>
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Table 3.2a: Correlation coefficients of median caterpillar biomass and predicted NDVI in 2013 and 2014 at different lags (biomass models). Column headers indicate lag positions. Zero indicates contemporaneous; negative lags indicate that caterpillar biomass precedes NDVI, positive lags indicate that NDVI precedes caterpillar biomass. Blue cells show the maximum correlation coefficient for all lags. Bold numbers a correlation coefficient or high (>0.6) correlation coefficient. Red denotes a high negative correlation; maximum coefficients that were not greater than 0.6 are in italics.

<table>
<thead>
<tr>
<th></th>
<th>-5</th>
<th>-4</th>
<th>-3</th>
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<td>-0.160</td>
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<td>0.486</td>
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<td><strong>0.671</strong></td>
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Figures 3.1 and 3.2

**Figure 3.1: NDVI for 2013 and 2014.** The red/blue curves show observed 2013/2014 NDVI values. Dashed lines represent the polynomial model predictions. Shaded areas represent the standard error for the given line.

**Figure 3.2: Average daily temperatures in Celsius for 2013 and 2014, March through August.** Red = 2013, Blue = 2014. In 2013, March temperatures were significantly warmer in 2013 than in 2014. Shaded areas represent the standard area for the given line.
DISCUSSION

The most striking finding in this study was the difference in NDVI correlation between years. While NDVI may be a perfectly reasonable predictor of food resources during a typical year, anomalous years, which are projected to increase in frequency as climate change progresses (Lovejoy and Hannah 2005), may be less accurately predicted. Since these anomalous years may be of high interest to researchers studying the effects of climate change on wildlife, I suggest NDVI be used with caution and perhaps confirm and further investigate the effects of anomalous temperatures on caterpillars.

The reason for a consistent peak correlation at lag 1 in 2013 and lag 0 in 2014 is likely due to the differences in degree-day thresholds for caterpillars and trees. The accumulated degree days required for the onset of spring differs between species and by location (Jenkins et al. 2002; White et al. 1997), with more degree days required in the south. Insect degree-day thresholds appear to be similarly governed by degree days, however, caterpillar phenology appears to be less sensitive to temperature than tree phenology (Schwartzberg et al. 2014).

Sugar Maple and White Pine had the highest correlations at higher lags in 2014. This is likely due to the shape of the biomass curves for these species. Sugar Maple and White Pine both have the highest biomass peaks later in the season, due to double-brooding and late-season lepidopterans such as Notodontidae. These species specialize on thicker late-season leaves, and have adaptations such as larger mandibles to compensate for this (Kunikichi and Masashi 2012).

Despite my general findings of NDVI correlating more strongly and synchronously to caterpillar biomass for most trees in 2014 and shifted in 2013, two exceptions were Eastern Hemlock (unadjusted biomass) and White Pine. For these species, NDVI and biomass had higher correlations coefficients during the 2013 season. It is likely that caterpillars feeding on coniferous trees are less susceptible to changes in weather that may alter tree phenology due to the ongoing availability of foraging materials. Caterpillars hatching early will still have food available, even if
tree phenology is behind. It may also be the case that because Hemlock made up a large proportion of canopy cover in some sites, NDVI tended to correlate stronger. However, this is an unlikely explanation for White Pine, as White Pines only made up a small proportion of canopy cover. Another likely explanation is that conifers have foliage year-round, phenological matching between caterpillars and coniferous trees may be less difficult than matching between caterpillars and deciduous trees.

Phenology models of Eastern North American tree species show that phenological events such as bud burst are best predicted by date and accumulated degree days (Richardson et al. 2006). What these findings suggest is that as tree phenology progresses, caterpillars do not necessarily follow. Although it is expected that they would track climate changes, as both caterpillars and trees tend to regulate phenology with accumulating warm temperatures, this does not appear to be the case at the Huyck Preserve.

NDVI likely correlates more strongly with trees that make up more of the canopy cover, as they will make up a larger proportion of the satellite images used in the algorithm to calculate NDVI. Thus, researchers using NDVI to predict resource abundance phenology must take foraging niche into account. The phenology of uncommon or understory trees may not be reflected by the NDVI, so when modeling resource abundance for specialist species, one must proceed with caution. Further studies could test how the strength of caterpillar biomass and NDVI relate to the proportion of each tree species in the landscape, or, even better, percent canopy cover.

If overall temperatures increase, caterpillars may move through lifecycles more quickly (Peñuelas et al. 2002), changing the shape of the peaks, perhaps making them more narrow and easily missed by any species that depend on them. Differences in phenological response to climate between Spruce Budworms, an irruptive caterpillar species in the family Tortricidae, and Douglas Firs have resulted in cases of higher caterpillar biomass (Chen et al. 2001). However, over a long
time period, this leads to the decline and death of the spruce trees, altering the landscape and food abundance in a negative way long-term.

**Future Priorities and Conclusion**

Before studies can fully implement NDVI as a proxy for caterpillar availability, several questions remain to be addressed. First, it is important to test whether the correlation between NDVI and caterpillar biomass holds for a tree species across latitudinal gradients. As both caterpillar species assemblages and phenology change across latitudes, this relationship between NDVI and caterpillar biomass maybe become uncoupled. Second, the influence of the tree species composition of the canopy on NDVI must be made known. A tree species that is less prevalent in the canopy logically has less influence on the overall NDVI value for a cell. If the phenology of an underrepresented tree species is unlike the phenology of the majority of the canopy, we may perceive a weak relationship between caterpillar biomass on this tree and NDVI when in reality we are observing a weak relationship between caterpillar biomass on this tree and the phenology of canopy-prevalent trees. There may be a strong relationship that is simply not detectible due to the lack of information in the NDVI value from this tree species. Collecting tree phenology data such as bud burst date can help researchers determine whether NDVI is indicative of phenology for a particular tree species. In fact, similar methods have shown that NDVI is not a particularly good indicator of the phenology of conifers in a boreal forest in Sweden (Jönsson et al. 2010). However, if new needle emergence in mixed forest conifers coincides with increases in greenness for more easily detected tree species, a strong correlation between NDVI and caterpillar biomass on conifers may still exist due to new-needle specialist caterpillars emerging and the NDVI signal from other increasingly greening trees.

Finally, work should be conducted to investigate the mismatches observed here between NDVI and caterpillar biomass. If the cause of this mismatch can be resolved, then NDVI can still be
used as an indicator of resource availability. Although the cause may be simply differential phenological responses to climate among tree species which was not detected by NDVI due to canopy composition, the inclusion of additional predictor variables such as temperature, date, or precipitation may reveal information on how to predict caterpillar biomass for a particular tree species. Although the results of this study show strong promise for the use of NDVI to predict caterpillar biomass, I conclude that more work is needed before this method can be used freely.
CHAPTER V – Conclusion

The work in this dissertation provides a foundation for future studies to successfully identify phenological mismatches in North America. Identifying the mechanisms driving species’ responses to climate change is vital – for both conservation and understanding ecological processes. In Chapter II, I show that 1) reproductive success in birds is driven by temperature, precipitation, and habitat cover; and 2) the availability of high quality habitat in the southern margins of the range is localized. These populations are likely at higher risk of local extinction, especially as climate change progresses and causes the lower margin of the range to shift northward (Sorte and Frank 2007). As Chapter II demonstrates, local tree composition and bird foraging niche combinations can result in the loss of food availability during the breeding season, which may contribute to range contractions. If caterpillar biomass is low on the primary foraging tree species for a bird in these southern regions, we would expect to observe declines in reproductive success. It may be that caterpillars peak earlier in the south, and breeding birds miss the peak in food abundance. As my Chapter IV discovered, local comparisons of NDVI and bird breeding date phenology can help test whether and where a species may be experiencing a mismatch in phenology.

The primary goal of these studies was to lay a foundation of work that facilitates remote detection of phenological mismatches and fitness-over-time as climate change progresses. This has been particularly well-studied in Europe, but North America has lagged behind. To my knowledge, phenological mismatches between birds and food during the breeding season have not been shown for any North American passerines to date. Tree Swallows (Tachycineta bicolor) in the United States, for example, have been shown to shift breeding dates to match flying insect abundance (Dunn et al. 2010). However, flying insects did not show a peak in abundance over time, but a gradual increase, while European studies, biomass availability was shown to have very narrow peaks of roughly fifteen days for birch (Veen et al. 2010) in Sweden. However, at this latitude it is
expected that peaks will be narrower than in New York State. Chapter III shows that the caterpillar biomass from my study site in the Northeastern United States have much wider peaks, with biomass above 2 mg/m²/day for more than forty days in 2014. Thus, birds in this region foraging on trees with wide biomass peaks are less likely to experience mismatches due to the overwhelming abundance in caterpillars. Dunn et al. (2010) suggested that perhaps a threshold amount of food abundance may be more useful in predicting mismatches than the location of the peak, and in cases like this where peaks are high and wide, I agree. Even a 96% experimental reduction in caterpillars has been shown to have no influence on the diets, survival, and growth of nestling Tennessee Warblers (*Oreothlypis peregrine*) in Ontario, Canada, although females did spend more time foraging than the control group (Holmes 1998). This suggests that original caterpillar abundance was so high that there were adequate resources even after the 96% reduction in caterpillars. At more northern latitudes, there may be more narrow peaks and increased risks for phenological mismatches, and more work is needed to determine whether this occurs in the northern latitudes of North America.

**Target locations and species at risk**

Not all species of migratory birds will be as resilient as the tree-gleaners of the eastern forests. Lilacs in the northwestern United States have had the highest occurrence of the largest shifts in bloom dates, especially in Montana, Saskatchewan, and British Columbia. In these areas, studies should focus on bird species that 1) occupy narrow foraging niches or habitats with low plant diversity or narrow NDVI peak; and 2) have shown declines in reproductive success or abundance. Whether a species has demonstrated phenological shifts may not be a good indicator of a phenological mismatch. Observed shifts suggest that selection is acting on the phenotype for this species, and it may or may not be enough to remain synchronous with its prey. Species that have not shifted either have not experienced selection pressure and thus have not shifted phenotype, or
they have experienced pressure, but constraints have prevented a shift in phenotype. Despite phenotypic plasticity, the genetic basis for phenology and responses to phenological cues are likely shaped by different selection pressures. Selection pressure may even be constrained by pleiotrophic genes regulating phenology (Visser et al. 2010). This could prevent selection for more synchronous phenology post-climate change. These selection pressures and ability to adapt will vary across the range of the species as well, thus highlighting the importance of monitoring at larger spatial scales.

The primary reason for collecting large-scale datasets and the disadvantage of using them are one and the same – local processes may greatly affect demography differently across regions. Local monitoring and extrapolation across a species’ range may not produce accurate predictions if a) different predictors act on the process of interest or b) selection has resulted in populations responding differently to predictors (Visser et al. 2010). Conversely, models containing data across a wide range may not make accurate predictions. However, simple wide-scale monitoring of populations separately may allow for the identification of local processes and areas of conservation concern.

**Monitoring over large spatial and temporal scales**

Monitoring phenology and demography over large temporal and spatial scales can account for change over time and the variations found across species’ ranges. Detecting change and the rate of change in phenology and demography as climate change progresses can allow us to make predictions into the future. Change should ideally be monitored over large spatial scales in order to detect regional patterns and to account for differences among regions are crucial due to the variability in climate, habitat, and local phenotypes.

As demonstrated by my Chapter II, demography varies regionally; however, predictors for reproductive success likely vary across very large scales, making it difficult to extrapolate
demographic predictions across a range using local data. An example of how extrapolation is
problematic can be seen in the Yellow Warbler – Yellow Warblers have been divided into 43
“subspecies”, which are lumped into three groups (Lowther et al. 1999). These subspecies show
genetic, morphological, and behavioral differentiation, suggesting local selection or genetic
isolation. Because of this, I recommend that range-wide genetic structure be examined before
extrapolating models across wide ranges. This can determine populations, their locations, and the
locations of sampling gaps in the monitoring program.

For large-scale monitoring of bird demography, the MAPS program used in Chapter II is a
valuable resource, but would benefit from several aspects of improvement. First, increased and
more even sampling across North America would improve models using these data. The dataset
suffers from missing years, likely due to funding or labor/volunteer shortages. Second, increased
availability of temporal trends within and among years would expand the types of analyses
possible. Currently, all data are compiled together as a single value for a station/species
combination, with the exception of the “trend” metrics. These metrics provide a coefficient of
variation, or regression slope along with r-squared and p-values for the regression slope for a
metric such as the number of hatch-year birds. However, without having the yearly values
accessible, testing for relationships between climate and NDVI are difficult, despite their potential
influence on phenology, which is the third suggested improvement: a better phenology metric.
Although MAPS calculates a mean date of capture for after-hatch-year birds and hatch-year birds,
which may be used to estimate breeding phenology, the dates of observed cloacal protuberances
may be more useful for estimating the breeding dates at a site. Using mean dates of capture
averaged across years is problematic because it assumes that these values are static for a location
and do not change over time. It prevents data users from testing for trends over time and
differences between years.
For migration phenology data, the Bird Phenology Program (BPP) is an alternative to MAPS that provides migratory bird arrival data from 1881 – 1970 (Zelt et al. 2012). These data would provide baseline migration dates for a number of bird species. However, migratory arrival dates such as those used in the BPP and many studies are not ideal for estimating bird phenology. Although they are useful measures that are easily obtained, migration observations assume that birds from the same winter populations pass through each year and are being observed in the same proportion each year (Møller et al. 2010). Additionally, the first arrival date is a potentially poor metric for phenology in birds, as it captures only a tail end (and possible outlier) of the population distribution (Miller-Rushing et al. 2010) and is prone to variation in sampling effort.

Another viable and potentially game-changing phenology data option is the USA National Phenology Program, which began around 2005 (Betancourt et al. 2005). The NPP is a citizen-science based program which solicits volunteers to submit phenology data on nearly every taxon. Even measures of behavior are recorded, such as feeding, breeding, and mating. If these types of measures are taken in high enough volume for birds along with phenological measures of plant and insects, this program has immense potential for researchers interested in phenological mismatches. Phenological observations from trees, caterpillars, and bird may be acquired from the same sites. However, this dataset is limited by the lack of historical data; however, the true strength of this dataset is the ability to compare large numbers of taxa over time and across large spatial scales. Volunteers and field stations should be encouraged to collect these data and submit any existing data to the database for researchers to use. With enough participating organizations, studies of enormous scales could be conducted on phenology of trees, insects, birds, and NDVI.

For remotely monitoring caterpillar phenology in particular, Chapter IV provides evidence for the potential of NDVI as a broad proxy for food availability. Although the inconsistencies found between 2013 and 2014 correlation coefficients suggest caution when using NDVI as such, they also highlight the phenological consequences of anomalous early spring temperatures. Abnormal NDVI
curves (like 2013, not a single peak as in 2014) should be used with caution by researchers.
Researchers should also consider the following before using NDVI as a proxy for food abundance: 1) the foraging niche of the species for which food abundance is being calculated – does NDVI reflect the phenology of this foraging substrate?; 2) whether the preferred foraging substrate’s phenology correlates with NDVI – does it have a presence in the canopy, or is it an understory or rare tree?; 3) whether the phenology of the food organism better tracks NDVI or another metric such as temperature; and 4) if the host plant and food organism rely on different cues to trigger phenological responses. Additional studies will further determine how these factors influence the relationship between NDVI and caterpillar biomass and facilitate its use with other data sources such as bird demography.

Summary

In sum, my work in this dissertation showed that birds exhibit regional variations in demography across their range, due to local predictors such as climate and land cover. As climate increases, monitoring these populations may be especially vital to species that forage on trees with narrow caterpillar biomass peaks. Working on developing new methods in remotely sensing food resources for birds, we can predict where phenological mismatches and population declines due to climate change are likely to occur.
LITERATURE CITED


